Herpetology FOURTH EDITION

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Herpetology



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Sinauer Associates, Inc. • Publishers Sunderland, Massachusetts • USA



About the Cover

A Neotropical reticulated glass frog (*Hyalinobatrachium valerioi*, Centrolenidae) guards a clutch of eggs on the underside of a leaf overhanging a stream. Male glass frogs remain with their clutches until they hatch, protecting them from egg-eating predators and releasing water to keep the eggs hydrated. The frog's pattern of yellow spots surrounded by green resembles the egg mass and may conceal it from predators such as birds. Photograph © Ingo Arndt/ Minden Pictures.

Herpetology, Fourth Edition

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Library of Congress Cataloging-in-Publication-Data

Pough, F. Harvey.

Herpetology / F. Harvey Pough, Rochester Institute of Technology, emeritus, Robin M. Andrews, Virginia Tech, emerita, Martha L. Crump, Utah State University, Alan H. Savitzky, Utah State University, Kentwood D. Wells, University of Connecticut, Matthew C. Brandley, University of Sydney. -- Fourth edition.

pages cm

Includes bibliographical references and index. ISBN 978-1-60535-233-6 (casebound)

1. Herpetology. I. Title. QL641.H47 2015 597.9--dc23

Printed in U.S.A.

654321

2015017774

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Preface

he striking and effective use of color throughout the book is merely the most conspicuous of the changes in this, the Fourth Edition of *Herpetology* and the first to be published by Sinauer Associates. All of the topics have been extensively revised to include new information and interpretations with extensive in-text citations, and color photographs now accompany all family-level descriptions.

What has not changed is the authors' appreciation of amphibians and reptiles as complex and fascinating organisms. Our perspective emphasizes the interactions at multiple levels of biological organization that shape the biology of a species of amphibian or reptile. We present these animals in a way that integrates all facets of their biology, from anatomy and physiology to ecology and behavior topics that are too frequently treated as independent fields of study. We believe that understanding these interrelationships is the key to understanding amphibians and reptiles.

Phylogeny, Systematics, and Numbers of Species

Advances in molecular phylogenetics have dramatically altered our understanding of the evolutionary relationships of many groups of amphibians and reptiles. Because phylogeny provides the context for interpreting the biology of extant species, we have expanded the explanation of cladistic methods and interpretations in Chapter 2. The power of molecular methods to trace evolutionary histories has produced a dramatic increase in the numbers of families, especially among amphibians. Chapters 3 and 4 describe the major lineages and the distinctive characteristics of each family, and Chapter 5 integrates this information with the historical and recent events that have determined the geographic distributions of extant lineages.

The past decade has seen tremendous progress inferring the phylogenies of amphibians and reptiles, with many evolutionary relationships strongly supported by large molecular and morphological datasets. However, phylogenies-representations of the sequence of divergences within an evolutionary lineage—are hypotheses, and like any scientific hypothesis they are continuously being tested and sometimes falsified by new information. As a result, the numbers and names of recognized taxa are constantly in flux. We have cited the total numbers of species of amphibians recognized by AmphibiaWeb (amphibiaweb.org) and the total number of species of reptiles recognized by The Reptile Database (www.reptile-database.org) as of our completion date, but we recognize that some of these numbers have doubtless already changed. Both sites are updated frequently, and we encourage students to visit them.

Sadly, the number of species of amphibians and reptiles that are considered threatened or endangered by the International Union for Conservation of Nature (IUCN) increases steadily. The numbers of species cited in this edition are based on version 2014.3 of the IUCN Red List; species data and definitions of categories can be found at www. iucnredlist.org.

Herpetology is well represented on the Web, with sites that range from scholarly to sensational, and herpetologyrelated items often appear on news sites. Viewing the videos that researchers post on YouTube can clarify and enliven descriptions of their studies, and open access is available to many journals and to important herpetological resources. We provide links to this information at **sites.sinauer.com/ herpetology4e**.

Acknowledgments

A textbook is far more than the sum of the contributions of its authors—we depend directly and indirectly on information, help, and inspiration from colleagues and students,

Denis V. Andrade Michael Archer Ion Barnes Aaron Bauer Steven J. Beaupre Anne Besson Andy Blaustein **James Bogart** Xavier Bonnet Frank Burbrink Warren Burggren Elizabeth L. Brainerd Jake Brashears Francois Brischoux Edmund D. Brodie Ir Edmund D. Brodie III Rafe Brown Stephen D. Busack Christopher Caprette Michael D. Cardwell Christopher Clark Alison Cree Sarah Crews David Cundall Kevin de Queiroz Stephen M. Deban Dale DeNardo

Alexandra Deufel Vladimir Dinets Wei-Guo Du Sylvain Dubey Robert E. Espinoza Danté Fenolio Craig E. Franklin Darrel Frost Margaret Fusari Theodore Garland **Justin Gerlach** Richard Glor Eli Greenbaum Harry W. Greene **Jovce** Gross Lisa C. Hazard Lindsay Hazley Matthew Heinicke Susan Herrick Paul Hertz Wen-San Huang Raymond B. Huey Christine M. Janis Bruce C. Jayne Scott Keogh Adam Leaché Manuel Leal

many of whom have made extraordinary efforts to answer questions, provide unpublished data, call our attention to important new information, and review drafts of chapters:

Alan Lemmon Emily Moriarty Lemmon Harvey B. Lillywhite Charles Linkem Ellis Loew Ionathan Losos Luke Mahler Jim McGuire Lindley McKay John Measev Jesse Meik Akira Mori Craig Moritz Suzanne L. Munns Alan Muth Kenneth Nagy Nicola Nelson Dina Newman Iim O'Reilly Susan Smith Pagano Greg Pauly Marion R. Preest Alex Pyron José Rosado Thomas Sanger Joseph J. Schall **Benjamin Scheele**

Kurt Schwenk Ainsley Seago Roger Seymour Glenn Shea Donald Shepard Wade C. Sherbrooke **Rick Shine** Cameron Siler Ulrich Sinsch Jacob Sivak Kathleen Smith Jake Socha Jan J. Sojka James R. Spotila Janet M. Storey Glenn J. Tattersall C. Richard Tracy Christopher R. Tracy Bruce Turner Peter Uetz Miguel Vences David B. Wake Marvalee H. Wake Tobias Wang Dan Warner Scott Waters Kelly Zamudio

We are also grateful to the very large number of colleagues who provided photographs:

Marlon Almeida-Santos Melissa Amarello Joana Amorim Christopher V. Anderson Denis V. Andrade Michael Archer Achmad Ariefiandy Ingo Arndt Kellar Autumn Jon Barnes R. D. Bartlett Bob Beale Steven J. Beaupre Gary Bell Sathyabhama Das Biju James Bogart Xavier Bonnet Elizabeth L. Brainerd Jake Brashears

Edmund D. Brodie Ir. Edmund D. Brodie III Gordon Burghardt Dale Burzacott Stephen D. Busack Philip Byrne Michael D. Cardwell Alessandro Catenazzi Mark Chappell Rebecca Chong René Clark Martin Cohn Luis A. Coloma Joseph C. Corbo Scott Corning Mircea Costina Alison Cree Laura Crothers David Cundall

Indraneil Das Kevin de Oueiroz Anslem de Silva Stephen M. Deban Dale DeNardo Alexandra Deufel Vladimir Dinets Erin Paul Donovan Wei-Guo Du Sylvain Dubey Melanie Elphick Dirk Erken Robert E. Espinoza Todd Esque Marty Feldner Martin Fischer Mark Fisher Craig E. Franklin Paul Freed

Nicole Friedenfelds Christopher Friesen Margaret Fusari Tony Gamble Theodore Garland Justin Gerlach Frank Glaw Claire Goiran Ulmar Grafe Eli Greenbaum Lee Grismer Wolfgang Grossmann Célio Haddad Mattias Hagman Winnifred Hallwachs Elizabeth Hane S. Blair Hedges José Juan Hernández Susan Herrick

Troy Hibbits Cindy Hitchcock Walter Hödl Leandro dos Santos Lima Hohl Masaki Hoso Wen-San Huang Kristiina Hurme Kate Jackson Daniel H. Janzen Bruce C. Jayne Carolyn Jenkins Fred Kraus Tobias Landberg Hugh Landsdown Jeffrey Lang A. Kristopher Lappin Manuel Leal Twan Leeders Andrew R. Lewis Russell Ligon Harvey B. Lillywhite Mariana Fiuza de Castro Loguercio

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Vishal Prassad Sarah Prvke Juan Carlos Rando Morley Read Sean Reilly Roger A. Repp Uli Rever Oscar Rocha-Barbosa Goncalo M. Rosa Robert Rothman Rodolfo Ruibal Joseph J. Schall Kurt Schwenk Aganto Seno David Sever Roger Seymour Wade C. Sherbrooke Barry Sinervo Skip Snow **Jake** Socha Ruchira Somaweera Margaret Stewart Rochelle Stiles Janet M. Storey

Adam Stow Devi Stuart-Fox John Sullivan Marc Sztatecsny Theodore L. Taigen Glenn I. Tattersall Mauro Teixeira Ir. Rory S. Telemeco Daniel S. Townsend Christopher R. Tracy Michael Tyler Wayne Van Devender Miguel Vences Pablo Venegas Marvalee H. Wake Tobias Wang Karen Warkentin **Richard Wassersug** Stacev Weiss Martin Wikelski Kenny Williams I. D. Wilson Wolfgang Wüster Stephen Zozaya

Expert librarians are essential to any scholarly undertaking, and we are fortunate to have had the outstanding assistance of Adwoa Boateng and Morna Hilderbrand (Rochester Institute of Technology) and Flora Shrode (Utah State University). In addition, we thank Larry Buckley (Rochester Institute of Technology) and Kami McNeil (Utah State University) for providing timely and much-needed assistance. Every page of this book testifies to the exceptional skill and dedication of the Sinauer team, especially Carol Wigg, David McIntyre, Elizabeth Pierson, Chris Small, Jason Dirks, Jefferson Johnson, Elizabeth Morales, Stephanie Bonner, and, of course, Andy Sinauer. Our gratitude and warmest thanks go to them all.

Media and Supplements to accompany **Herpetology**, FOURTH EDITION

eBook

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For the Student

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- Links to videos illustrating topics discussed in the textbook
- Important open-source publications in the field of herpetology
- Links to news items related to herpetology

For the Instructor

INSTRUCTOR'S RESOURCE LIBRARY (available to qualified adopters)

The *Herpetology*, Fourth Edition Instructor's Resource Library includes a collection of visual resources from the textbook for use in preparing lectures and other course materials. The textbook figures have all been sized and formatted for optimal legibility when projected. The IRL includes all textbook figures and tables in JPEG (both high- and low-resolution) and PowerPoint formats.

PART I What Are Amphibians and Reptiles?

CHAPTER 1 Why Study Herpetology?

CHAPTER 2

Phylogenetic Systematics and the Origins of Amphibians and Reptiles

CHAPTER 3

Systematics and Diversity of Extant Amphibians

CHAPTER 4

Systematics and Diversity of Extant Reptiles

CHAPTER 5

The Biogeography of Amphibians and Reptiles





1

Why Study Herpetology?

o the authors of this book, who share a lifelong fascination with amphibians and reptiles, the immediate answer to this question is "Because they are so interesting." More objectively, we would point out that the study of amphibians and reptiles reveals a way of being a terrestrial vertebrate that is different from the more familiar examples of birds and mammals. Furthermore, because of these differences amphibians and reptiles have a critical role in energy and nutrient flow in terrestrial ecosystems. And, sadly, we would add that an alarmingly high proportion of species in both groups, and especially amphibians, are classified as at risk in the Red List of the International Union for Conservation of Nature (IUCN).

The word "herpetology" is based on the Greek root herpes, meaning "a creeping thing." The name may not sound like an enthusiastic way to describe an animal, but the ancient world held some reptiles in high esteem. Alexander the Great, who conquered much of the known world around 300 BCE, encouraged the legend that he derived some of his power from a god-sent serpent that protected him in its coils when he was a baby.

Some ancient legends are preserved even today. The staff entwined by a serpent carried by Aesculapius, the Roman god of healing, appears as the caduceus—a winged staff entwined by two snakes—of modern medicine. The Romans built shrines to Aesculapius throughout their empire and released Aesculapian snakes (*Zamenis longissimus*, formerly *Elaphe longissima*) at the shrines. This species is native to southern Europe, including Italy and Asia Minor, but has isolated populations in central Europe, far to the north of other occurrences of the species. These northern populations may be descendants of snakes released 2,000 years ago at shrines to Aesculapius.

Herpetology also plays a role in modern medicine. Peptides isolated from reptile venoms can treat some chronic conditions without side effects, and compounds from the skin of amphibians have antibacterial properties superior to those of conventional antibiotics. Thus, the study of herpetology encompasses both basic and applied biology, at levels extending from molecules to the global environment.

1.1 Changing Perspectives

The great 18th-century Scandinavian biologist Carl von Linné had a low opinion of the creeping animals. Writing under the Latinized version of his name, Carolus Linnaeus, he initiated the hierarchical method of naming organisms that we are familiar with as the binominal classification system. His work *Systema Naturae* (*The System of Nature*) assembled organisms in groups. Linnaeus did not distinguish amphibians from reptiles, referring to both groups as amphibians and characterizing them as "foul and loathsome." He noted that for this reason "their Creator has not exerted his powers to make many of them."

Now we know that Linnaeus was sadly mistaken in both those statements. Herpetologists have found amphibians and reptiles to be model organisms for studies in many areas of biology, and they have identified a large number of species to study—about 7,300 amphibians (salamanders, frogs and toads, and caecilians) and 10,000 reptiles (turtles, crocodylians, tuatara, lizards, and snakes). For comparison, there are about 5,500 species of mammals and 10,500 species of birds. Thus, the study of herpetology covers more species of animals than does either ornithology or mammalogy (Figure 1.1), and it includes a greater range of body forms, behaviors, and life-history patterns.

Studies of amphibians and reptiles have played key roles in biological specializations as diverse as developmental biology, behavior, ecology, and medicine. Many of these contributions are the result of unique characteristics that make a certain species of amphibian or reptile suitable for a particular technique. For example, the large eggs of many frogs and salamanders allow embryonic development to be observed under a light microscope. Much of our understanding of the way cells move during gastrulation (when an embryo changes from a hollow ball of undifferentiated



Figure 1.1 Herpetology includes more than half of the species of extant tetrapods. Herpetologists have more species in their field study than ornithologists and mammalogists combined.

cells to a structure with distinct layers of endoderm, mesoderm, and ectoderm) resulted from studies in which early embryologists marked individual cells of frog and salamander embryos with dye and observed their movements.

In a similar manner, the easily observed diurnal (daytime) activity patterns of many lizards (especially *Anolis* species) and their use of color and movement in social behavior have made these animals central figures in studies of behavioral ecology (Johnson et al. 2010; Baird 2013) and evolutionary ecology (Losos 2009; Camargo et al. 2010; Hertz et al. 2013; Mahler et al. 2013; Thompson 2013) (see Chapters 13 and 16).

Herpetological studies have also contributed to advances in molecular biology and medicine. Molecules with specific functional properties have been used as probes to map biochemical pathways (McCleary and Kini 2013). For example, phosphodiesterase from the venom of the cottonmouth water moccasin (*Agkistrodon piscivorus*) played a key role in the pioneering studies of the cell cycle for which Stanley Cohen and Rita Levi-Montalcini received the 1986 Nobel Prize in Physiology or Medicine.

Some molecules from venoms have therapeutic applications (Kupferschmidt 2013). Peptides in the venom of the African black mamba (*Dendroaspis polylepis*) block pain impulses by inhibiting acid-sensing ion channels in neurons of the central and peripheral nervous systems. These peptides, called mambalgins, are as effective as morphine and do not have morphine's undesirable side effects of habituation and inhibition of respiration (Diochot et al. 2013). A peptide from the venom of the Gila monster (*Heloderma suspectum*) increases insulin secretion by the pancreas, and a synthetic form of that molecule is used to treat type II diabetes (Furman 2012).

The skins of amphibians synthesize a wealth of biologically active compounds. Antimicrobial host defense peptides provide a first line of defense against pathogens in the environment, including the chytrid fungi *Batrachochytrium dendrobatidis* and *B. salamandrivorans* (Conlon 2011). These small molecules (18–48 amino acid residues) have both hydrophobic and hydrophilic regions. This amphipathic structure allows them to penetrate the plasma membranes of bacterial and fungal cells, leading to lysis and cell death.

The host defense peptides of amphibians are diverse, and every new species of amphibian tested reveals previously unknown peptides. Synthetic analogs of host defense peptides are being developed to treat inflammation, infection, and cancer (Conlon et al. 2013). Because these peptides interact with the plasma membrane as a whole rather than with a specific receptor molecule, pathogenic organisms are unlikely to evolve resistance to them. Thus, these peptides offer promise for treating infections caused by multidrugresistant bacteria such as methicillin-resistant *Staphylococcus aureus* (MRSA) (Sang and Blecha 2008; Conlon and Sonnenvend 2011; Park et al. 2011; Afacan et al. 2012).

1.2 ■ The Diversity of Amphibians and Reptiles

Many people are familiar with the major groups of amphibians and reptiles—salamanders, frogs and toads, turtles, crocodylians, and lizards and snakes—from visits to zoos or from televised nature programs. This chapter provides an overview of some basic characteristics of these familiar groups. Detailed descriptions of amphibians and reptiles and their evolutionary relationships will be presented in Chapters 2, 3, and 4.

Amphibians

Modern amphibians are grouped as the Lissamphibia. The Greek prefix *liss* means "smooth" and refers to amphibians' scaleless skin. The lack of a protective scaly covering and other characteristics of amphibian skin shape many aspects of their lives. Different types of glands in amphibian skin produce peptides that deter pathogens, pheromones used in courtship, and a variety of toxins.

The skin of amphibians has a thin stratum corneum (outermost layer) and little keratin (the structural protein that stiffens skin and scales) (Lillywhite 2006). As a consequence, amphibian skin is very permeable to water and gases, and this permeability shapes much of the behavior and physiology of terrestrial amphibians (see Chapter 6). The high rate at which water evaporates from the skin of most terrestrial amphibians limits their activity in time and space. Most amphibians can be active only when the rate of evaporation is low—that is, when humidity is high and wind speed is low. Thus, amphibians typically are active at night (especially on rainy nights), and amphibian faunas are most diverse in moist environments.

Skin permeability has a paradoxical aspect, however, that allows amphibians to live in dry places. Amphibians do not

drink water. They absorb water through the skin and can take up water from moist soil. Anurans and salamanders that live in desert habitats spend many months in underground burrows, absorbing water from the soil around them to maintain their water balance. Amphibians would not be able to exist in arid environments if their skin were not permeable.

Amphibians are the only terrestrial vertebrates with a complex **life history**—the series of changes or stages an individual passes through over the course of its lifetime. An aquatic larval stage followed by **metamorphosis** (a change of form) into a terrestrial adult stage is an ancestral character of amphibians, and the name of the group is derived from the Greek *amphi*, "double" or "both," and *bios*, "life." **Direct development**, which bypasses the larval stage and metamorphosis, has evolved independently in many amphibian lineages, but many species retain the ancestral mode of development.

The extant (currently living) species of amphibians include three groups: Caudata (salamanders), Anura (frogs and toads), and Gymnophiona (caecilians). The more than 7,300 amphibian species encompass enormous diversity in body form, size, ecology, and behavior (see Wells 2007).

CAUDATA All of the more than 650 species of salamanders have elongate trunks and tails (**Figure 1.2**). Most salamanders have four legs, although the limbs of some aquatic species are greatly reduced. Aquatic eggs that hatch into aquatic larvae is the ancestral mode of reproduction for salamanders, but some lineages lay eggs on land and others retain the eggs and give birth to fully formed young (see Chapter 8). Two contrasting trends are prominent in the evolution of salamanders: specialization for an entirely terrestrial life, and specialization for a purely aquatic life.

Many members of the family Plethodontidae, the most terrestrial lineage of salamanders, lay eggs on land and the embryos pass through the larval stage of development within the egg before they hatch into miniature versions of adults (Bruce et al. 2000). The absence of lungs is an important element of the terrestrial specializations of plethodontids, and is possible because the skin of salamanders is a major site of gas exchange (see Chapter 7). The entire family Plethodontidae is characterized by lunglessness, and extremely small lungs are found in some other lineages of salamanders as well.

The evolution of life histories among the plethodontids is a study in complexity. Most terrestrial egg-laying salamanders belong to the Plethodontidae, which nevertheless displays the full range of reproductive modes: aquatic eggs and larvae (e.g., *Eurycea, Gyrinophilus, Pseudotriton*), terrestrial eggs and aquatic larvae (*Hemidactylium* and some *Desmognathus*), and terrestrial eggs with direct development (no larval stage; *Aneides, Ensatina, Bolitoglossa,* and some *Desmognathus*). The surprise lies in the evolutionary sequence of these modes. Rather than a straightforward transition











from aquatic eggs and larvae to terrestrial eggs and direct development, phylogenetic analysis of Plethodontidae reveals reversion from direct development to aquatic larvae within the genus *Desmognathus* and raises the possibility that there have been two additional reversions to aquatic larvae within the family (Chippindale et al. 2004).

While the plethodontid salamanders have adapted to terrestrial life, a completely aquatic life history has evolved in some other groups. Specialization for purely aquatic life includes a phenomenon called paedomorphosis (from the Greek paedos, "child," and morph, "form"), which is, in a sense, the mirror image of direct development. That is, instead of losing the aquatic larval stage, paedomorphic species have lost the terrestrial adult stage. Paedomorphosis is an example of an evolutionary process known as heterochrony (from the Greek heteros, "different," and chronos, "time"), discussed in Chapters 2 and 8. Heterochrony refers to alterations in the timing and rate of developmental processes (primarily during embryonic life) that change the body form of adults. Paedomorphic adults are aquatic and have larval characteristics, such as the presence of external gills and lateral line systems and the absence of eyelids and adult tooth patterns. Paedomorphosis is characteristic of some entire families of aquatic salamanders, such

as the Proteidae (*Proteus*, the European cave salamander, and *Necturus*, the North American mudpuppy; see Figure 1.2A). In other families, such as the Ambystomatidae (North American mole salamanders), some species are paedomorphic, whereas others metamorphose into terrestrial adults. Paedomorphosis is facultative in some species; certain populations—or even only certain individuals within a population—retain larval characteristics, whereas other populations or individuals metamorphose.

ANURA The anurans, with about 6,500 species worldwide, form the largest group of amphibians, and they are the most ecologically diverse. The immediately distinctive characteristic of all anurans is the absence of a tail, and the name "Anura" is formed from two Greek words (*an oura*) meaning "without a tail."

Most anurans have short bodies, large heads, and four well-developed limbs. Although this basic body form functions well in many habitats (Vidal-García et al. 2014), body shape and the relative lengths of the forelimbs and hindlimbs help sort anurans into categories based on their mode of locomotion (**Figure 1.3**). Species with short hindlimbs are generally runners, hoppers, or walkers, whereas those with long hindlimbs are swimmers or jump-



ers (moving ten body lengths or more in a single leap). Among jumping frogs, large hindlimb muscles relative to total body mass identify good jumpers. Long hindlimbs are often associated with climbing frogs (Emerson 1988).

Anurans have an enormous variety of reproductive modes, extending from aquatic larvae (tadpoles) to direct development (eggs that hatch into tiny frogs without a free-living tadpole stage) and even to viviparity (a female gives birth to tiny frogs) (see Chapter 8). Free-living aquatic larvae that metamorphose into adults are the ancestral condition and remains the most common reproductive mode (Jamieson 2003). Tadpoles are very different animals from frogs, with complex specializations associated with feeding (see Chapter 11). Most tadpoles are herbivores, and they are extremely efficient filter feeders. A tadpole is basically a swimming sieve attached to a gut, and enormous anatomical changes occur at metamorphosis when a tadpole changes to a frog.

GYMNOPHIONA This least familiar amphibian group comprises the caecilians—elongate, legless, burrowing and aquatic animals found in tropical habitats around the world (**Figure 1.4**). Most of these animals spend their entire lives underground or in the water and thus are difficult to study (Nussbaum 1992; Gower and Wilkinson 2005). Relatively little is known about their natural history, but work with captive animals has revealed elaborate reproductive specializations (Exbrayat 2006; Gomes et al. 2012). Among the most remarkable are species in which the embryos develop within the mother, feeding on a lipid-rich substance they scrape from the walls of the oviducts with specialized fetal teeth. In other species, the young remain with the mother after birth and feed by scraping lipid-rich cells from her skin (see Chapter 8).

Reptiles

The extant reptiles, in the sense covered by herpetology, include turtles, crocodylians, tuatara, and squamates (lizards and snakes). The qualifier "in the sense covered by herpetology" is needed because the groups of animals listed do not include all the forms descended from a common ancestor. Birds are closely related to crocodylians, so a complete list of the extant reptiles would include birds. Birds are so different from the other groups of reptiles, however, that they are normally excluded from herpetology, and we will use the term "reptiles" to mean non-avian reptiles—that is, all extant reptiles except birds. Chapter 2 describes the relationships of living and extinct amphibians and reptiles (including dinosaurs and birds) in more detail.

All reptiles (in the herpetological sense) except the crocodylians have a heart with a single ventricle (i.e., a threechambered heart), as do amphibians and fish. Oxygenated blood from the lungs and deoxygenated blood from the veins both enter the single ventricle of a reptile. Despite the lack of a septum, the two bloodstreams are normally kept separate in the heart: oxygenated blood is pumped to



Figure 1.4 Caecilians are elongate, legless amphibians. This Central American species (*Gymnopis multiplicata*) is viviparous. The embryos consume lipid-rich cells that they scrape from the walls of the oviduct. (Photograph © Michael & Patricia Fogden/Corbis.)

the head and body via the aortic arches, and deoxygenated blood is sent to the lungs via the pulmonary artery (see Chapter 7).

While it is true that an undivided ventricle is an ancestral character for reptiles (i.e., one that was present in the ancestor of the groups), being ancestral does not mean that a three-chambered heart is inferior to a four-chambered heart. On the contrary, a structure must work well to remain unchanged for 300 million years, and a threechambered heart can do something that a four-chambered heart cannot-adjust the proportion of blood that goes to the body versus to the lungs. This phenomenon is called an intracardiac (within the heart) blood shunt, and reptiles use intracardiac shunts to facilitate a variety of physiological processes (Hicks and Wang 2012). Thus, this primitive characteristic-the absence of a ventricular septum-is advantageous to extant reptiles. In fact, crocodylians, which do have a ventricular septum, use a different method of creating an intracardiac shunt during diving when they are adjusting blood flow to accelerate warming and to facilitate digestion. We will discuss intracardiac shunts further in Chapter 7.

TESTUDINES Just about everybody can recognize a turtle. The shell, which is a distinguishing feature of turtles, is a remarkable structure that encloses the entire animal in a bony case with openings only at the front and rear. The shell has limited the morphological diversity of turtles—there are aquatic and terrestrial turtles, but no arboreal or gliding species (Wyneken et al. 2007).

The habits of a turtle can often be deduced from its appearance (Figure 1.5). Terrestrial turtles, especially most



Figure 1.5 The body forms of turtles reflect their habits and habitats. (A) The carapace (dorsal shell) of many tortoises, like that of this Galápagos giant tortoise (*Chelonoidis nigra*), are domed, with elephant-like forelimbs. (B) The shells of aquatic swimmers such as the loggerhead sea turtle (*Caretta caretta*) are flatter and hence more streamlined. That relationship is not invariable, however, as seen in the next two images.

species of tortoises (*Astrochelys, Chelonoidis, Geochelone, Testudo,* and several other genera), have high domed shells, sturdy limbs, and elephant-like feet. Species of tortoises that construct burrows have flatter shells and spadelike front feet. The burrows of the gopher tortoise (*Gopherus polyphemus*), which extend for 10 m or more and reach depths greater than 4 m, provide shelter for more than 300 species of vertebrates and invertebrates (Kinlaw and Grasmueck 2012).

Aquatic turtles usually have webbed feet and relatively flat shells that offer less resistance to movement in water than would the domed shells of terrestrial species. Some aquatic turtles, such as musk turtles (*Sternotherus*) and mud turtles (*Kinosternon*), spend more time walking on the bottom than they do swimming, however, and these species have more domed shells than do turtles that swim quickly to capture prey or escape predators. Some aquatic turtles are still more specialized. Soft-shelled turtles



(D)



(C) Tortoises that construct burrows, like this gopher tortoise (*Gopherus polyphemus*) have relatively low dorsal shells. (D) Aquatic turtles that walk on the bottom of ponds, like the musk turtle (*Sternotherus odoratus*), have domed shells. (Photographs: A, © Steve Bloom Images/Alamy; B, © Amar and Isabelle Guillen/Guillen Photo LLC/Alamy; C, © FLPA/Alamy; D, © blick-winkel/Alamy.)

(*Apalone* and about 14 other genera) have flat shells without a bony layer or an external covering of scales. The leatherback sea turtle (*Dermochelys coriacea*) is another species in which the dermal bones are greatly reduced, and the stiff dermal scales have been replaced by a flexible covering of skin.

CROCODYLIA Only 25 species of crocodylians survive today, and most of them are classified as threatened or endangered on the IUCN Red List. The largest living reptiles are the Australian saltwater crocodile (*Crocodylus porosus*) and the Indian gharial (*Gavialis gangeticus*), both of which probably reach lengths of 7 m. Large as they are, however, they are small compared with some Mesozoic crocodylians Grigg and Kirshner 2015). *Sarcosuchus imperator* lived in Africa during the Early Cretaceous, and *Deinosuchus rugosus* in North America in the Late Cretaceous. Both species probably reached lengths of 11 to 12 m and may have weighed

as much as 8,000 kg (Erickson and Brochu 1999; Sereno et al. 2001). They were slightly larger than *Tyrannosaurus rex*, and could have preyed on dinosaurs.

Not all crocodylians are large; male dwarf caimans (*Paleosuchus palpebrosus*) are only 1.5 to 1.6 m long, and the females are even smaller. Estimating the maximum size of crocodylians is difficult because they continue to grow—albeit slowly—long after they reach maturity. Thus, among crocodylian populations the largest individuals are also the oldest. In a world with human predators, however, few crocodylians live long enough to grow to their maximum size.

The most conspicuous morphological differences among crocodylians involve the shape of the snout (**Figure 1.6**). Broad-snouted species, including the American alligator (*Alligator mississippiensis*), are generalized feeders that eat a wide variety of aquatic animals as well as an occasional bird or small mammal. Some crocodylians, such as the broad-snouted caiman (*Caiman latirostris*) can crush

(A) Dietary generalist (Alligator mississippiensis)



(C) Generalist piscivore (Crocodylus niloticus)



Figure 1.6 Crocodylians' jaws provide information about their food habits. (A) Dietary generalists such as the American alligator (*Alligator mississippiensis*) have moderately broad snouts and consume a wide variety of terrestrial and aquatic prey. (B) Specialists on armored prey such as the broad-snouted caiman (*Caiman latirostris*) have even stouter jaws with which they crush the shells of snails and turtles. (C) Generalist fish

hard-shelled prey, such as turtles. Long-snouted species, of which the Indian gharial (*Gavialis gangeticus*) is the prime example, are fish-eating specialists that capture fast-moving prey with a rapid sideways movement of the head. Some crocodiles (*Crocodylus*) with broad snouts prey on mammals, seizing them when they come near the water to drink, and large crocodiles have been known to attack and kill humans.

Crocodylians are members of the archosaurian lineage, which also includes dinosaurs and birds (see Chapter 2). As such, they provide a basis for understanding the ecology, behavior, and physiology of dinosaurs (Brazaitis and Watanabe 2011). Crocodylians provide extensive parental care to their young, and evidence is emerging of social structures among crocodylians that may involve many individuals (Lang 1989; Dinets 2013). These observations support the hypothesis that similar kinds of parental care and social behavior were characteristic of dinosaurs.

(B) Armoured prey specialist (Caiman latirostris)



(D) Specialist piscivore (Gavialis gangeticus)



eaters (piscivores) such as the Nile crocodile (*Crocodylus niloticus*) have moderately narrow snouts. Fish make up a large part of their diets, but generalist fish eaters also consume a wide variety of other vertebrates. (D) A specialist piscivore, the Indian gharial (*Gavialis gangeticus*) has an extremely narrow snout and uses a rapid sideward swipe of the head to capture fish, on which it feeds almost exclusively. (After Wermuth and Fuchs 1978.)



Figure 1.7 Henry, a tuatara (Sphenodon punctatus). Henry has lived at the Southland Museum in Invercargill, New Zealand, since 1970 and was the model for the tuatara on the New Zealand 5-cent coin. Sadly, these coins have been



removed from circulation, but in 2009 Henry became a father at an estimated age of more than a century. (Photographs by Harvey Pough.)

RHYNCHOCEPHALIA Commonly known by the Maori name "tuatara," the Rhynchocephalia contains only one species, *Sphenodon punctatus*, although there is substantial genetic variation among populations (Hay et al. 2010). Tuatara (the Maori language does not add an *s* to form the plural) are lizardlike in appearance (**Figure 1.7**) but are distinguished from lizards by several primitive features of their skeletal anatomy (see Chapter 4). As recently as 800 to 1,000 years ago, tuatara occurred on the North and South Islands of New Zealand, but predation by introduced mammals and habitat destruction wiped out those populations, and the species is now restricted to 30 offshore islands (Cree 2014).

Tuatara are colonial nesters (Thompson et al. 1996; Refsnider et al. 2010, 2013). Females breed every 2 to 4 years, migrating more than 300 m from their residential burrows to rookeries in open areas, and usually returning to the same rookery time after time. Clutches average 9 eggs, which take 11 to 16 months to hatch. The hatchlings become reproductively mature in 11 to 13 years but require 25 years or more to grow to the adult size of 50 cm, and they live for at least 60 years (Castanet et al. 1988; Alison Cree and Nicola Nelson, pers. com.). Sex is determined by the temperature in the nest during incubation-low nest temperatures produce females, and high temperatures produce males (Cree et al. 1995). (This phenomenon is known as temperature-dependent sex determination, or TSD, and also occurs in turtles, lizards, and crocodylians; see Chapter 9.) The combination of small clutch sizes, slow growth to maturity, and long intervals between successive clutches makes populations of tuatara vulnerable to extinction on islands with rats, and global climate change might interact with TSD to produce an excess of male hatchlings (Cree et al. 1995; Nelson et al. 2004).

SQUAMATA Squamates, the largest group of reptiles, are an enormously diverse group. Squamate species live

in habitats extending from below ground to the treetops, from deserts to the ocean, and from the Equator to the Arctic Circle. Two body forms are included in the Squamata, lizards (about 6,000 species) and snakes (about 3,500 species). Snakes and lizards are part of the same evolutionary lineage (Hedges and Vidal 2009). That is, in an evolutionary sense the animals known as snakes are specialized lizards (see Chapter 4), and there is no correct name for a group that includes only the animals popularly called lizards. The term "squamates" can be used in many cases when the phenomenon being discussed is common to both lineages. In other cases, however, we will use "lizards" or "snakes" to make distinctions between the groups.

Many lizards are diurnal, brightly colored, and use conspicuous visual displays in their social behavior. These characters have made lizards familiar elements of the fauna and important subjects for behavioral and ecological studies (Pianka and Vitt 2003). Snakes are often secretive and rely on scent rather than vision in their predatory and social behavior. As a result, snakes are usually a less conspicuous part of the fauna than are lizards. Nonetheless, snakes are important components of ecosystems in many parts of the world and display a broad range of specializations (Greene 1997; Lillywhite 2014).

A generalized lizard has a more or less cylindrical body, a long tail, and moderately long legs (**Figure 1.8**). Most lizards can climb, and the most arboreal species, the African chameleons (*Chamaeleo* and other genera), have digits that are organized into two sets that oppose each other to grasp a branch. Herbivorous species, such as ground iguanas (*Cyclura*) and mastigures (*Uromastyx*), have bulky bodies that accommodate the digestive apparatus needed to cope with a plant diet.

Many lizards enter water to escape from predators, but only a few species actually forage underwater. The best-





Figure 1.8 Body forms of lizards. (A) Lizards that live primarily on the ground, such as the North American desert iguana (*Dipsosaurus dorsalis*), often have cylindrical bodies and tails and stout limbs. (B) Specialized arboreal lizards, especially chameleons (a veiled chameleon, *Chamaeleo calyptratus*, is shown here), have laterally flattened bodies and their heads are often adorned with crests. Chameleons have prehensile tails and zygodactylus feet—that is, the toes are arranged in opposing groups that close to grip a twig. (C) Lizards that have reduced limbs, or no limbs at all, such as the European slow worm (*Anguis fragilis*), are typically elongate. (Photographs: A, Harvey Pough; B, © Matthijs Kuijpers/Alamy; C, © David Boag/Alamy.)

known aquatic species is the Galápagos marine iguana (*Amblyrhynchus cristatus*), which feeds on marine algae that it scrapes from rocks, diving as deep as 10 m in the process.

Leglessness has evolved repeatedly among squamates (Wiens and Slingluff 2001). All snakes are legless (**Figure 1.9**), and several families of lizards include species that are functionally or actually legless. Legless squamates must be elongate because they form curves along the length of the body to push against the substrate during locomotion (see Chapter 10). Snakes have elongated trunks with very high numbers of presacral vertebrae (i.e., anterior to where the hip would be if snakes had hips) and relatively few postsacral (i.e., tail) vertebrae. Legless lizards, in contrast, have relatively short trunks and very long tails.

Many legless squamates are surface dwellers. Their slim bodies allow them to move easily through dense vegetation or leaf litter. Other legless species are fossorial (burrowing). Some of these animals construct open tunnels in compact soils, whereas others move through loose soil by a process known as sand swimming. Amphisbaenians are an evolutionary lineage of specialized burrowing squamates that occur in tropical habitats around the world (Gans 1992; Navas et al. 2004). Only 3 of the approximately 150 species of amphisbaenians retain limbs.

Specialized arboreal snakes, such as the South American vine snake *Philodryas argentea*, hunt lizards and frogs that perch at the tips of branches. Their extremely elongate bodies and tails spread their weight over a large area and allow them to crawl across leaves and twigs (see Figure 1.9B). Vine snakes represent an extreme development of elongation among snakes, but other arboreal snakes—including boas, pythons, and vipers—are slimmer than their terrestrial relatives.

Not all snakes are long and thin. In fact, being short and fat has some definite advantages. Snakes swallow their prey whole, and the cartoon image of a snake with a lump representing a large meal in its stomach is based on fact. A stout body allows snakes to swallow large prey, and stout bodies are one of several specializations of nonarboreal vipers. The stoutest vipers are members of the African genus *Bitis*, such as the puff adder (*B. arietans*; see Figure 1.9C) and Gaboon viper (*B. gabonica*). The Gaboon viper grows to a mere 1.2 m in length, but there is a record of one eating an antelope.

The distinction between aquatic and terrestrial species is blurred among snakes. Many genera, including water snakes of the genera *Nerodia* and *Natrix* and some garter snakes (*Thamnophis*), forage both in and out of water. More specialized aquatic snakes, such as the homalopsines (swamp and water snakes of Asia and Australia), have nostrils with valves that exclude water. The most specialized aquatic snakes, the acrochordids (Indo-Australian wart snakes) and hydrophiines (sea snakes), lack enlarged ventral scales and never emerge from the water (Figure 1.9D).



Figure 1.9 Body forms of snakes. (A) A generalized terrestrial snake, the San Francisco garter snake (*Thamnophis sirtalis tetrataenia*) is a colorful subspecies that occurs in San Mateo County, California. (B) The striped long-nosed snake (*Philo-dryas argentea*) from northern South America shows the long,

thin body typical of specialized arboreal snakes. (C) The African puff adder (*Bitis arietans*) is a heavy-bodied terrestrial viper. (D) The spiny-headed sea snake (*Hydrophis peronii*) shows the valvular nostrils and flattened tail characteristic of sea snakes. (Photographs: A and B, R. D. Bartlett; C and D, Harvey Pough.)

1.3 ■ Shared Characteristics of Amphibians and Reptiles

By now you should be convinced that the more than 17,000 species of amphibians and reptiles display an enormous diversity of behavioral and morphological features. But if that's so, why is there an area of biological specialization called herpetology that includes both amphibians and reptiles? After all, reptiles are more closely related to mammals than they are to amphibians, so why should one taxonomic discipline study two such distantly related groups as amphibians and reptiles?

Historical accident is partly the reason that herpetology includes both amphibians and reptiles. Remember that in the 18th century, Linnaeus lumped amphibians and reptiles together with other vertebrates that were neither bony fishes, birds, nor mammals. But historical inertia is not the only reason herpetologists have continued to study both amphibians and reptiles; there is a biological reason as well. These two groups share a key ancestral character that makes them different from birds or mammals in many aspects of their ecology, physiology, and behavior.

Amphibians and reptiles are ectotherms (from the Greek ecto, "outside," and thermos, "heat"). That is, ectotherms obtain the energy needed to raise their body temperature to levels that permit normal activity from an outside source: the sun, either directly (by basking in the sunlight) or indirectly (by resting on a warm surface such as a rock heated by the sun). In contrast, endotherms (birds and mammals) produce heat internally, by biochemically metabolizing carbohydrates, lipids, and proteins from the food they eat. Because ectothermy has consequences for nearly all aspects of an animal's life, amphibians and reptiles are more similar to each other in many aspects of their biology than either group is to birds or mammals. Understanding the significance of ectothermy is key to understanding how and why the ecology, behavior, morphology, and physiology of amphibians and reptiles are so different from those of birds and mammals, and why ectotherms and endotherms play different roles in ecosystems (Pough 1980, 1983). The mechanics of ectothermal temperature regulation are complex, as we will discuss in Chapter 6, but a brief explanation of some features of ectothermy shows why ectotherms are so different from endotherms.



Ectothermal thermoregulation

Many ectotherms control their body temperature at high levels and within narrow limits during their periods of activity. Lizards, especially species that live in open, sunny habitats, provide the best examples of how effective ectothermal thermoregulation can be. Many species of lizards maintain body temperatures between 35°C and 40°C while they are thermoregulating. That is as warm as the body temperatures of most birds and mammals.

Figure 1.10 shows thermoregulation by a male Central American whiptail lizard (*Holcosus festivus*, formerly *Ameiva festiva*). The lizard moved back and forth between the edge and interior of a forest, basking in the sun at the forest edge to raise its body temperature and then moving under the tree canopy and cooling as it foraged in the shade before returning to the sun to bask again. During the 35-minute period charted in Figure 1.10, the lizard maintained its body temperature between an average upper limit of 39.4°C and an average lower limit of 34.5°C (van Berkum et al. 1986).

Costs and benefits of ectothermy and endothermy

A lizard has two important energy-saving features compared with a mammal that lives in the same habitat as the lizard. The first advantage is that the lizard uses sunlight to maintain a high body temperature, whereas the mam**Figure 1.10 Thermoregulation by a Central American whiptail lizard.** (A) *Holcosus festivus* is a terrestrial species that lives in habitats that provide sun and shade. (B) The body temperature of a male *H. festivus* was recorded as it shuttled between sun at the edge of a forest and the shaded interior of the forest. The lizard basked in the sun until its body temperature reached an average of 39.4°C, then foraged for prey in the shade, cooling to an average of 34.5°C, at which point it moved back to the forest edge to bask. (After van Berkum et al. 1986; photograph by Martin Feldner.)

mal relies on metabolic heat production. As a result of the difference in the metabolic requirements of ectotherms and endotherms, the rates of energy use by ectotherms are one-seventh to one-tenth those of an endotherm of the same body size (**Figure 1.11**).

The total difference in the daily energy requirement for a lizard and a mammal of the same size is more than the seven- to tenfold difference in their metabolic rates,

however, because of the daily cycle of body temperature the lizard experiences. At night, when its body temperature is low, a lizard's energy use falls to about one-third of its daytime rate. A mammal also shows a change in energy expenditure at night, but in the opposite direction from the lizard because the mammal is producing heat by metabolism to replace the heat it loses to the environment. When the environment cools at night, a mammal loses heat faster and must increase its metabolic rate to produce the additional heat it needs. Thus, the difference between energy use by a lizard and by a mammal is greater at night than it is during the day.

A third factor enters the equation: activity. Mammals are usually more active than lizards, and activity requires energy. The combined effects of the three factors—the use of solar energy rather than metabolic energy by a lizard to keep itself warm, the reduction in a lizard's body temperature at night, and the sedentary behavior of a lizard compared with a mammal—are dramatic. A lizard uses only about 3% as much energy in a day as a mammal of the same body size (Bennett and Nagy 1977). That lower metabolic requirement of the lizard translates into lower daily food requirements.

Body size and shape

A striking feature of amphibians and reptiles is how small most of them are compared with birds and mammals. More



Figure 1.11 Mass-specific energy use.

Metabolic rates (in J/h per gram of body weight) of ectothermal and endothermal vertebrates are shown as a function of body size (measured as body mass and shown on a logarithmic scale). The metabolic rates of endotherms (birds and mammals) are 7 to 10 times higher than those of ectotherms (salamanders, all reptiles, lizards) of the same body size. The mass-specific metabolic rates of both ectotherms and endotherms increase at small body sizes, and the rates for small ectotherms are substantially lower than those for small endotherms. Very few species of birds and mammals are smaller than 10 g. (After Pough 1980.)

than half of the extant species of salamanders, caecilians, anurans, lizards, and amphisbaenians weigh less than 10 g as adults. (Figure 1.12). Only among snakes, turtles, and crocodylians are larger species the norm. Thus, the smallest species of amphibians and reptiles are ten times smaller than the smallest birds and mammals. Mice, bats, chickadees, and sparrows weigh 10 to 20 g. Very few birds and mammals weigh less than 5 g, but that is a common body size for amphibians and reptiles. In fact, adults of many small species of amphibians and reptiles weigh less than 0.5 g.

In a pattern that is characteristic of both endotherms and ectotherms, energy use increases at small body sizes. To put that relationship into words, the energy requirement of a gram of tissue (called the **mass-specific energy requirement**) is greater for a small animal than for a larger animal of the same kind. For example, at a body temperature of 30°C, a reptile weighing 100 g has a mass-specific energy requirement of 1.98 J/h per gram of body weight, whereas for a 10-g reptile the value is 3.14 J/h per gram of body weight. (The symbol J indicates joule, a unit of energy equal to 0.24 international calories.) That is, the mass-specific energy requirement becomes progressively greater as body size gets smaller.

The increase in the mass-specific energy requirement at small body sizes applies to both endotherms and ectotherms, but endotherm metabolic rates are 7 to 10 times greater than those of ectotherms. Thus, a 5-g ectotherm uses about 600 J/day, a 5-g placental mammal about 6,000 J/day, and a 5-g passerine bird about 15,000 J/day. The amount of food an animal must eat is proportional to its energy use, so a small mammal or bird must find and eat much more food each day than an amphibian or reptile of the same size would require. The increase in mass-specific metabolic rates at small body sizes, combined with the already higher energy requirements of endotherms, means that being a very small endotherm is both energetically expensive and ecologically difficult. In fact, it is so difficult to be a very small endotherm that there are very few such species (e.g., some of the smallest shrews and hummingbirds), and these species save energy by lowering their body temperature at night and also during the day when food is scarce.

In contrast, it is relatively easy to be a small ectotherm, and many species of amphibians and reptiles live in a bodysize range well below that of any bird or mammal species. The competitive and predatory interactions of these very small amphibians and reptiles are primarily with each other and with invertebrates such as spiders, scorpions, and centipedes.

Ectothermy and efficiency

One more consequence of ectothermy leads to a major difference in the way amphibians and reptiles function in ecosystems compared with birds and mammals: ectothermy is an efficient way of life in terms of how an organism uses the energy in the food it eats.

Ecologists and organismal biologists are concerned with the way an organism partitions the energy it obtains in its food—that is, how much of the energy goes to maintenance (processes that keep an organism alive, such as respiration, circulation, and transporting molecules in and out of cells) and how much goes to secondary production (growth of an individual or development of eggs and embryos). It is in the *balance* between the two major categories of energy use—maintenance and production—that ectotherms differ from endotherms.



Because endotherms rely on heat generated by metabolic processes, they devote a large proportion of the food they consume to keeping themselves warm. In fact, nearly 99% of the energy that most birds and mammals obtain from their food is used to generate heat. Less than 2% is available for production of new tissue. In contrast, ectotherms get heat from the sun without having to use energy from their food. As a result of ectothermy, the proportion of the energy amphibians and reptiles consume that is converted to new animal tissue (their **production efficiency**) is about 25 times higher than the production efficiency of birds and mammals.

1.4 ■ Amphibians and Reptiles in Terrestrial Ecosystems

The difference in production efficiency between amphibians and reptiles on the one hand, and birds and mammals on the other, has important implications for the pathways that energy and nutrients follow through ecosystems. An example that illustrates this principle is the Hubbard Brook Experimental Forest in New Hampshire, the site of ecosystem studies since the 1960s. The numbers of different kinds of animals have been counted, the amount of food each species consumes has been measured, the amount of energy each species uses for maintenance has been calculated, and the annual production of young and the growth



Figure 1.12 Amphibians and reptiles are small compared with birds and mammals. More than 50% of anurans, salamanders,, and lizards weigh less than 10 g. In contrast, about 90% percent of birds and 95% of mammals weigh more than 10 g. The contrast is even more dramatic at the low end of the scale about 20% of salamanders and anurans and 10% of lizards weigh less than 1 g, but no species of birds or mammals are that small. (Data from Pough 1980; Eisenberg 1981; Dunning 2008.)

of adults have been recorded. The values of all these variables can be compared by converting them to megajoules per hectare (MJ/ha) of forest.

Thomas Burton studied the role of salamanders in energy flow through the Hubbard Brook ecosystem (Burton and Likens 1975). One species, the eastern red-backed salamander (*Plethodon cinereus*), makes up about 90% of the total salamander community in the Hubbard Brook forest. Burton concentrated on *P. cinereus*, for comparison using information about birds and mammals gathered by other ecologists working at Hubbard Brook.

In the Hubbard Brook ecosystem, salamanders consume only about 20% as much energy as birds, and from that perspective, the salamanders don't seem very important. The picture changes, however, when the annual production of new tissue by salamanders and birds is compared (**Figure 1.13**). The efficiency of salamanders is so high (about 60%) that they produce more than five times as much new animal biomass every year as the birds. This new biomass is a source of protein and energy for predators. Farther south, the biomass of salamanders is as much as ten times greater than at Hubbard Brook, making them an even more important component of the forest food web (Semlitsch et al. 2014). The question that interests a predator is, "What is there to eat?" and the answer is, "Salamanders!"



Figure 1.13 Energy flow through the bird and salamander communities at Hubbard Brook. Birds consume nearly five times as much energy as salamanders, but birds devote almost 99% of that energy to maintenance. In contrast, salamanders use only 40% of the energy in their food for maintenance. As a result, the annual production of new biomass by salamanders is five times greater than that of birds. (Data from Burton and Likens 1975.)

In addition to their importance in biomass conversion, the salamanders occupy a critical niche in the forest ecosystem. Eastern red-backed salamanders, like so many species of amphibians and reptiles, are very small. Adults weigh about 1 g—much smaller than the smallest birds and mammals at Hubbard Brook. The salamanders feed on invertebrates that are too small for a bird or mammal to eat, efficiently converting tiny prey into salamander biomass. Thus, in the context of the Hubbard Brook ecosystem, salamanders harvest the energy in prey that is not directly available to birds and mammals because it comes in small packages, and convert that energy into salamander-size packages that birds and mammals can consume. Both the small body size of the salamanders and their high production efficiencies are direct results of ectothermy (Pough 1980, 1983).

1.5 ■ The Future of Amphibians and Reptiles

Just as we are coming to appreciate the unique characteristics of amphibians and reptiles, many species are facing unprecedented threats to their survival, and some are already extinct. (For reviews see Gibbons et al. 2000; Lannoo 2005; Wake and Vredenburg 2008; Collins and Crump 2009; Allentoft and O'Brien 2010; Reading et al. 2010; Böhm et al. 2013.)

The current extinction rate of amphibians is more than 200 times the background extinction rate (McCallum 2007). *Incilius periglenes*, the golden toad of Costa Rica (**Figure 1.14**), has the sad distinction of being one of the first well-documented cases of extinction of an amphibian species. This brightly colored montane toad was first described in 1967 (Savage 1967). At that time golden toads were abundant, and they remained so for two decades. In 1987 more than 1,500 toads gathered at the main breeding site, but in 1988 and 1989 only a single toad appeared at those pools. Intensive surveys from 1990 to 1992 did not locate any golden toads, and the species has not been seen since then (Pounds and Crump 1994).



Figure 1.14 A recently extinct amphibian species. This breeding assemblage of male golden toads (*Incilius periglenes*) was photographed in the 1980s at Monte Verde Cloud Forest Preserve, Costa Rica. No individual of this species has been sighted since the early 1990s, and it represents one of the first fully documented cases of modern-day extinction. (Photograph © Michael & Patricia Fogden/Corbis.) Most of the anthropogenic (human-caused) pressures faced by amphibians and reptiles confront other animals as well, but aspects of the life history and ecology of amphibians and reptiles makes them particularly susceptible to certain threats.

- Habitat destruction and alteration caused by the inexorable increase in human population threatens many populations and species of amphibians and reptiles (Hof et al. 2011). Amphibians with complex life histories are especially vulnerable. Not only do they have two critical habitats—the aquatic breeding and larval habitat and the terrestrial adult habitat—but they must also be able to move between those two habitats.
- Many human activities release chemical pollutants into the environment. Some of these pollutants are immediately toxic to amphibians and reptiles, whereas others interfere with physiological processes or with embryonic development and sex determination (e.g., Denoël et al. 2010; Hayes et al. 2010; James and Semlitsch 2011; Karraker and Gibbs 2011; Moore et al. 2012; Wijesinge 2012). Again, amphibians are especially vulnerable because of their aquatic larvae and permeable skins.
- Epidemic diseases are spreading more rapidly as the speed and volume of global transportation increase. In the past two decades fungal diseases have emerged as a threat to the species diversity of animals and plants and to food production for humans (Fisher et al. 2012). Global com-

merce in African pipid frogs (*Xenopus*) for medical research and American bullfrogs (*Rana catesbeiana*) to be farmed as food may have contributed to the spread of a fungus, *Batrachochytrium dendrobatidis* (Bd), that has infected anurans around the world (Schloegel et al. 2012). Worse still, anthropogenic mixing of different strains of Bd has generated a hypervirulent strain of the fungus (Farrer et al. 2011).

As ectotherms, amphibians and reptiles depend on the environment to maintain body temperatures (Paaijmans et al. 2013). For this reason, changes in temperature could be detrimental to some species. Range distributions may change. Temperature-dependent sex determination could also be affected: an increase or decrease in the temperature of nests could result in skewing the sex ratio in populations of species with temperature-dependent sex determination (Mitchell and Janzen 2010).

Habitat loss, pollution, and disease are not separate problems, and disentangling their interactions is challenging (Blaustein et al. 2010; Buckley 2013). The responses that amphibians and reptiles can deploy in the face of these challenges include behavior, physiology, and even morphology (Williams et al. 2008; Clusella-Trullas et al. 2011; Huey et al. 2012). Multifactorial studies are required to identify the mechanisms underlying the responses of populations to these stresses (Blaustein et al. 2009; Buckley 2013), and these studies must be based on an understanding of the biology of amphibians and reptiles—that is, on herpetology.

SUMMARY

Our understanding of the biology of amphibians and reptiles has increased greatly in the last three centuries.

In the 18th century, Linnaeus lumped amphibians and reptiles together, calling them "foul and loathsome" and saying there are very few of them. Today we know that amphibians and reptiles are as diverse as birds or mammals, and that the unique characteristics of some species make them model organisms for modern biology.

Extant amphibians include about 7,300 species in three lineages.

Caudata (salamanders; 655 species) have elongated trunks and tails and, in most species, four limbs.

Anurans (frogs and toads; 6,438 species) have short bodies, no tails, and four well-developed limbs used for walking, running, hopping, jumping, climbing, burrowing, and swimming.

Gymnophiona (caecilians; 200 species) are elongated, legless, burrowing, and aquatic animals.

Because they share a unique common ancestor, extant reptiles technically include the birds, but herpetology focuses on four lineages of non-avian reptiles, with a total of more than 10,000 species.

Testudines (turtles; 341 species) are distinguished by the shell that encloses the trunk.

- Rhynchocephalia is represented by a single species (*Sphenodon punctatus*, the tuatara of New Zealand).
- Squamates include the lizards (6,175 species) and snakes (3,496 species).
- Crocodylians (alligators and crocodiles; 25 species) are mostly large, semiaquatic predators.

Although historical accident is part of the reason two lineages as phylogenetically distant as amphibians and reptiles are combined in the specialty of herpetology, the consequences of ectothermy, an ancestral character retained in both groups, is critically important.

As ectotherms, amphibians and reptiles rely primarily on environmental sources of heat for thermoregulation, rather than on heat produced inside their bodies by metabolism. As a result of ectothermy, the daily energy requirement of an amphibian or reptile is only one-tenth to oneseventh that of a bird or mammal of the same body size, and because of this low energy requirement amphibians and reptiles differ from birds and mammals in important ways:

- Most species of amphibians and reptiles are much smaller than birds or mammals, with 10 g as a convenient dividing line—that is, most species of amphibians and reptiles are smaller than 10 g, whereas most species of birds and mammals are larger.
- Amphibians and reptiles are more efficient at converting energy in their food into new tissue (i.e., secondary production) than are birds and mammals. In general, amphibians and reptiles convert more than 50% of the energy they ingest into new tissue (growth and reproduction), whereas birds and mammals convert less than 2% of that energy.

Small body size and efficient secondary production allow amphibians and reptiles to occupy a distinct ecological niche, consuming prey items that are too small for birds and mammals and efficiently repackaging the energy in their prey into organisms that are large enough for birds and mammals to consume.

Human activities are responsible for most of the risks facing all forms of life, and features of their ecology make amphibians and reptiles especially vulnerable to certain threats.

Amphibians have the unfortunate distinction of being the tetrapod group with the highest proportion of species (nearly one-third) in the categories at risk of extinction in the 2014.2 IUCN Red List. More than 20% of reptiles are at risk.

Habitat destruction and degradation resulting from the pressures of human population increase threatens many species of amphibians and reptiles. Amphibians with complex life histories are especially vulnerable because they rely on both aquatic (larvae) and terrestrial (adult) habitats, and must travel between the two.

The reliance of amphibians and reptiles on environmental sources of heat and shelter from extreme temperatures renders them vulnerable to the changes in climate that are occurring on a global scale.

Interactions among risk factors can magnify their effects and increase the impact of climate change.

Go to the **Herpetology** Companion Website at **sites.sinauer.com/herpetology4e** for links to videos and other material related to this chapter.

2 Phylogenetic Systematics and the Origins of Amphibians and Reptiles

The extant amphibians and reptiles are a diverse collection of animals with evolutionary histories dating back to the Early Carboniferous period. A phylogenetic perspective helps us visualize the relationships among these organisms and interpret the evolution of their physiological, morphological, and behavioral characteristics. To gain this perspective, it is important to understand how phylogenies are created and used. Thus, we begin with a brief review of phylogenetic systematics and taxonomy and then use this framework to examine the transition from fishlike aquatic vertebrates to the earliest terrestrial tetrapods (from the Greek *tetra*, "four," + *podos*, "foot") and the origins of modern amphibian and reptile groups.

Taxonomy is the science of categorizing, or classifying, Earth's living organisms. A **phylogeny** is a hypothesis of the evolutionary relationships of these categories of organisms, usually presented in the form of a branching diagram. Phylogenies, sometimes called **cladograms** or **phylogenetic trees**, are similar to human family trees in that they show the splitting of an ancestor and its descendants through time, but instead of several familial generations, these splitting events cover millions to hundreds of millions of years.

The appearance in 1966 of an English translation of the work of the German biologist Willi Hennig was the start of a revolution in the way evolutionary relationships are analyzed. Hennig's method, known as **phylogenetic systematics** or **cladistics**, emphasizes the importance of monophyletic groups and shared derived characters. The many terms used in phylogenetic systematics can be confusing, but the concept of **monophyly** (from the Greek *mono*, "one" or "single," + *phylon*, "tribe") is critical to understanding any discussion of modern phylogeny and taxonomy.

2.1 ■ Principles of Phylogenetics and Taxonomy

Phylogenies are the basis of the taxonomic structure of reptiles and amphibians. A **taxon** (plural *taxa*; from the Greek *tax*, "to put in order") is any unit of organisms given a formal name. For example, the common five-lined skink (*Plestiodon fasciatus*) from eastern North America is a taxon, as is its entire genus (*Plestiodon*), the group containing all skinks (Scincidae), and several more inclusive, larger taxonomic groups (Squamata, Reptilia, Tetrapoda, Vertebrata, etc.) to which it belongs. A monophyletic taxon, or **clade**, is made up of a **common ancestor** and all of its descendant taxa.

Phylogenies can be depicted in a variety of styles (**Figure 2.1**). A **node** is the point at which a common ancestor gives rise to two **sister lineages**, or **branches**. The region of a phylogeny between two nodes is called a **stem**. The stem is an important concept because the term is often used when discussing extinct lineages. Depending on the type of analysis used to infer the phylogeny, the length of branches may represent the amount of genetic change or be scaled with time and accompanied by a timescale. Such a timescale is usually depicted in terms of the geological eras and periods of Earth's evolutionary history (**Table 2.1**; **Figure 2.2**).

A phylogeny is one of the most powerful tools in biology. With knowledge of a group's phylogeny, we can track the evolution of morphology, behavior, and ecology among the organisms in that group. For example, both the mantellid frogs of Madagascar and the dendrobatid frogs of Central and South America are small, leaf-litter dwelling anurans that are brightly colored and have evolved the ability to secrete powerful defensive alkaloid toxins in their skin (see Chapter 15). Both groups sequester many of the same types of alkaloids (Clark et al. 2005), and both groups de**Figure 2.1 Common formats and terminology for presenting a phylogeny (cladogram).** This simple phylogeny of four hypothetical taxa is shown in three different styles. Taxa 1 and 2 form a clade, as do Taxa 3 and 4 and all four taxa together. Not shown are numerous stem lineages between nodes A and B (and others between A and C). These lineages may be extinct or simply were not sampled in the phylogenetic analysis. (A) Squared horizontal presentation, read from left to right with terminal taxa on the right. This is the style used most frequently in this book. (B) Squared vertical presentation, with terminal taxa at the top. (C) Diagonal presentation.



rive these alkaloids from their prey, usually ants. With no phylogenetic information, we would assume that these two groups are more closely related to each other than to other frog groups, and that the ability to sequester defensive alkaloids from arthropod prey evolved once in their com-

mon ancestor. However, phylogenetic analysis shows that mantellids and dendrobatids are only distantly related, and that both groups have close relatives that do not secrete defensive alkaloids (**Figure 2.3**). Thus, sequestration of toxins evolved independently in mantellids and dendrobatids, a phenomenon known as **convergent evolution**.

In phylogenetic systematics, only clades—monophyletic taxa—are formally recognized and given names. Following this convention produces taxonomic groups that also represent evolutionary history. For example, precladistic taxonomy recognized birds and reptiles as separate taxa. However, modern phylogenetic analysis has shown that birds share a common ancestor with all the other reptile taxa (crocodiles, lizards, snakes, tuatara, and turtles). In other words, if we exclude birds from Reptilia, then Reptilia is not monophyletic; in the context of phylogenetic systematics, Reptilia without birds is **paraphyletic** (from the Greek *para,* "beside" or "except") because it contains only some, not all, of the descendants of the common ancestor of the traditional reptiles (**Figure 2.4**).

A similar concept is **polyphyly** (from the Greek *poly*, "many"), the situation in which a taxonomic group does not contain the most recent common ancestor of all the members of that group. For example, a hypothetical taxonomic group comprising the endothermal ("warm-blooded") vertebrates—mammals and birds—would be polyphyletic because it would not include the most recent common ancestor of each group, birds and mammals having arisen from different common ancestors (diapsids and synapsids; see Section 2.5). Paraphyletic and polyphyletic groups are not given formal taxonomic names but are sometimes named informally, in which case the taxonomic name is put in quo-







Mantella laevigata



Dendrobates tinctorius

Figure 2.3 Phylogeny reveals convergent evolution.

Both the Neotropical Dendrobatidae and the Madagascan Mantellidae comprise small, brightly colored frogs that live in leaf litter on the tropical forest floor, as seen in these photos of typical species. Both dendrobatids and mantellids obtain alkaloid toxins from the insects they eat and sequester these toxins in their skin as a defense against predators. These similarities could logically lead to the hypothesis that dendrobatids and mantellids are sister taxa, and that sequestration

TABLE 2.1 The geological time scale ^a				
Era	Period	Epoch		
	Oustanaa 24 mus	Holocene ~11 kya		
	Quaternary 2.6 mya	Pleistocene 2.6 mya		
	Anter strand Dame and	Pliocene 5.3 mya		
Cenozoic 66.0 mva		Miocene 23.0 mya		
oo.o mya	Tertiary 66.0 mya	Oligocene 33.9 mya		
	and the carries of a string	Eocene 56.0 mya		
	The second s	Paleocene 66.0 mya		
	Cretaceous 145 mya			
Mesozoic 252 mva	Jurassic 201 mya			
	Triassic 252 mya			
	Permian 299 mya			
	Carboniferous 359 mya			
Paleozoic	Devonian 419 mya			
541 mya	Silurian 444 mya			
	Ordovician 485 mya			
	Cambrian 541 mya			

^a Dates are from Geological Society of America (2012) and represent the ^s starting times of the intervals shown.

ability evolved a single time in their common ancestor. However, phylogeny reveals that these frogs belong to two distinct evolutionary lineages—Hyloidea and Ranoidea—that separated some 170 mya, and the defensive use of toxins evolved independently in the two taxa. Solid triangles are shorthand for multiple taxa; the complete anuran phylogeny is shown in Figure 3.22. (Photographs: *Mantella* © All Canada Photos/ Alamy; *Dendrobates* © Dirk Ercken/Alamy.)

tation marks (as "Reptilia" in Figure 2.4B). Many researchers do not make a distinction between para- and polyphyletic and simply use the term non-monophyletic.

Because only monophyletic groups are given formal taxonomic names, many changes in the names of taxonomic groups such as genera and species are the results of phylogenetic analysis showing that an existing named taxon is not monophyletic. As with all scientific hypotheses, the relationships depicted by a phylogenetic tree are subject to falsification by new evidence or a better analysis of existing evidence. Alternative hypotheses about evolutionary relationships are common, as we will see in this and the next two chapters.

In some cases, groups that are clearly monophyletic can be defined by shared derived characters (see below), but it has not yet been possible to determine the sequence in which the descendant lineages separated (e.g., neobatrachian frogs or pleurodont lizards; see Figures 3.22 and 4.12, respectively). When the branching sequence of three or more lineages cannot be determined, that situation is unresolved and is called a **polytomy** (from the Greek *tom*, a "cut" or "slice"). For example, iguanian lizards, anguimorph lizards, and snakes form a polytomy because the phylogenetic interrelationships of these major clades remain unclear (see Figure 4.12).

Before we discuss how phylogenies are constructed, we wish to emphasize that the branching pattern of life is



Figure 2.4 Definitions of Reptilia. (A) Modern phylogenetic systematics includes Aves in a monophyletic Reptilia. (B) The antiquated paraphyletic definition of Reptilia excludes Aves.

continuous whether a phylogeny includes extinct or extant taxa, and there are numerous lineages that are not shown in a phylogeny simply because we do not have any fossil evidence of those lineages. Thus, for every branch of a phylogeny, there are countless other branches for which we have no information, so no phylogeny can completely capture the true diversity of life over Earth's enire history.

Building phylogenies

Deciphering the phylogenetic histories of taxa is a surprisingly complex task. Profound advances in how we construct phylogenies have been made since Hennig's development of cladistics. The use of DNA data and increasingly sophisticated statistical methods of phylogenetic analysis (e.g., maximum likelihood and related Bayesian methods) have been especially influential. In general, however, phylogenetic systematics uses characters to identify clades and to discover the order in which they branched over evolutionary time. A character is simply any heritable trait and can include morphology, behavior, physiology, DNA sequences, and virtually anything else observable about organisms. A derived character is a character that differs in form from its ancestral character. For example, all amniotes (mammals and reptiles) possess a specialized amniotic egg, which is characterized by a tough shell and four structures called extraembryonic membranes (see Chapter 9). This type of egg is unique to amniotes, and because it evolved from an egg that lacks a shell and extraembryonic membranes (the ancestral state seen in fish and amphibians), the amniotic egg is a derived character.

An ancestral character is also called a **plesiomorphy** (from the Greek *ples*, "close to" + *morph*, "form"). A derived character is an **apomorphy** (from the Greek *ap*, "away from"). In other words, an apomorphy is a structure that has moved away from the ancestral form. A derived character shared by two or more taxa is called a **synapomorphy** (from the Greek *syn*, "together"), or shared derived character. Synapomorphies are evidence that taxa share a common ancestor—that is, they form a clade. The amniotic egg is a synapomorphy supporting the monophyly of Amniota. Additional examples of synapomorphies defining a clade include the presence of a shell in turtles and the absence of lungs that is characteristic of plethodontid salamanders.

Sometimes, as we saw in Figure 2.3, the same derived character evolves independently in different groups; that is, the character appears in two groups that do not share a recent common ancestor. Derived characters arising from such convergent evolution are called **homoplasies** (from the Greek *homo*, "alike," + *plastos*, "moulding"). For example, ectothermy—relying on the environment rather than internal mechanisms to regulate body temperature—is the ancestral condition for all tetrapods. Both mammals and birds are endotherms, which is a derived state. However, endothermy is a homoplastic trait in the context of tetrapod phylogeny because it evolved convergently (i.e., separately and independently) in birds and mammals—it is a derived character in both groups, but it is not a *shared* derived character.

Although plesiomorphies do not provide any information about evolutionary relationships, this does not mean they are unimportant. On the contrary, ancestral characters can be profoundly important in how an animal lives. Ectothermy is plesiomorphic for amphibians and reptiles and has ramifications in many aspects of their ecology and behavior. Thus, it is essential to understand the mechanisms and implications of ectothermy to understand the biology and ecology of salamanders and lizards, even though the fact that both salamanders and lizards are ectotherms does not provide any information about the evolutionary relationship of these two groups.

To further confuse matters, a given character may be seen as either a plesiomorphy or a synapomorphy, depending on the taxonomic scale. For example, the shell is a synapomorphy of turtles, evidence that turtles form a clade relative to all other reptiles. However, if one is interested in the interrelationships of the different turtle lineages, the presence of a shell is not informative because all turtles have the ancestral condition of a shell; in this case, the shell is a plesiomorphy.

The examples of characters given above are all aspects of an organism's physical phenotype and are called morphological or phenotypic characters. Before scientists had the ability to collect biochemical data such as DNA, morphological characters were the only data used for phylogenetic construction. Morphological data—typically features of the skeleton—are usually the only data available from fossils of extinct taxa. The collection of morphological data has
been greatly aided by X-ray microtomography that allows the scanning of three-dimensional images of skeletons and even of fossils embedded in rock.

Just as the morphology of organisms changes over time and leaves signatures of evolutionary history, so too does DNA. The vast majority of phylogenetic analyses of extant taxa today rely on differences in DNA characters among taxa. Mutations in DNA that substitute one nucleotide for another (e.g., adenine for guanine) occur in all lineages of life. Modern phylogenetic analysis tries to determine the sequence in which these substitutions occurred over evolutionary time, and therefore the sequence in which lineages split from other lineages.*

The most obvious advantage to using DNA data for phylogenetic reconstruction is the number of characters one can analyze. With the vast numbers of genes for which DNA sequences are available, and the ever increasing number of organisms for which complete genomes have been sequenced, it is now easy to obtain thousands or hundreds of thousands of characters rather than the tens to hundreds of characters used in phylogenetic analyses based on morphological data. The use of DNA also allows a researcher to study evolutionary questions that would be difficult to answer with only morphological data. For example, DNA sequence analysis allows one to study the phylogenetic history of species that have few visible phenotypic differences (known as cryptic species). Analysis of DNA can also determine whether two populations of a species have recently or are currently exchanging genes, or if both populations are reproductively isolated from each other, and thus may be on the road to becoming distinct species. DNA data can rarely be collected from fossils, however, so studies incorporating extinct taxa must rely on morphological data collected from fossil specimens.

Rank-free taxonomy and phylogenetic nomenclature

Many students may recall having memorized the hierarchical Linnean ranks (kingdom, phylum, class, order, family, genus, and species), but there is an increasing trend in mod-

*The details of how phylogenies based on DNA data are constructed are fascinating but beyond the scope of this brief overview. Specialized coverage can be found in a number of sources, including Felsenstein 2003, Hall 2011, and Baum and Smith 2013.

Figure 2.5 Node-based versus stem-based

taxonomic names. The node-based name Tetrapoda (red) is a crown group defined by the node that represents the common ancestor of *Acanthostega* and all extinct and extant tetrapods (the amphibians, mammals, and reptiles). The stem-based name Tetrapodomorpha (blue) includes the crown group (i.e., Tetrapoda) and all taxa including extinct lineages—that are more closely related to Tetrapoda than to lungfish. ern taxonomy to use **rank-free** taxonomic names above the genus level. Thus, instead of referring to the Class Reptilia, we simply say Reptilia.

There are multiple reasons for adopting rank-free taxonomy. The first is that Linnean ranks are not comparable with respect to either diversity or time. For example, the amphibian lineage Cryptobranchidae (giant salamanders) is approximately 175 million years old and contains 3 extant species, but the lineage Bufonidae (true toads) is less than 50 million years old and contains almost 600 species. In this case, to rank both these lineages as families has no meaning in terms of biological diversity. Second, because we now have substantial amounts of phylogenetic information (including DNA sequences) for many organisms, especially vertebrates, taxonomists can make highly detailed taxonomies, to the point of naming every node on a phylogeny. Using the more inclusive Linnean ranks in this situation quickly becomes cumbersome because of the proliferation of rank prefixes such as magnaorder, infraclass, superfamily, and so on. In other words, the meaningful part of a taxonomic name is the name itself, not the Linnean rank.

This book uses a mostly rank-free taxonomy, although we do refer to families and subfamilies, primarily because these terms have long been used for higher-level taxonomy and continue to be used extensively in scientific literature. As in all taxonomic literature, whether Linnean or rankfree, we specify genus and species.

The proliferation of phylogenetic information has also changed how we define taxonomic groups, specifically the use of node-based and stem-based definitions of taxonomic names. A **node-based definition** names a group that includes the most recent common ancestor of at least two taxa (called specifiers) and all of its descendants. This type of group is also sometimes called a **crown group**. For example, the name Tetrapoda defines a taxonomic group that contains the common ancestor of mammals, reptiles, lissamphibians, and the extinct *Acanthostega*, and all of its descendants (**Figure 2.5**). This group contains all extant taxa, plus



any extinct relatives of extant lineages (e.g., fossil reptiles and mammals). It does not include any stem lineages (see below) that diverged before the split between *Acanthostega* and other tetrapods.

The alternative to a node-based definition is a **stembased definition**. In phylogenetic terms, **stem lineages** are those that diverge before the crown group. Stem-based definitions also use specifier taxa, but instead of identifying a specific node in the tree, a stem-based definition defines a group more closely related to at least one taxon than another. For example, Tetrapodomorpha is a stembased name defining all organisms more closely related to extant tetrapods (Tetrapoda) than to lungfish (see Figure 2.4). It includes Tetrapoda and all lineages that arose on this branch of the phylogeny after it split with the ancestor of extant lungfish. In other words, a stem-based definition includes the crown group and lineages that diverged before the crown group.

There is a third type of taxonomic definition, called an **apomorphy-based definition**, that includes members of a group that all share a specific apomorphy. However, this definition is rarely used.

Discovering and describing new species

A fundamental goal of taxonomy is discovering and describing new species, and this continues to be an active field of herpetology. For example, approximately 1,800 species of amphibians were described between 2004 and 2013 (see amphibiaweb.org), representing about 25% of all named, extant species. Much of this biodiversity has been discovered in tropical forests, especially in South America, equatorial Africa, Southeast Asia, and Madagascar (see Chapter 5).

Both historically and today, the species discovery process often begins when a researcher finds a group of organisms in the wild that differs in some way from existing species. Most often these are morphological differences; in reptiles they can be such characters as color or scale patterns. For frogs, advertisement calls are important because they are strong predictors of reproductive isolation (see Chapter 13). The researcher then compares the potential new species to other presumably closely related species to assess whether there are enough consistent, distinctive differences to warrant recognizing a new species. If so, the species is officially described using a strict set of rules governed by the International Code of Zoological Nomenclature (ICZN). A single specimen is designated as the holotype, and it serves as the individual that possesses all the characters of that species. The holotype, and any other individuals collected with it, must be deposited in a museum that other researchers can access in the future. The species must be described in a scientific journal in an article that defines the holotype and that provides a unique binomial species name (typically Greek or Latin), the meaning of the name, a morphological description of the new species, and an explanation of how this new species differs from other species.

• A large measure of subjectivity remains in the species description process, and can be summed up by the question "How much difference is enough to call the organism a new species?" The answer is left up to the researchers and can depend on which of several definitions of species, or **species concepts**, they use (see Coyne and Orr 2004). It is useful to think of a species as a testable hypothesis subject to falsification by further data rather than as an immutable form. Species are sometimes no longer recognized when additional data, especially DNA data, reveal that a recognized species is not consistently different from other species.

Some lineages do not fit comfortably into binomial taxonomy. For example, some *Ambystoma* salamanders, as well as several species of lizards, are composed entirely of females that reproduce clonally (i.e., as matrilineages). In practice, they are named as species (e.g., *Aspidoscelis neomexicana*, a tetraploid hybrid between two species of whiptail lizard; see Figure 9.5), but they do not fit the biological species definition of a group of actually or potentially interbreeding organisms. Each individual reproduces parthenogenetically, and there is no exchange of genetic material among the members of this unisexual species.

Molecular data and species identification

Since the advent of DNA sequencing in the late 20th century, DNA data have profoundly changed how we identify new species. Researchers can compare DNA sequences to determine whether an organism is similar to an existing named species. This can be a complex process, and a thorough discussion is beyond the scope of this chapter (see Fujita et al. 2012; Leaché et al. 2014), but researchers typically use a phylogenetic analysis of the DNA to determine if individuals from a putative new species are part of clades formed by other known species.

For example, a researcher may discover one or more populations of lizards with a unique brown body coloration that differs from the green body coloration seen in another, physically similar and presumably closely related, species. If a phylogenetic analysis of DNA shows that the brown lizards are a lineage derived within the clade of already described green species, the researcher may conclude that the brown animals are not a new species but represent a color polymorphism of the existing green species (**Figure 2.6A**). However, if the phylogenetic analysis of DNA shows that the brown and green populations are genetically distinct and form reciprocal monophyletic groups, then the researcher may describe the brown morphs as a new species (**Figure 2.6B**).

DNA data may also show large genetic differences between populations of an already described species, but there may be no diagnosable morphological characters that distinguish them. Are these morphologically indistinguishable animals multiple cryptic species rather than a single species? A growing consensus holds that DNA data alone can be used to delimit species because genetic divergence



is evidence of the reproductive isolation of populations. In other words, although we humans may not be able to tell two species apart, each species recognizes individuals of its own species as distinct from those of other species.

2.2 ■ Evolutionary Origins and Processes of Amphibian and Reptile Diversity

In this section we discuss the origins of terrestriality from aquatic ancestors and the subsequent diversification of amphibian and reptile groups, many of which are extinct and have left no descendants living today. Throughout this discussion, you may find it useful to refer to Figure 2.2 and Table 2.1, which describe the geological time periods we frequently refer to. It is also important to understand that, for every group of animals that we discuss here and in Chapters 3 and 4, there are countless extinct stem lineages that we do not discuss.

As we noted in Chapter 1, inclusion of organisms as different as frogs and crocodiles in the discipline of herpetology is partly historical accident and partly recognition that the shared ancestral character of ectothermy creates important functional similarities among the groups. Although we discuss taxonomic groups separately, remember that many of these extinct groups, or ancestors of extant groups, were contemporaneous and formed ecological communities that were functionally equivalent to those we see now. If you wade through a swamp today, you will see a variety of amphibians and reptiles, including some that are fully aquatic or terrestrial; small, gracile insectivores; and large, plodding herbivores. You might hear amphibians calling and watch lizards aggressively defending their territory. If you could have made the same walk in a Late Carboniferous forest, you would have experienced the same phenomena, but you would have been watching the earliest relatives of modern amphibians and reptiles, along with organisms from lineages that subsequently became extinct and have no direct descendants today.

The numerous taxonomic names are the most frustrating aspect of discussing both extinct and extant diversity. We have limited our discussion to those groups that are critical to understanding amphibian and reptile diversity (**Table 2.2**). It is useful to visualize these groups on the phylogenetic tree to understand how they are related (**Figure 2.7**).

The ecological transition from water to land

Before discussing the origins of terrestrial tetrapods, it is necessary to understand the many challenges of transitioning from an aquatic to terrestrial mode of life and how morphological and physiological adaptations to land were shaped by natural selection. A major difference between living in water and on land is the effect of gravity on the skeletal system. Changes in the body forms and proportions of early tetrapods are coincident with changes in the skeleton and reflect increasing support for life on land.

Fish have a comparatively weaker skeleton than tetrapods because a fish's buoyancy counteracts the downward force of gravity and there is little selective pressure to evolve robust skeletons, even in large fish. In contrast, terrestrial animals must support their entire mass against the force of gravity, and thus the most obvious adaptations to living on land are seen in the skeleton and associated musculature, especially in the vertebrae, limbs, and pectoral and pelvic girdles—the bony structures that support the forelimbs and hindlimbs (see Figure 2.8). Terrestrial animals have robust, interlocking vertebrae that can bear the weight of the entire axial skeleton, organs, and muscles of the trunk. These limb girdles must be large enough to support the body mass and configured to allow the limbs to move. Finally, one or both sets of limbs must have the strength to move the animal.

The evolution of terrestrial feeding modes need not have involved radical reorganization of the ancestral feeding apparatus, but only the addition of components associated with terrestriality. Some modern tetrapods (e.g., some salamanders) migrate annually between a terrestrial and an aquatic medium, using the tongue to acquire food on land and suction feeding in water. Experiments show that the

TABLE 2.2 Major extant taxonomic groups in the evolution of amphibians and reptiles

Sarcopterygii: Bony fish with fins or limbs supported internally by bones and intrinsic musculature. Sarcopyterygii arose in the Late Silurian and includes Actinistia, Dipnoi, and Tetrapoda.

Actinistia: A diverse group of fish extending back to the Paleozoic, now represented by only two species of coelacanths (genus Latimeria).

Dipnoi: Three genera of extant lungfish in Africa, South America, and Australia, as well as diverse fossil species extending well back to the Paleozoic.

Tetrapoda: Vertebrates with four limbs. Includes Lissamphibia, Amniota, and the extinct Acanthostega and all of its descendants.

Lissamphibia: Anura (frogs), Caudata (salamanders), and Gymnophiona (caecilians). We use Lissamphibia for the clade name and informally refer to them by the more common term amphibians.

Amniota: Vertebrates with (ancestrally) a shelled egg and four extraembryonic membranes.

Synapsida: Mammalia (mammals) and extinct non-mammalian fossil species

Diapsida: Includes all extant Reptilia as well as several extinct lineages.

Archosauria: Testudines^a (turtles), Crocodylia (alligators, crocodiles, and gharials), and Aves^b (birds). Lepidosauria: Squamata (lizards and snakes) and Rhynchocephalia (tuatara).

^a The inclusion of Testudines in Archosauria is debated (see Section 2.7).

^b Aves is included because this clade is nested deep within the archosaur branch of Reptilia. Among extant amniotes, birds are the closest relatives of crocodylians. Neither birds nor mammals are subjects of this textbook.

mechanics of this transition in feeding mode are quite simple. Terrestrial adult salamanders retain the basic structural and functional components of their larval feeding system and simply add components (such as a tongue) for feeding on land (Lauder and Reilly 1994). Both feeding modes are possible for adult salamanders that passed through an aquatic larval stage.

Preventing desiccation is critically important in the dryness of the terrestrial environment. While this challenge can be met by staying close to water (as many modern amphibians do), other adaptations are necessary for an animal to remain terrestrial for extended periods of time. This has been achieved by the evolution of wax-producing glands in the skin of amphibians and increased keratinization and lipids in the skin of amniotes.

Gills are not suitable for terrestrial life because the gill filaments collapse onto each other when they are not supported by water, drastically reducing the surface area available for gas exchange. Terrestrial gas exchange occurs via the skin, buccopharynx, and lungs. We know from examining modern lungfish that it is possible to possess both functional gills and lungs, and lungs are an ancestral character of tetrapods.

Many other functional and anatomical changes required for the evolution of terrestriality have left no evidence in the fossil record. Sensory systems, in particular the eyes and ears, would have changed to accommodate differences in the transmission of sensory signals through air and water (e.g., Fritzsch et al. 2013). The evolution of terrestrial hearing, including a stapes associated with a tympanum, seems to have occurred later in land vertebrate evolution than in *Acanthostega* and *Ichthyostega*, two early aquatic tetrapods. By the time temnospondyls appeared some 30 million years later (see Figure 2.7), the structure of the hearing apparatus approached that of extant salamanders (Christensen et al. 2015).

It is important to note that these suites of morphological and physiological adaptations did not have to evolve at the same time. The earliest tetrapods would have made very brief forays out of water, and thus any of the above adaptations would have conferred a small selective advantage. Accumulation of small changes over millions of years would have ultimately allowed tetrapods to occupy terrestrial environments.

The transition from fish to tetrapods

Morphological, paleontological, and molecular phylogenetic studies show that tetrapods arose from sarcopterygian fish ancestors. Sarcopterygian (from the Greek *sarc*, "fleshy," + *pterys*, "fin" or "wing") fish, including modern lungfish and

Figure 2.7 Phylogeny of Tetrapodomorpha. This phylogeny includes the lineages discussed in the chapter text; countless extinct stem lineages are not depicted. Node ages are estimates derived from Ruta and Coates 2007, Anderson et al. 2008, Shedlock and Edwards 2009, Sigurdsen and Bolt 2009, Jones et al. 2013, and Benton 2014.



coelacanths, have fins that articulate with the limb girdles via a single bone. In tetrapods this same bone develops into the humerus of the arm and the femur of the leg. In evolutionary terms, we call these structures **homologous** because they are both derived from the same fundamental structure. Although tetrapods, lungfish, and coelacanths share a common ancestor, neither of the latter two fish groups resembles the earliest ancestors of tetrapods because both have undergone more than 400 million years of independent evolution and developed their own unique traits. Thus, fossil data provide the strongest clues to the origin of tetrapods and the ecological context in which they evolved.

Before continuing, recall the distinction between stemand node-based taxonomic names (see Section 2.1). The stem-based clade Tetrapodomorpha includes all taxa that are more closely related to modern amphibians, reptiles, and mammals than to lungfish (see Figure 2.5). This clade includes modern tetrapods and their more fishlike fossil ancestors. The definition of Tetrapoda has changed over the years (see Laurin 2002; Laurin and Anderson 2004) but is now most commonly used as a node-based name for the clade containing the ancestor of *Acanthostega* and all descendants of this common ancestor: modern-day amphibians, reptiles, and mammals, including extinct lineages such as *Ichthyostega*.

Interest in tetrapod origins has generated a rich literature with the identification of numerous extinct lineages and hypotheses of their phylogenetic relationships. Below we discuss only a selection of fossil taxa most relevant to the origin and evolution of tetrapods (see Schoch 2014 for a comprehensive review).

Early tetrapodomorphs

Tristopterid and elpistostegalid fish are the most important extinct lineages for understanding the evolution of early tetrapodomorphs. *Eusthenopteron*, a tristopterid, was a large (up to 1.8 m) predatory fish that inhabited shallow marine or estuarine waters in the Late Devonian (385–380 million years ago). *Eusthenopteron* is notable because its teeth have extensive folding of enamel (labyrinthodont dentition) like those of other early tetrapods. More important, its pectoral and pelvic fins contain bones homologous to the radius, ulna, tibia, and fibula of modern tetrapods (**Figure 2.8A**). *Eusthenopteron* was probably fully aquatic (Clack 2002; Laurin et al. 2007).

The Late Devonian (~385 mya) elpistostegalid fish *Panderichthys* (Figure 2.8B) was contemporaneous with *Eusthenopteron* and displayed more tetrapod-like features (Boisvert 2005; Boisvert et al. 2008). Its body was dorso-laterally flattened and lacked dorsal and anal fins, and the tail fin was greatly reduced. Its pectoral girdle was more robust than that of *Eusthenopteron*, and *Panderichthys* may have walked on the bottom of shallow water bodies. Its eyes were located dorsally on a rather crocodile-like skull, and *Panderichthys* may have foraged at the water surface. More-

over, the middle-ear architecture of *Panderichthys* shows modifications that may represent the early transition to a tetrapod-like middle ear (Brazeau and Ahlberg 2006).

The elpistostegalid Tiktaalik (Figure 2.8C) has been profoundly important to interpreting the transition from water to land in early tetrapodomorphs (Daeschler et al. 2006). Although distinctly a fish that inhabited shallow water bodies, Tiktaalik possessed a suite of morphological characters that represents a transitional stage between aquatic and terrestrial modes of living. Tiktaalik lacks the bony sheath (operculum) that covers the gills in other fish. This change is functionally important because loss of the operculum eliminates the rigid connection between the body and head, creating a flexible neck. Thus, Tiktaalik could probably raise its head out of the water and turn it from side to side. Perhaps more important, the pectoral and pelvic girdles were stronger than those of other tetrapodomorph fish, thus allowing Tiktaalik to prop itself up on its fins, use them for aquatic propulsion, and maybe even make brief terrestrial forays along the water's edge (Shubin et al. 2006, 2014).

Early tetrapods

Even casual observation reveals that the skeletons of Acanthostega (Figure 2.8D) and Ichthyostega (Figure 2.8E), animals that lived during the Late Devonian (~365 mya), were far more like our own terrestrially adapted skeletons than the skeletons of fish. They had well-developed pectoral and pelvic girdles and distinct neck regions that allowed movement of the head independent of the trunk. They also possessed limbs with bony digits-seven on the hindlimb of Ichthyostega (the forelimb of Ichthyostega is unknown) and eight on both the forelimb and hindlimb of Acanthostega (Coates and Clack 1990). Ichthyostega had additional skeletal modifications that suggest partially terrestrial habits (Pierce et al. 2013). For example, the pectoral and pelvic girdles of Ichthyostega were far more robust than those of Acanthostega (Coates 1996), the elbow was bendable (Pierce et al. 2012), the vertebral column was reinforced by strong connections between vertebrae (zygopophyses), and the ribs were expanded and overlapping, thereby forming a distinct rib cage.

All of these features suggest that *Ichthyostega* could drag itself out of the water with its forelimbs (the hindlimbs were smaller and more paddlelike) and support its weight in terrestrial environments, although it not possible to know how long it could remain out of the water. Like lungfish today, these genera probably had lungs, but they also retained fishlike internal gills and were primarily aquatic (Coates and Clack 1991; Clack et al. 2003).

In summary, a 20-million-year time span in the Late Devonian saw a dramatic transition from fully aquatic fish to animals with structures found in all tetrapods today. Although these features initially evolved in response to selective pressures specific to inhabiting shallow water bodies, they provided the basic building blocks that eventually allowed tetrapods to invade and diversify on land. (A) Eusthenopteron



Figure 2.8 Reconstructed skeletons and limbs of extinct tetrapodomorphs and tetrapods. The reconstructed dorsal view of the forelimb of each species is shown, except for Ichthyostega (E), whose hindlimb is shown (the forelimb is unknown for this genus). Homologous bones are color-coded. (A,D after Coates et al. 2008; B after Boisvert 2005; C after Coates et al. 2008, Shubin et al. 2014; E after Coates and Clack 1990.)

2.3 Three Hypotheses for the **Origin of Extant Amphibians**

Extant amphibians (caecilians, frogs, and salamanders) form a clade named Lissamphibia (see the diphyly hypothesis below for a different interpretation). The origin of Lissamphibia has been debated for decades and continues to produce copious literature. The debate centers around whether caecilians, frogs, and salamanders are derived from one or both of two early tetrapod lineages, temnospondyls and lepospondyls (Figure 2.9). As with tetrapod origins, we do not discuss the many other stem amphibian lineages (see Schoch 2014 for an extensive review).

The temnospondyl hypothesis

The most widely accepted hypothesis for the origin of extant amphibians is that they form a clade (Lissamphibia; see Section 2.4) and are derived from temnospondyl ancestors (Milner 1988, 1993), specifically the Dissorophoidea (see Figure 2.9A) (e.g., Ruta and Coates 2007; Sigurdsen and Bolt 2009, 2010; Sigurdsen and Green 2011).

Temnospondyls (from the Greek temn, "cut," + spondyl, "vertebra") are so named because the centrum (body) of their vertebrae consists of two distinct regions that surround the notochord (Figure 2.10A). The intercentrum is a wedge-shaped ventral structure, and the pleurocentra are two wedge-shaped dorsal structures.

Temnospondyls are represented by almost 200 genera from the Early Carboniferous to the Middle Cretaceous (~330–130 mya). They ranged in length from a few centimeters to a few meters. Many species were crocodile-like, with large, flat skulls and dorsally positioned eyes. Mastodonsaurus, which grew to 6 m and had two massive fangs on the mandible, is an extreme example of this phenotype (Figure 2.11A). The teeth of temnospondyls are labyrinthodont, a condition seen in other tetrapodomorphs (e.g., Eusthenopteron). Temnospondyls inhabited both freshwater and marine habitats. (See Ruta et al. 2007 and Schoch 2013 for information about the phylogenetics of Temnospondyli.)

Numerous characters support a temnospondyl origin of Lissamphibia. Both groups have, among other characters, pedicellate teeth (see Section 2.4), wide openings in the palate that permit retraction of the eye into the skull, two occipital condyles on the skull that articulate with the first cervical vertebra (the atlas), and short ribs.

The lepospondyl hypothesis

Some phylogenetic studies support the origin of a monophyletic Lissamphibia within lepospondyls, usually within a paraphyletic assemblage of small, lizardlike animals called "microsaurs" (see Marjanovič and Laurin 2009, 2014). Unlike the divided three-part vertebrae of temnospondyls, the vertebrae of lepospondyls consist only of a centrum (derived from the pleurocentrum) fused with the neural arch into a single unit (Figure 2.10B). Lepospondyls comprise about 60 genera







Figure 2.10 Vertebrae distinguish temnospondyls and lepospondyls. (A) The vertebrae of temnospondyls consist of a wedge-shaped ventral structure, the intercentrum, and two dorsal pleurocentra (the second pleurocentrum is behind the notochord in this view). (B) In lepospondyls, the intercentrum, pleurocentra, and neural arch are fused into a single structure.

from the Early Carboniferous to the Early Permian (~340–275 mya). Aïstopods and lysorophids were nearly or entirely limbless, nectrideans were aquatic with strongly compressed tails, and "microsaurs" had a variety of body forms. In contrast to many temnospondyls, lepospondyls were small animals with skulls typically no longer than 5 cm (**Figure 2.11B**). However, one of them—*Diplocaulus*—is famous for its large (~35 cm) boomerang-shaped head and large body (up to 1.5 m). Probably a flap of skin extended from the head to the sides of the body. This unusual structure may have been a hydrofoil to aid swimming, or a way to increase the surface area for cutaneous gas exchange (Cruickshank and Skews 1980), although these and other hypotheses, such as sexual selection, are not mutually exclusive. (See Anderson 2001 for information on the phylogenetics of Lepospondyli.)

Both lissamphibians and lepospondyls lack numerous bones of the skull, including the ectopterygoid and postorbital bones, as well as the cleithrum from the pectoral girdle. These losses may be interpreted as synapomorphies that support inclusion of both groups in a clade. A study that included morphological data for both extinct and extant taxa and molecular data for extant taxa also supports the lepospondyl hypothesis (Vallin and Laurin 2004; Pyron 2011). However, it is worth noting that only Vallin and Laurin's (2004) data support the lepospondyl hypothesis, and it is unclear whether Pyron's (2011) results would differ if alternate data sets that support the temnospondyl hypothesis were used. Moreover, loss of skull bones is often correlated with the evolution of miniaturization, a common phenomenon in numerous groups of amphibians (see Section 2.4).

The diphyly hypothesis

The diphyly (from the Greek *di*, "two") hypothesis of lissamphibian origin is a hybrid between the temnospondyl and lepospondyl hypotheses and proposes that Lissamphibia is not monophyletic (Carroll 2007, 2009; Anderson 2008). It proposes that frogs and salamanders are derived from dissorophoid temnospondyls and that caecilians are



Figure 2.11 Temnospondyls and lepospondyls of the Late Paleozoic. (A) Two representative temnospondyls. *Mastodonsaurus* was huge and superficially resembled a crocodylian. The much smaller *Cacops* was a more typical size temnospondyl. (B) Two lepospondyls. The unique head shape of *Diplocaulus* may

have helped the animal glide through the water. The tiny *Microbrachis* may have appeared similar to some modern salamanders. The graph, keyed to the colored bars beneath the skeletons, shows the relative sizes of the animals compared with a very tall adult human. (After Bolt 1977; Schloch 1999.)

derived from lepospondyl "microsaurs" (see Figure 2.9C). An important fossil supporting the diphyly hypothesis is that of the caecilian *Eocaecilia*. Some studies have suggested that *Eocaecilia*, and therefore modern caecilians, are derived from lepospondyl ancestors (e.g., Carroll 2007; Anderson et al. 2008). However, a recent X-ray microtomography analysis of the skull of *Eocaecilia* (see Figure 3.65) has revealed additional characters that reject the diphyly hypothesis and instead support a monophyletic Lissamphibia derived from temnospondyls, a hypothesis also supported by inner ear structure and other phylogenetic analyses (e.g., Sigurdsen and Green 2011; Maddin and Anderson 2012; Maddin et al. 2012). Thus, the diphyly hypothesis is not widely accepted.

These alternative hypotheses do not affect our concept of relationships among extant tetrapods; they apply only to interrelationships among extant and fossil taxa. Nonetheless, these alternative phylogenetic hypotheses bear critically on the interpretation of evolutionary processes involved in the evolution of lissamphibians (Bolt 1977, 1979; Laurin 1998).

Why do different analyses support different hypotheses of lissamphibian origins?

Perhaps the most important cause of the lissamphibian origins debate is also a frustrating aspect of almost all phylogenetic analyses of paleontological data—the incomplete fossil record. The fossil record of early caecilians, Carboniferous stem tetrapods, and early lissamphibians from the Permian–Jurassic boundary is extremely poor. As a result, relationships at these regions of the phylogeny may be ambiguous or highly variable across studies simply due to lack of data.

There is discrepancy between molecular and paleontological age estimates of Lissamphibia. Molecular divergence age estimates generally support a Late Carboniferous age of Lissamphibia (~315–300 mya) (San Mauro 2010; Pyron 2011). However, divergence ages based on fossil data suggest a much younger age, in the Late Permian (~260–255 mya) (Marjanovič and Laurin 2014). However, there is a frustrating 30-million-year gap (called Romer's Gap) between the appearance of *Acanthostega, Ichthyostega,* and *Tiktaalik* in the Late Devonian and the explosion of tetrapod diversity in the Early Carboniferous. This period is critical for understanding early amphibian and amniote evolution, for it is when several tetrapod groups—including temnospondyls, lepospondyls, and the earliest amniotes—appear in the fossil record.

The wildly varying quality of fossil preservation is another factor that accounts for different results from phylogenetic studies of fossil taxa. While there are some exceptionally well preserved fossils with fully articulated skeletons, fossil specimens are usually incomplete, or the skeleton is crushed and in multiple pieces. Therefore, not all relevant morphological characters may be identified in every specimen, and researchers may disagree in their identification of certain characters that affect phylogenetic reconstruction (e.g., McGowan 2002; Marjanovič and Laurin 2008). In addition, researchers must determine whether a fossil has enough identifiable characters to be included in an analysis, and the choice of specimens, taxa, and characters strongly influences phylogenetic results. As with the origins of tetrapods, a better resolution of the origin of Lissamphibia awaits more fossil discoveries.

2.4 ■ Relationships among Extant Lissamphibian Lineages

Given the controversy concerning the relationships between lissamphibians and Paleozoic amphibians, it should not be surprising that relationships among frogs, salamanders, and caecilians have also been debated extensively. Although most morphological studies support the sister relationships between frogs and salamanders (Batrachia), researchers have also found putative derived morphological characters that support salamander + caecilian or frog + caecilian clades (Trueb and Cloutier 1991; Jenkins and Walsh 1993; McGowan and Evans 1995; Laurin 1998a). Because of the highly derived morphology of the three lissamphibian groups, it is often difficult to apply morphological characters across all three groups.

However, three or more decades of molecular phylogenetic analyses have converged on a phylogeny of Lissamphibia that supports the sister relationship between frogs and salamanders (Batrachia) that together are sister to caecilians. The presence of an opercular apparatus is a synapomorphy for Batrachia (see Figure 2.12B). True dermal scales are absent in frogs and salamanders (whereas they are present in caecilians and in Paleozoic tetrapods), and ectopterygoid and postfrontal bones are absent from their skulls (see Figure 2.13). Finally, two developmental characters—absence of segmentation of the sclerotome and reduction or loss of male Müllerian ducts—are shared by frogs and salamanders but not caecilians.

For the purposes of further discussion, we follow most phylogenetic studies and assume that Lissamphibia (caecilians, frogs, and salamanders) is monophyletic and derived from temnospondyl ancestors (see Figure 2.9A). The earliest fossil that can clearly be assigned to an extant lissamphibian clade is *Triadobatrachus* from the Early Triassic (~245 mya; see Figure 3.21). *Triadobatrachus* was thus an early ancestor of frogs (although it is unclear whether *Triadobatrachus* had the ability to jump; Sigurdsen et al. 2012), and therefore the earliest ancestors of Lissamphibia must be older than 245 million years.

Monophyly of Lissamphibia

Numerous morphological synapomorphies support lissamphibian monophyly (Schoch 2014). The following characters are some of the derived features that are shared by, and in many cases are unique to, extant amphibians:

- 1. The teeth are pedicellate and bicuspid (Figure 2.12A). Each tooth crown sits on a base (pedicel), from which the crown is separated by a fibrous connection. Moreover, the teeth have two cusps, one on the lingual (inner) side of the jaw and one on the labial (outer) side. Such a tooth structure is unique to Lissamphibia and some temnospondyls.
- 2. The sound-conducting apparatus of the middle ear consists of two elements: the stapes (columella), which is the usual element in tetrapods, and the operculum. The operculum (not homologous to the operculum in fish) consists of a bony or cartilaginous structure that attaches to the ear capsule and is connected to the suprascapula via the opercular muscle (Figure 2.12B). Functionally, this allows ground vibrations to be transmitted from the forelimb to the inner ear. Inside the inner ear are two sensory epithelial patches (not shown), the papilla basilaris, found in other tetrapods, and the papilla amphibiorum, unique to lissamphibians. The papilla basilaris receives relatively high-frequency sound input via the stapes. The papilla amphibiorum receives relatively low-frequency input via the opercular apparatus. The opercular apparatus is lost in caecilians, perhaps as a result of limb loss, and is reduced in salamanders by the loss of one or more components in various groups.
- 3. The stapes is directed dorsolaterally from the fenestra ovalis, a character shared by some of the lissamphibians' presumed Paleozoic relatives.
- The fat bodies develop from the germinal ridge (which also gives rise to the gonads), a developmental origin unique among tetrapods.
- 5. The skin contains both mucus and poison (granular) glands that are broadly similar in structure.
- Specialized receptor cells in the retina of the eye, called green rods, are present in frogs and salamanders. Caecilians apparently lack green rods, perhaps because of their highly reduced eyes.
- 7. A sheet of muscle, the levator bulbi muscle, lies under the eye and permits lissamphibians to elevate the eye.
- 8. All extant amphibians employ cutaneous and buccopharyngeal respiration.
- 9. The ribs are short, straight, and do not encircle the body. The ribs of Paleozoic stem tetrapods (other than some temnospondyls) are long, robust, and encircle the viscera.
- Two occipital condyles at the base of the skull articulate with two cotyles on the first cervical vertebra (the atlas). Most other extant tetrapods have a single occipital condyle, but two condyles are found in some temnospondyls.



Replacement crown growing within pedicel



Figure 2.12 Two shared derived characters of Lissam-

phibia. (A) Pedicellate teeth. Each tooth crown sits on a base (pedicel); the two elements are separated by a fibrous connection. The teeth are bicuspid, with one cusp (point) on the lingual (inner) side of the jaw and a second on the labial (outer) side.
(B) The opercular apparatus is part of the lissamphibian sound-conducting system, allowing ground vibrations to be transmitted from the forelimb to the inner ear. This apparatus is a synapomorphy of frogs and salamanders (Batrachia), although it is reduced in salamanders; it has been secondarily lost in caecilians. (A after Parsons and Williams 1963.)

11. The radius and ulna articulate with a single structure on the humerus called a radial condyle. This character has been lost in caecilians, which are limbless (Sigurdsen and Bolt 2009). 12. Lissamphibians share similar reductions in skull bones and fenestration patterns compared with Paleozoic tetrapods (Figure 2.13). These shared derived characters include loss of the supratemporals, intertemporals, tabular, postparietals, jugals, and postorbitals. Other elements, such as the pterygoid and parasphenoid bones in the palate, are reduced, producing a similar configuration of bones among the three modern amphibian groups. Nonetheless, the skull morphology of caecilians is highly unusual compared with that of frogs and salamanders, reflecting the caecilians' very different life history.

Some of these characters (e.g., characters 4–8) are difficult or impossible to evaluate in extinct taxa because soft anatomy is rarely preserved in fossils. Moreover, not all of these characters are unique to Lissamphibia. Nonetheless, the preponderance of morphological evidence supports lissamphibian monophyly. Although molecular studies cannot sample extinct taxa, no recent molecular phylogenetic analyses reject lissamphibian monophyly. In summary, the most comprehensive molecular and morphological analyses support the hypothesis that salamanders and frogs are more closely related to one another than to caecilians.

Paedomorphosis in lissamphibian evolution

Although the contrasting hypotheses of lissamphibian origins (see Section 2.3) affect our interpretation of lissamphibian evolution, miniaturization and heterochrony have probably been a pervasive influence on the evolution of the highly derived skeletal morphology of lissamphibians regardless of their origins (Bolt 1977, 1979; Laurin 1998b). **Heterochrony** (from the Greek *hetero*, "different," + *chronos*, "time") is a change in the timing of embryonic and juvenile development that affects the sexually mature adult phenotype.

Paedomorphosis (from the Greek *paed*, "child," + *morph*, "form") is a type of heterochrony and refers to the retention of juvenile characters in adult stages of an organism (see Chapter 8). For example, some salamanders retain the juvenile conditions of having gills and being fully aquatic in adulthood despite being sexually mature, and we infer that these salamanders are derived from ancestors with the ability to transform to the adult form. In essence, these salamanders have arrested metamorphosis and retain some juvenile features, despite the sexual maturation of their gonads.

If lissamphibians are derived from temnospondyls, then paedomorphosis can explain many of their unusual shared morphological characters. One common result of paedomorphosis is size reduction (juveniles are smaller than adults), and extant amphibians are very small (~5–15 cm) compared with many Paleozoic tetrapods. Temnospondyls show an astounding diversity of body sizes (see Figure 2.11), but there is a striking evolutionary trend toward size reduc-



Figure 2.13 Skulls of lissamphibians and a temnospondyl. Dorsal views are shown above and ventral views below. (A) *Dendrerpeton*, an edopoid temnospondyl from the Paleozoic. (B) The salamander *Phaeognathus hubrichti* (Caudata: Plethodontidae) (C) The frog *Gastrotheca walkeri* (Anura: Hylidae).

tion, of which dissorophoids and lissamphibians are simply the end point. In other words, lissamphibians may be miniaturized temnospondyls.

The heterochronic process left many other imprints on the morphology of lissamphibians. In fact, some of the most characteristic features of lissamphibians can be interpreted as paedomorphic features (Schoch 2009, 2010). We give just three examples here, made possible by the remarkable preservation of developmental sequences, including larvae, juveniles, and adults, of some dissorophoid temnospondyls known as branchiosaurs from the Early Permian of Germany. Ontogenetic series of branchiosaurs are so well preserved that it is possible to examine the sequence in which the bones of the skull ossified during development. Compared with *Dendrerpeton*, the two lissamphibians have lost many skull elements and evolved larger orbits, both manifestations of paedomorphosis. (After Duellman and Trueb 1986; Carroll 1998.)

- Skull bones such as the supratemporals, postfrontals, prefrontals, jugals, postorbitals, and ectopterygoids were the last to appear during the development of branchiosaur temnospondyls. It is precisely these bones that are absent from lissamphibian skulls, suggesting that frogs, caecilians, and salamanders have arrested their development at a stage before these bones form. All of the skull bones appearing early in the development of branchiosaurs (nasals, frontals, parietals, lacrimals, etc.) are present in lissamphibians.
- The eye orbits of lissamphibians and dissorophoids are large relative to those of other Paleozoic forms. Sensory organs, such as the eyes, form relatively early in development and are relatively large in early developmental stages. As a result of paedomorpho-

sis, lissamphibians and derived dissorophoid temnospondyls have large eyes compared with those of many other Paleozoic temnospondyls.

3. The bicuspid, pedicellate teeth of lissamphibians may be a retained juvenile condition observed in dissorophoid temnospondyls. Tooth development in dissorophoids and lissamphibians undergoes a sequence in which larvae have nonpedicellate, monocuspid teeth. At metamorphosis these teeth are replaced by bicuspid, pedicellate teeth. In dissorophoids, but not lissamphibians, these bicuspid, pedicellate teeth are gradually replaced by adult teeth that are monocuspid and have the characteristic labyrinthodont structure. Thus, the adult lissamphibian tooth condition (pedicellate, bicuspid, and lacking labyrinthodont structure) is that shown by juvenile dissorophoids. In other words, adult lissamphibians retain the juvenile condition shown by ancestral temnospondyls.

Many peculiar aspects of morphology are comprehensible when lissamphibians are viewed as paedomorphic relative to Paleozoic stem tetrapods. Understanding paedomorphosis sheds light on a fundamental evolutionary process governing morphological evolution in many tetrapods.

2.5 ■ Characteristics and Origin of the Amniotes

We have traced the phylogeny of tetrapods from their origins to the basic split among the extant groups Lissamphibia and Amniota and considered the evolutionary relationships of taxa associated with the amphibian clade. Now we turn to Amniota, the reptiles (including birds) and mammals.

The origins of Amniota

Amniotes are named for their highly specialized amniotic egg (see Chapter 9). The evolution of the amniote egg allowed vertebrates to move into new ecological niches, most notably land, as it freed reproduction from dependence on external water. The amniote egg consists of an outer flexible or hard shell and contains the embryo and four extraembryonic membranes: the yolk sac, which stores energy; the fluid-filled amnion, which surrounds and cushions the embryo; and the chorion and allantois, which perform multiple functions, including gas exchange and, in the case of the allantois, storage of nitrogenous waste. In viviparous amniotes (many squamates and most mammals), the chorion and sometimes the allantois are modified into the embryonic portion of the placenta.

In addition to the shell and extraembryonic membranes, characters supporting the monophyly of Amniota include derived characters of the skull, pectoral girdle, and appendicular skeleton (Laurin and Reisz 1995), as well as molecular data. Some aspects of soft anatomy that may be derived characters have probably been secondarily lost over evolutionary time in certain groups (Gauthier et al. 1988). For example, a penis with erectile tissue is found among male crocodylians, mammals, turtles, and some birds. However, the single penis was secondarily lost in the ancestor of Lepidosauria (tuatara, lizards, and snakes) as well as most birds. Tuatara reproduce by cloacal apposition without the assistance of an intromittent organ. Squamates (lizards and snakes) evolved paired hemipenes, but it remains unclear whether the hemipenes are completely or partially homologous to the ancestral amniote penis (Gredler et al. 2014; Leal and Cohn 2015). Despite its secondary loss in lepidosaurs and birds, the male penis is considered a shared derived character of Amniota. Within the amniotes, reptilian monophyly is supported by characters of the skull and limbs (deBraga and Rieppel 1997) and by countless phylogenetic analyses of DNA data.

The earliest extinct relatives of Amniota are the Late Carboniferous reptilomorphs (e.g., Diadectes; Figure 2.14A). All of the extant amniote groups can be traced to the Permian or Early Triassic. Thus, amniotes appear in the fossil record at approximately the same time as early stem-group lissamphibians. The earliest identified fossil amniote is Casineria, a small (~85 mm) lizardlike animal from the Late Carboniferous (~340 mya), and numerous taxa (e.g., Paleothyris; Figure 2.14B) have been discovered in slightly younger fossil deposits (~310–300 mya). Paton et al. (1999) speculated that the amniote lineage is even older, possibly dating back to approximately 360-350 mya, dates also supported by molecular clock studies (Hedges 2009). Therefore, Lissamphibia and Amniota probably diverged within 30 million years after the origin of the earliest tetrapods. Early Carboniferous limestone deposits in Scotland contain fossil amniotes, temnospondyls, lepospondyls, and several specimens that have a mixture of amniote and temnospondyl characters, and constitute one of the oldest terrestrial vertebrate assemblages known (Milner and Sequeira 1994; Clack 1998; Paton et al. 1999).

The major amniote lineages: Synapsida and Diapsida

The phylogeny of the amniotes has been extensively studied using morphological and molecular data sets and, with the exception of the turtles, there is broad agreement on the relationships among the major groups (see Figure 2.7). During the Early Carboniferous, amniotes split into two lineages, Synapsida and Reptilia. Synapsida gave rise to the mammals and the extinct therapsids that were the dominant terrestrial megafauna of the Permian. The Reptilia diversified into numerous Carboniferous and Permian lineages, all of which became extinct except the Diapsida—the group that includes extant reptiles (including birds) as well as the extinct pterosaurs and dinosaurs.

Synapsida and Diapsida are named for the number of holes, called **fenestrae** (Latin *fenestra* "window"), in the temporal region of the skull. Turtles and some extinct amniotes lack these openings, a condition called anapsid, from the Greek *an*, "without" + *apsid*, "arch" (Figure 2.15A).



Synapsids (from the Greek *syn*, "together") have a single temporal fenestra (**Figure 2.15B**). In humans, this fenestra can be seen as the opening between the cheekbone (the zy-gomatic arch) and the temporal and sphenoid bones of the cranium. The evolution of synapsids is beyond the scope of this book, other than to briefly mention the stem synapsids that dominated the Permian prior to the rise of dinosaurs. These early synapsids, sometimes called "mammal-like reptiles" because of their superficial resemblance to extant and extinct mammals, include iconic animals such as

the sail-finned *Dimetrodon* (see Figure 2.14E) and multiple lineages of large, predatory therapsids. However, these extinct lineages are more closely related to mammals than to reptiles, and are thus more properly referred to as non-mammalian syapsids.

Diapsids have two temporal fenestrae (Figure 2.15C), but the lower temporal fenestra has been secondarily lost in lizards (Figure 2.15D) and in the extinct rhynchocephalian lineages, and both fenestrae have been lost in the highly modified snake skull. In both diapsids and synapsids, the



temporal fenestrae permit space for bulging jaw muscles and are important adaptations that allow a strong bite force. Indeed, you can locate your own fenestra by clenching your teeth and feeling the bulge of the temporalis muscle that passes through the fenestra behind the cheekbone.

bar, resulting in a single fenestra.

Thus, extant reptiles have either an anapsid skull condition (turtles only) or a diapsid skull (lizards, snakes, tuatara, crocodylians, and birds). It is generally agreed that the anapsid skull is the ancestral condition for amniotes, and therein lies one of the most disputed aspects of amniote phylogeny: Where do turtles fit into the reptile phylogeny? Because the anapsid condition is ancestral for amniotes, the fact that turtles have an anapsid skull gives no clue to their relationships. We will return to this question after first outlining the radiation of diapsids.

2.6 ■ Diapsida: Lepidosauria and Archosauria

The clade Diapsida includes most, and perhaps all, extant reptiles (depending on whether turtles are diapsids; see Section 2.7). Diapsids are an extraordinary radiation that produced major components of terrestrial and marine ecosystems from the Late Carboniferous (e.g., *Petrolacosaurus*; see Figure 2.14D) to the present. Of the extraordinary radiation of diapsids in the Mesozoic, only a few major groups of Lepidosauria and Archosauria are still extant, although birds and squamates account for more species than all other extant amniotes combined. The number of extant diapsid species—more than 19,000—far surpasses that of their sister group Mammalia (Synapsida), which numbers about 5,400 species.

The taxonomic nomenclature of diapsids can be confusing not only because of the many clade names, but also because the name Sauria (rather than Diapsida) is often used to refer to extant reptiles. Both names are correct in that they refer to clades that contain extant reptiles. The distinction between the two is that Sauria contains only extant diapsids, whereas Diapsida includes Sauria and extinct stem lineages. We will use the name Diapsida for the remainder of this chapter.

Diapsida includes many familiar fossil groups, including those highly modified for a marine existence such as ichthyosaurs and plesiosaurs, but two other lineages, Lepidosauria and Archosauria, are most relevant to this discussion. Lepidosauria includes Squamata (lizards and snakes), Rhynchocephalia (tuatara), and several fossil groups. Archosauria includes Crurotarsi (crocodiles and extinct relatives) and Avemetatarsalia, which contains Pterosauria (extinct flying reptiles), Dinosauria (dinosaurs and birds), and the highly aquatic Ichthyosauria and Plesiosauria. To make matters more confusing, Crurotarsi is sometimes called Pseudosuchia and Avemetatarsalia is called Ornithodira in the literature (see Nesbitt 2011). Molecular dating indicates that Lepidosauria and Archosauria split in the Early to Middle Permian (~285–260 mya) (Jones et al. 2013).

Lepidosauria

Lepidosauria includes Squamata (lizards and snakes) and Rhynchocephalia (tuatara). Characters of both the skull and appendages support the monophyly of Lepidosauria (e.g., Gauthier et al. 1988; Evans 2003; Hill 2005), as do all recent phylogenetic analyses of molecular data (e.g., Crawford et al. 2012; Mulcahy et al. 2012). The soft anatomical characters of Lepidosauria are the major characters by which we recognize squamates and tuatara. Lepidosaurs have a transverse cloacal slit (versus an anteroposterior orientation in other tetrapods), loss of a single penis and subsequent evolution of paired penes (hemipenes) or their homologs residing in the tail base, and regular cycles of shedding (ecdysis) of the outer layer of the epidermis (see Chapter 4).

Most early ancestors of Lepidosauria (the Lepidosauromorpha) were small and did not fossilize well. The oldest lepidosaur fossils are a jaw fragment, skull, and anterior skeleton of *Megachirella wachtleri* (Renesto and Bernardi 2013), both from the Middle Triassic (-240 mya) (Jones et al. 2013). Although both rhynchocephalians and squamates were both present through the rest of the Mesozoic, the Late Triassic and Early Jurassic rhynchocephalian fauna is far better represented in the fossil record (Evans and Jones 2010; see Chapter 4). Although some Jurassic squamate fossils exist, modern, morphologically diverse families are not widely represented until the Middle Cretaceous. Thus, the fossil record suggests that the early history of Lepidosauria was dominated by rhynchocephalians that were later replaced by squamates. However, given the poor fossil record of early squamates, this generalization should be viewed with skepticism until more data are collected.

Archosauria

Archosauria include Crurotarsi (crocodylians) and Avemetatarsalia (pterosaurs, dinosaurs, and birds). Characters of both the skull and appendages support the monophyly of Archosauria (e.g., Benton 1985; Brusatte et al. 2010; Nesbitt 2011), as do all recent phylogenetic analyses of molecular data (e.g., Chiari et al. 2012; Crawford et al. 2012; Fong et al. 2012; Field et al. 2014).

Early archosaurs were typically large and robust and left a more complete fossil record than did the contemporaneous lepidosaurs (Nesbitt 2011). The earliest member of Archosauria is the Early Triassic (~249 mya) *Xilousuchus*, a pseudosuchian with a sail-like dorsal structure similar to that of the synapsid *Dimetrodon* (see Figure 2.14E) (Nestbitt et al. 2010). Both major lineages of archosaurs, Crurotarsi and Avemetatarsalia, experienced their greatest diversity in the Late Triassic (~228–209 mya) and then suffered a marked loss of diversity during the Triassic–Jurassic extinction, although avemetatarsalians, represented mostly by pterosaurs and dinosaurs, remained diverse throughout the Jurassic and Cretaceous, the last two-thirds of the age of dinosaurs (Brusatte et al. 2011).

The radiation of Archosauria was marked by two notable morphological trends. First, early members of the clade show derived cranial modifications associated with increased predatory efficiency, including elaborated cranial musculature and sharp, thecodont dentition (i.e., teeth set in sockets in the jaw bones). These and other modifications reached their culmination in some dinosaurs, which added features such as raptorial forelimbs suitable for grabbing prey. Many features of birds that are associated with flight-long forelimbs and birdlike wrists, fused clavicles (furcula), a fused bony sternum, hollow bones, and long forelimbs—evolved earlier in the archosaur radiation in association with predatory habits (Gauthier and Padian 1985). Even feathers evolved in pre-avian dinosaurs (e.g., Padian and Chiappe 1998; Xu et al. 2003; Godefroit et al. 2014). Second, modifications in the postcranial skeleton of archosaurs permitted an erect stance, a narrow-track gait, and the ability to breathe while running (Parrish 1986). The evolution of locomotor specializations, a hallmark of the archosaur radiation, indicates evolutionary trends toward more active lifestyles than observed in the lepidosaur radiation. Dinosaurs were an extraordinarily diverse group comprising major components of terrestrial vertebrate life in the Mesozoic. More than 1,400 species of extinct dinosaurs have been discovered, and extant dinosaurs are represented today by the more than 10,000 species of birds.

2.7 ■ The Debated Origins of Turtles

Notably absent from our discussion of reptile phylogeny is the origin of turtles, a long-debated topic that has produced numerous papers supporting different phylogenetic resolutions (see Carroll 2013 and Scheyer et al. 2013 for reviews). The highly modified body plan of turtles makes assessing homology of morphological characters difficult.

All studies agree that turtles, archosaurs, and lepidosaurs form a clade (Reptilia), but they disagree on the sister lineage to turtles. Turtles lack temporal fenestrae (the anapsid condition; Figure 2.16A) and therefore may be related to a group of reptiles that share this anapsid condition and that diverged before the origin of diapsids-the "parareptilia" (see Scutosaurus, Figure 2.14C). Indeed, numerous recent studies based on extensive morphological data sets that include both extinct and extant taxa support this relationship (e.g., Gauthier 1988; Werneburg and Sánchez-Villagra 2009; Lyson et al. 2010, 2013). However, no modern phylogeny based on molecular data supports this relationship. Rather, essentially all molecular studies support a sister relationship between archosaurs and turtles (Figure 2.16B). Finally, some morphological studies (e.g., deBraga and Rieppel 1997; Rieppel 2000; Hill 2005) support a third possible position of turtles as sister to lepidosaurs (Figure 2.16C). If either of the latter two hypotheses is correct, the anapsid condition of the turtle skull must be secondarily derived from an ancestral diapsid condition and therefore convergent with the anapsid skull condition seen in "parareptiles."

There are many possible explanations for the differing results among the phylogenetic studies based on morphological data, but which taxa are included in the analysis is probably the most important. Given their aquatic nature and heavily ossified body plan, turtles have an extensive fossil record, thereby allowing morphological analysis of both extinct and extant species. However, the homologies of some morphological characters are debated, and phylogenetic analysis of these data is sensitive to which taxa are included. It is more difficult to explain the differing results of the molecular and morphological analyses. The molecular analyses may be the best representation of turtle phylogenetic relationships because they include far more characters (thousands) than those based on morphological data (hundreds), and are arguably less biased to the interpretation of homology by the investigator. However, because molecular data cannot be collected from fossil taxa, studies based on morphological data can better capture stem lineages that are phylogenetically informative. Although it is highly unlikely that phylogenies estimated from turtle morphology and DNA will reach a consensus, the archosaur origin of turtles is increasingly accepted.

2.7 The Debated Origins of Turtles 39

(A) Anapsid hypothesis







(C) Lepidosaur hypothesis



Figure 2.16 Three hypotheses of turtle origins. (A) The anapsid hypothesis proposes that turtles are most closely related to early-diverging "parareptile" lineages that had no temporal fenestration. Although morphological data support this hypothesis, no analysis of molecular data upholds it. (B) The hypothesis supported by almost all phylogenetic analyses of DNA data is that turtles are diapsids and the sister lineage to extant archosaurs (crocodiles and birds). (C) The hypothesis that turtles are diapsids and the sister lineage to lepidosaurs (lizards, snakes, and tuatara) is supported by some morphological data but is not widely accepted.

SUMMARY

Phylogenies are a critical tool in understanding the evolutionary history of life.

Phylogenetic systematics, also known as cladistics, emphasizes the importance of derived characters (characters that have changed from the ancestral condition) shared among taxa in recognizing monophyletic groups (clades).

Phylogenies can be reconstructed using many different kinds of data. Skeletal features and DNA data are most commonly used.

DNA has become the predominant type of data to infer phylogenies of extant organisms because of the larger data sets that can be constructed compared with morphological data. However, only morphological (mostly skeletal) data can be collected for fossil taxa.

The use of DNA data allows researchers to study the evolutionary history of organisms that may not display substantial morphological differences and allows estimation of when lineages diverged.

Rank-free taxonomy dispenses with the use of Linnean ranks above the genus level.

Equal Linnean ranks do not necessarily represent groups that are equal in diversity or age.

A node-based taxonomic name (e.g., Tetrapoda) includes the most recent common ancestor of at least two taxa and all of its descendants. A stem-based taxonomic name (e.g., Tetrapodomorpha) includes a group more closely related to one taxon than to another.

Discovering and describing new species is a fundamental goal of phylogenetic systematics.

The morphology, and often DNA, of a putative new species is compared to that of existing described species to identify potential differences.

Multiple criteria are used to decide whether or not an organism is a new species. These usually consist of morphological features such as coloration or scale patterns (in reptiles), or of advertisement calls (in frogs), but new species can also be identified by phylogenetic analysis of DNA.

New species are described in a scientific paper that defines a holotype (the individual specimen that possesses all the characters of that species) and that provides a unique binomial species name, a morphological description of the new species, and an explanation of how this new species differs from other species.

Tetrapods are evolutionarily derived from Late Devonian sarcopterygian fish.

The transition from water to land was a gradual process over the span of approximately 20 million years. Increasing adaptations to terrestriality are preserved in the fossil record in multiple aquatic taxa, including Eusthenopteron, Pandericthys, Tiktaalik, Acanthostega, and Ichthyostega.

The greater effect of gravity on land compared with water required the evolution of skeletal adaptations to bear the mass of the animal. These adaptations included extensively interlocking vertebrae and robust limbs and pelvic and pectoral girdles.

The loss of gills and the evolution of oil- and waxproducing glands are adaptations to living in a dry terrestrial environment.

Terrestrial living also required changes to sensory systems, especially hearing.

Extant amphibians, which include salamanders, frogs, and caecilians, form a clade called Lissamphibia.

Numerous characters, including features of the teeth, sensory systems, musculature, and skeleton, support the monophyly of Lissamphibia.

The evolutionary origins of Lissamphibia are debated. The temnospondyl hypothesis is the most widely accepted and states that lissamphibians are derived from the temnospondyls—amphibians with vertebrae composed of two distinct centra.

The lepospondyl hypothesis states that lissamphibians are derived from the lepospondyls—amphibians with a single circular centrum.

The diphyly hypothesis states that Lissamphibia is not monophyletic and that caecilians are derived from lepospondyls, and frogs and salamanders from temnospondyls. This hypothesis is not widely accepted.

Most phylogenetic studies support a clade composed of frogs and salamanders (Batrachia) that is the sister lineage to caecilians. Many of the morphological features of Lissamphibia can be explained by paedomorphosis.

Reptiles and mammals form the clade Amniota.

Amniotes are defined primarily by their possession of the amniotic egg—a specialized structure composed of a protective eggshell and four extraembryonic membranes.

The earliest fossil amniote is from the Late Carboniferous and was contemporaneous with lissamphibians.

With the possible exception of turtles, all extant amniotes are classified in two clades, Synapsida and Diapsida.

- Synapsida includes mammals and extinct nonmammalian species identifiable by the possession of a single temporal fenestra in the skull.
- Diapsida includes two major clades: Archosauria (crocodylians, dinosaurs, and birds) and Lepidosauria (lizards, snakes, and rhynchocephalians). Diapsids are identifiable by the possession of two temporal fenestrae in the skull, although this condition has been secondarily lost in all squamates and some extinct rhyncocephalians.

There are three major hypotheses of turtle origins.

Most phylogenetic analyses of morphological data support the sister relationship of turtles and Diapsida.

Essentially all phylogenetic analyses of molecular data support the sister relationship between turtles and Archosauria.

Some morphological studies support the sister relationship of turtles and Lepidosauria, although this hypothesis is not widely accepted.

Go to the *Herpetology* Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

3 Systematics and Diversity of Extant Amphibians

The three extant lissamphibian lineages (hereafter referred to by the more common term amphibians) are descendants of a common ancestor that lived during (or soon after) the Early Carboniferous. Since the three lineages diverged, each has evolved unique features that define the group; however, salamanders, frogs, and caecelians also share many traits that are evidence of their common ancestry. Two of the most definitive of these traits are:

- Nearly all amphibians have complex life histories. Most species undergo metamorphosis from an aquatic larva to a terrestrial adult, and even species that lay terrestrial eggs require moist nest sites to prevent desiccation. Thus, regardless of the habitat of the adult, all species of amphibians are fundamentally tied to water.
- 2. The permeable skin of amphibians acts as a respiratory organ that, in addition to the lungs, exchanges oxygen and carbon dioxide with the environment. This exchange can occur only when the skin is moist, and the thin, moist skins of nearly all amphibians render them susceptible to evaporative water loss.

Because of their reliance on water for respiration and reproduction, amphibians are particularly sensitive both to water pollution and to increasing aridity caused by climate change.

In this chapter, we first discuss several important morphological and physiological traits that characterize amphibians. We then explore amphibian diversity on a finer scale by discussing general biological features of each family, as well as its geographic distribution and conservation status. We provide detailed discussions of taxonomy when appropriate, and provide references for the most recent systematics studies and sometimes examples of classic systematics papers. We present widely used common names of groups in addition to scientific names, noting also that herpetologists colloquially refer to most clades by their scientific name (e.g., ranids, ambystomatids, typhlonectids).

A total of 7,303 species of amphibians are recognized and new species-primarily tropical frogs and salamanders-continue to be described. Frogs are far more diverse than salamanders and caecelians combined: more than 6,400 (~88%) of extant amphibian species are frogs, almost 25% of which have been described in the past 15 years. Salamanders comprise more than 660 species, and there are 200 species of caecilians. Amphibian diversity is not evenly distributed within families. For example, more than 65% of extant salamanders are in the family Plethodontidae, and more than 50% of all frogs are in just six families (Hylidae, Craugastoridae, Bufonidae, Microhylidae, Ranidae, and Rhacophoridae). Amphibian populations worldwide have been devastated by the introduction of the chytrid fungus, as well as by habitat loss, pollution, and poaching or harvesting for folk remedies (see Chapter 17).

3.1 What Is an Amphibian?

Herpetologists use two different measurements of amphibian body length (**Figure 3.1**), and most amphibians are small in terms of both length and weight. Amphibians share numerous other traits, including ectothermy (see Chapter 1), but their life histories and skin structure are central in defining the ways these animals interact with their environments.

Amphibian life histories

The ancestral reproductive mode of amphibians is aquatic, a trait inherited from their tetrapod forebears. Eggs are laid



(A) The total length reptiles and amphibians is measured from the tip of the snout to the tip of the tail. However, loss of a portion of the tail (caudal autotomy) is common in some groups (notably salamanders and lizards), so snout-vent length, or SVL—the distance from the tip of the snout to the posterior margin of the cloaca—is often used in preference to total length. (B) Almost all adult anurans lack tails, so total length and SVL are generally the same, measured from the tip of the snout to the end of the urostyle (the fused caudal vertebrae; see Figure 3.18). (Photographs: A, © Francesco de Marco/ Shutterstock; B, © Eric Isselee/Shutterstock.)

in water and hatch into aquatic larvae that grow for some period and ultimately metamorphose into terrestrial adults. This complex life history allows an individual to harvest energy and nutrients from two different habitats, and amphibians therefore play an important ecological role in transporting nutrients from aquatic to terrestrial habitats. Because the larva and adult have different lifestyles, selection acts independently on these two life stages. The counteracting forces of selection are evident in tadpoles, which are very different from adult frogs. During metamorphosis, practically every body structure of a tadpole is broken down and reconstituted into the adult form. The body forms of salamander and caecilian larvae are similar to those of adults, and the changes that occur during metamorphosis are correspondingly less dramatic.

Variations on the ancestral life-history pattern are widespread. For example, among direct-developing species, the embryo passes through an abbreviated larval period before hatching and emerges from the egg as a miniature of the adult. Some direct-developing species are viviparous, retaining the embryos within the oviducts and giving birth to fully formed young. Paedomorphic species retain larval characters (such as external gills) throughout life and reproduce without metamorphosing to a fully adult form.

Amphibian skin

The basic structure of the skin is similar among the three major clades of amphibians. The permeable, glandular nature of amphibian skin plays crucial roles in respiration, defense, courtship, locomotion, and reproduction. These characteristics of the skin also render amphibians susceptible to pollution in aquatic habitats and to dehydration in terrestrial habitats.

As in other vertebrates, amphibian skin is composed of an outer epidermis and an underlying dermis. The glands, nerves, muscles, scales (in caecilians), and pigment cells associated with the skin are located in the dermis, although their processes and ducts may extend to the skin surface. Functionally, developmentally, and anatomically, the epidermis and dermis are highly integrated. The thin, moist skin of amphibians allows exchange of carbon dioxide and oxygen with the atmosphere. Indeed, cutaneous gas exchange is the only mode of respiration for plethodontid salamanders and a few other species that lack lungs entirely.

Cutaneous mucus and granular glands are synapomorphies of Lissamphibia. Amphibian skin contains two types of **mucus glands** that secrete mucoproteins (see Figure 6.4). Ordinary mucus glands provide a moist coating over the body surface that is critical for cutaneous gas exchange and for limiting water loss. Some frog species use this mucus and shed epidermis to form a cocoon that allows the frog to **estivate**, a prolonged state of of dormancy, during dry periods. The skin overlying the skull of some frogs becomes inseparably fused with the underlying bone. This condition, called co-ossification, also inhibits evaporative water loss (Seibert et al. 1974), and is often associated with the presence of bony crests in the skull.

Sexually dimorphic mucus glands, or **breeding glands**, differ structurally and chemically from ordinary mucus glands (Thomas et al. 1993; de Perez and Ruiz 1996). In response to increased levels of androgen hormones during the breeding season, males of many frog species develop clusters of mucus glands (Emerson et al. 1999). When present on the hands and/or forearms, breeding glands are called **nuptial pads**, and they often develop a dark, highly keratinized (even spiny) overlying epidermis (**Figure 3.2**). Nuptial pads help males grasp females securely during amplexus. In some frogs, they are used in male–male combat and may bear enlarged bony spines projecting from the base of the thumb (prepollical spines). These spines can inflict lethal wounds during encounters between males (Kluge 1981).

Granular glands produce defensive secretions in the form of toxic amines, peptides, proteins, steroids, or alka-

Figure 3.2 Nuptial pad of a male frog. During the breeding season, males of some frog species develop thick, rough, or even spiny areas of skin on the prepollex and forearm. These nuptial pads assist them in grasping a female during amplexus (mating). Shown is a nuptial pad of Perez's frog (*Pelophylax perezi*, Ranidae). (Photograph © Wildlife GmbH/Alamy.)

loids (Daly 1995; Conlon 2011a). Like mucus glands, the granular glands of amphibian skin are often concentrated into macroscopic clusters. The most obvious examples are the **parotoid glands** (and dorsal warts) of many frogs, especially bufonid toads and some salamanders (e.g., *Salamandra*), that may secrete copious quantities of toxin when disturbed. In addition, the sticky granular gland secretions of most amphibians play a role in defense (e.g., Evans and Brodie 1994).

Colors and color changes of amphibians are produced by specialized cells called chromatophores in the skin. Three types of chromatophores are usually present and are organized into discrete structures called dermal **chromatophore units** (Figure 3.3). Xanthophores are located just below the basement membrane separating the epidermis and dermis. These cells contain pteridine or carotenoid pigments and impart red, yellow, or orange colors. Iridophores reflect white, silver, or blue coloration depending on the size of purine granules in the cell, and may emphasize or change the colors of overlying tissue. The cell bodies of **me**-



lanophores have dendritic processes extending toward the skin surface that cover the upper surfaces of the iridophores. Melanophores contain the pigment melanin, which gives rise to dark brown or black coloration.

Interactions among the different chromatophore types account for both color and color change of amphibians. For example, the blue color of some frogs results from reflective properties of iridophores in the absence of overlying xantho-

Figure 3.3 Chromatophore units are the color-producing components of an amphibian's

skin. (A) The chromatophore units of the dermis are made up of a regular arrangement of xanthophores, iridophores, and melanophores. (B) The typical green color of the red-eved treefrog (Agalychnis callidryas) is produced by interaction between blue light reflected from the iridophores and from yellow xanthophore pigments. Myriad other interactions among chromatophore units produce the diverse colors of amphibians. (C) This A. callidryas individual is missing xanthophores from its dorsal surface, and the regions without xanthophores appear blue. (A after Bagnara et al. 1969. Photographs: B, © bluedogroom/Shutterstock; C, Harvey Pough.)



(B)



(C)



phores. However, if overlying xanthophores contain yellow pigments, the interaction between the reflected blue light from the iridophores and the yellow xanthophore pigments produces the green of many frogs. Indeed, many museum specimens that initially are green turn blue over time because the ethanol preservative washes away the yellow pigments.

Physiological color changes (i.e., those that occur on the order of seconds to minutes) are the result of changes in the distribution of pigments within cells by intracellular transport (Schliwa and Euteneuer 1983). Pale colors result from concentration of melanin in the central part of the melanophores, exposing the overlying iridophores. Conversely, when melanin is dispersed throughout the dendritic processes of the melanophores, the iridophores are obscured and the animal appears dark. These changes are mediated hormonally, primarily by circulating levels of melanocytestimulating hormone (MSH).

3.2 Caudata: Salamanders

Caudata (from the Latin *cauda*, "tail") is the node-based name for the ancestor of extant salamander lineages, and Urodela (from the Greek *ur*, "tail," + *delos*, "conspicuous") is the stem-based name for all lineages more closely related to Caudata than to other amphibians, and includes extinct lineages that diverged before modern salamanders. Salamanders are found on every continent except Australia, but are most phylogenetically diverse in North America, which hosts representatives of all but one family of salamanders (Hynobiidae).

Morphology

Typical salamanders have four limbs and a long tail (see Figure 3.1A). The SVLs of adult salamanders vary from 15 mm (*Thorius*; Plethodontidae) to >1 m (*Andrias davidianus*; Cryptobranchidae). Many species are terrestrial as adults but return to water to breed. Other species are entirely terrestrial or entirely aquatic, while many plethodontids are arboreal or fossorial. Cave- or crevice-dwelling species occur in the Plethodontidae and Proteidae.

The trunk of salamanders is superficially segmented by **costal grooves** (Figure 3.4) that facilitate water movement over the body surface (Lopez and Brodie 1977). The limbs of some elongate species, including *Amphiuma* (Amphiumidae) and *Siren* (Sirenidae), are reduced, and the pelvic girdle and hindlimbs are lost entirely in sirenids. Salamanders have lost many of the ancestral lissamphibian skull roofing bones (compare Figure 2.13A and B).

Salamanders lack middle ear cavities and tympana (eardrums). Instead, the ancestral salamander hearing apparatus is the opercular apparatus, which has two components: the columella (stapes), which is found in other tetrapods; and the operculum and associated opercular muscle, which are unique to salamanders and frogs. The columella and the operculum are bony or cartilaginous elements associ-



Figure 3.4 Costal grooves facilitate water movement. These external grooves lie above the rib cage and enhance the amphibian's ability to maintain vital moisture in the skin. (Photograph © blickwinkel/Alamy.)

ated with the fenestra ovalis of the inner ear. The columella receives relatively high-frequency airborne sound. The operculum, which is connected via the opercular muscle to the suprascapula of the pectoral girdle (see Figure 2.12), receives low-frequency sound from the air or substrate. One or more components of the opercular apparatus are absent in some salamander families.

Reproduction and life history

Fertilization is external in cryptobranchids, hynobiids, and sirenids and internal via **spermatophores** in all other salamanders. The spermatophore is a mushroom-shaped packet of sperm that the male places on the substrate (see Figure 8.4). The ancestral reproductive mode, retained in most salamander families, is to deposit aquatic eggs that proceed to an aquatic larval stage. However, direct development is the most common reproductive mode at the species level, occurring in more than 300 species of plethodontids. Viviparity occurs in some species of *Salamandra*, which give birth to advanced larvae in water or to fully metamorphosed young, depending on the species and population.

Salamander larvae have a body form almost identical to that of adults, with the exception of larval features associated with an aquatic existence, such as external gills, gill slits, and tail fins (see Figure 8.22). In contrast to frog larvae, in which the skeleton is entirely cartilaginous and no true teeth are present, salamander larvae have both bony skeletons and teeth. Pond-dwelling larvae in the families Ambystomatidae, Hynobiidae, and Salamandridae develop rodlike **balancers** in the region of the jaw joint anterior to the developing limbs. Composed of collagen and other tissues, balancers provide physical support for the limbless larva and secrete adhesive mucus (Crawford and Wake 1998). In contrast to adults, salamander larvae lack eyelids and have

Costal grooves



10 mm

histologically different skin. These features change into the adult conditions at metamorphosis. The palate of salamanders is also completely remodeled during metamorphosis, a synapomorphy of the group.

Some salamanders, including all cryptobranchids, proteids, sirenids, and some dicamptodontids, plethodontids, and ambystomid species (notably the Mexican axolotl, *Ambystoma mexicanum*; see Figure 8.30A) never completely metamorphose, but become reproductively mature while retaining a larval body form. This evolutionarily important phenomenon is known as **paedomorphosis**. Other salamanders exhibit facultative metamorphosis—that is, the occurrence of metamorphosis depends on environmental cues. Individual salamanders in a population, or entire populations, may show facultative metamorphosis (see Section 8.9).

Fossil record

Salamanders from the Middle Jurassic (~170–159 mya) are known from England and Kyrgyzstan (Evans et al. 1988; Nessov 1988). Most salamander fossils are from the Holarctic, but a few Cretaceous fossils are known from Gondwanan localities in Bolivia, Sudan, and Niger (Evans et al. 1996; Skutschas and Martin 2011). For many years, the only

Figure 3.5 A fossil cryptobranchid salamander (Chunerpeton

tianyiensis). Discovery of these Middle Jurassic fossil salamanders in China extended the fossil record of Caudata back more than 100 million years. (From Gao and Shubin 2003).

articulated (jointed) salamander fossil was Karaurus sharovi from Late Jurassic (~150 mya) deposits of Kazakhstan (Ivachnenko 1978). However, hundreds of articulated fossils have been discovered in a pond deposit of Late Jurassic age in China (Gao et al. 1998; Gao and Shubin 2001). These fossils are so well preserved that some of the soft anatomy and larval traits such as gill filaments are visible. The deposit, the result of mass mortality caused by a volcanic eruption, includes two species, one (Sinerpeton fengshanenesis) with aquatic larvae and metamorphosed terrestrial adults, the other (Laccotriton subsolanus) apparently a paedomorphic species that reproduced in a larval state. The earliest examples of modern salamander groups are also from China, and include complete skeletons of cryptobranchids (Chunerpeton; Figure 3.5) (Gao and Shubin 2003). The discovery of these specimens extended the fossil record of cryptobranchids by more than 100 million years, to the Middle Jurassic (~161 mya), and showed that cryptobranchids and hynobiids had diverged by that time.

Systematics and Phylogeny of Salamanders

Evidence for the monophyly of Urodela includes derived characters of the jaw adductor musculature, the ossification sequence of the skull bones, the late appearance of the maxillae, and a unique fusion of distal mesopodial (ankle and wrist) elements supporting the first two digits (Milner 1988; Shubin et al. 1995; Gao and Shubin 2001). Paedomorphosis produces convergent evolution of many morphological characters (D. Wake 1991b), and its pervasiveness in salamanders has made it difficult to achieve robust phylogenies for the major groups using only morphological characters (Wiens et al. 2005), although individual families and some larger clades are supported by both morphological and molecular data.

Numerous phylogenetic analyses of molecular data have consistently supported the relationship shown in **Figure 3.6**. One notable exception is the relationship of Sirenidae to other salamanders. Molecular data support the hypothesis that sirens are either the sister group to all other salamanders (Zhang and Wake 2009) or to Salamandroidea (Wiens et al. 2005; Roelants et al. 2007; Pyron and Wiens 2011). We favor the latter phylogenetic resolution because it is corroborated by multiple nuclear loci, but the question requires further study.

Classification, distribution, and conservation 10 families, 66 genera, 665 extant species. Salamanders occur principal-

Figure 3.6 Phylogeny of salamander families. These relationships are based on phylogenetic analysis of DNA data. (Data from Roelants et al 2007; Zhang and Wake 2009; Pyron and Wiens 2011; Zheng et al 2011.)



ly in North America and temperate Eurasia, but one clade of plethodontids, the Bolitoglossini has radiated extensively in tropical Central and South America, and its 270 species comprise more than 40% of all known salamander species (Wake 2012). No salamanders occur in sub-Saharan Africa, Australasia, much of tropical Asia, or most islands (e.g., West Indies, Oceania, Madagascar).

Cryptobranchidae Hellbenders and Giant Salamanders

Cryptobranchids are the largest extant salamanders, with adult total lengths reaching 1.5–1.8 m for *Andrias* (**Figure 3.7A**) and 75 cm for *Cryptobranchus*. All species inhabit cold

streams. They undergo incomplete metamorphosis and adults retain larval features, including lidless eyes and the absence of a tongue pad (tongues are used for terrestrial feeding in salamanders and are small to absent in salamander larvae or in fully aquatic adults). *Cryptobranchus* retains one pair of gill slits, but no external gills. The gill slits are completely closed in

Figure 3.7 Cryptobranchidae.

(A) Japanese giant salamander, Andrias japonicus. (B) The family has a disjunct distribution in Asia and North America. (Photograph by Kelly Sweet, courtesy of Brady Barr.) (A)







Fertilization is external. Males of *Cryptobranchus* construct nests under rocks in streams into which several females may deposit eggs, whereas males of *A. japonicus* construct nests at the end of long tunnels in riverbanks (Kawamichi and Ueda 1998).

Classification, distribution, and conservation 2 genera, 3 species. Species include *Andrias davidianus* (central China), *A. japonicus* (Japan), and *Cryptobranchus alleganiensis* (eastern North America) (**Figure 3.7B**). *Andrias davidianus is* listed as Critically Endangered by the IUCN and *A. japonicus* is Near Threatened, primarily because of human consumption and habitat destruction. *Cryptobranchus alleganiensis*, which requires clear, unpolluted streams to survive, is also Near Threatened. Silting of streams due to runoff and destruction of habitat that would otherwise prevent the release of soil into streams are major contributors to the population decline.

Systematics references Matsui et al. (2008), Sabatino and Routman (2009), Crowhurst et al. (2011).

Hynobiidae • Asian Salamanders

Hynobiids are relatively small salamanders (10–25 cm total length; **Figure 3.8A**). They undergo complete metamorphosis and therefore have eyelids and lack gill slits as adults. Lungs are reduced in several genera and absent in *Onychodactylus*, which is a streamside salamander. Adults





of *Batrachuperus* permanently inhabit mountain streams. In most other species, adults are terrestrial and migrate to breeding sites.

Fertilization in hynobiids is external. Males of most species release sperm into the water as the female releases eggs, but females of Ranodon sibericus deposit eggs on top of a spermatophore previously deposited by a male. Eggs are laid in gelatinous egg sacs attached to rocks or vegetation in ponds, streams, or marshes. Some species breed while wetlands are still covered with snow and ice (e.g., Salamandrella keyserlingii in Japan; Hasumi and Kanda 1998). Mating systems vary in Hynobius. In some species, males maintain territories and females lay egg sacs within this territory; whereas in other species several males court a female simultaneously, sometimes forming a mating ball. A striking increase in male head width occurs during the aquatic breeding phase of these species, apparently due to swelling of subcutaneous connective tissue (Hasumi and Iwasawa 1990: Hasumi 1994). The function of this swelling is unclear. The larvae of Hynobius retardatus exist in two morphs. The normal morph feeds on detritus and plant matter, and a much larger, broad-headed carnivorous morph eats tough prey and cannibalizes other larvae. This phenomenon is very similar to cannibalism in some populations of Ambystoma tigrinum and scaphiopodid frogs.

Classification, distribution, and conservation 9 genera, 59 species. Representative genera include *Batrachuperus*, *Hynobius, Onychodactylus, Paradactylodon, Pseudohynobius*, and *Salamandrella*. Hynobiids have a disjunct distribution in Asia from west of the Ural Mountains to the Pacific Ocean, and south to China (including Taiwan), Japan, Afghanistan, and Iran (**Figure 3.8B**). The IUCN lists 14 species as Critically Endangered or Endangered and 15 species as Near Threatened or Vulnerable.

Systematics references Dunn (1923), Zeng et al. (2006), Zhang et al. (2006), Fu and Zeng (2008), Poyarkov et al. (2012), Weisrock et al. (2013), Xiong et al. (2013).

Sirenidae • Sirens

Sirenids are long, slender, eel-like salamanders that have reduced forelimbs and lack pelvic girdles and hindlimbs entirely. *Siren lacertina* (**Figure 3.9A**) reaches nearly 1 m in total length, but other species are much smaller. Adult *Pseudobranchus* are 15–20 cm long. Other unusual sirenid features include a keratinized beak, nonpedicellate teeth (see Section 2.4), external gills, and adult skin that is histologically

Figure 3.8 Hynobiidae. Gensan salamander, *Hynobius leechi*. (B) Distribution. (Photograph courtesy of Todd W. Pierson.)



Figure 3.9 Sirenidae. (A) Greater siren, *Siren lacertina*, which can reach 1 m in total length. (B) Distribution. (Photograph by Wayne Van Devender.)

similar to larval skin. Sirenids lack marginal teeth and eyelids, and the maxillae are absent (*Pseudobranchus*) or dramatically reduced (*Siren*).

Sirenids are obligately aquatic and inhabit swamps, lakes, and marshes with slow-moving water. They prey on invertebrates such as crayfish and other crustaceans, insects, and worms. During droughts, sirenids burrow into mud in drying ponds, secrete a mucus cocoon, and estivate. *Siren intermedia* estivates for up to 1 year, and the larger *S. lacertina* can probably estivate longer (Gehlbach et al. 1973; Etheridge 1990; Aresco 2001). Sirenids fertilize their eggs externally (thereby making internal fertilization a synapomorphy for Salamandroidea; see Figure 3.6), but this reproductive mode and the courtship behavior of sirenids have only recently been documented (Reinhard et al 2013).

Classification, distribution, and conservation 2 genera (*Siren, Pseudobranchus*), 4 species. They inhabit the coastal plain and Mississippi Valley of the southeastern United States and extreme northeastern Mexico (**Figure 3.9B**). No sirenid species are listed by the IUCN as an extinction risk.

Systematics references Moler and Kezer (1993), Gardner (2003), Liu et al. (2006).

Salamandroidea

Ninety percent of described salamander species are Salamandroidea, all of which share the synapomorphy of internal fertilization via spermatophores. The monophyly of Salamandroidea is also strongly supported by recent phylogenetic analyses of DNA, as are the phylogenetic interrelationships of the salamandroid families.

Salamandridae • Newts

Salamandrids are usually up to 20 cm in total length (although some species exceed 30 cm) and have smooth to extremely rugose skin (Figure 3.10A,B). Salamandra, Chioglossa, and Salamandrina are terrestrial as adults, whereas adults of Pachytriton are totally aquatic. The remaining genera of newts move between terrestrial and aquatic environments annually or are aquatic for an extended portion of their life history. Corresponding to these different modes of life history, the morphology of the feeding apparatus is particularly variable among salamandrids (Deban and Wake 2000; Wake and Deban 2000). Salamandrids use both suction feeding in aquatic situations and tongue protrusion feeding mechanisms in terrestrial environments. Feeding mechanisms (and even some aspects of the morphology) change depending on the life-history stage and vary seasonally in newts that migrate to breeding ponds. Some salamandrids, especially Ommatotriton and Triturus, are notable for dorsal crests that play a role in courtship (see Figure 13.11).

Life histories of salamandrids are highly varied. Courtship behaviors are often elaborate, usually involving prolonged interaction between partners, as described in Section 13.4. Fertilization is internal via spermatophores, and eggs of most oviparous species are deposited in ponds or streams. Females of the European genus Salamandra retain developing eggs within the body, either depositing advanced larvae into water (some populations of Salamandra salamandra) or giving birth to fully metamorphosed young (S. atra, S. luschani, and some populations of S. salamandra). In the northern Iberian Peninsula of Europe, the reproductive mode of S. salamandra varies among populations. In some populations, females give birth to a small number (1-15) of fully metamorphosed offspring, whereas in other populations females deposit 20-60 eggs that hatch either as they are being laid or just prior to parturition. In these latter populations, the larvae spend from several weeks to 2 years in the water prior to metamorphosis (Dopazo et al. 1998).

Adults of many North American and Eurasian salamandrids are terrestrial and migrate to ponds for breeding (e.g., *Taricha* and *Triturus*). *Notophthalmus* (eastern North America) and several Eurasian newts have a more complex life cycle. Adults are permanently aquatic, and ontogeny may involve larval and adult stages only, or the larvae may metamorphose into an immature **eft** stage, which is terrestrial. The eft stage of *N. viridescens* lasts from 1 to 14 years, varying among populations (Healy 1974; Gill 1978).



The efts eventually return to ponds and transform into the adult stage. Some populations of both *N. viridescens* and *N. perstriatus*, and populations of several species of *Triturus*, are paedomorphic and reproduce in a larval state.

Many salamandrids have conspicuous skin glands that produce highly neurotoxic secretions (e.g., tetrodotoxin, TTX, in *Taricha* and *Notophthalmus*, salamandarine in *Salamandra*), often accompanied by aposematic coloration and elaborate defensive displays (Brodie 1977; Daly et al. 1987). Some predators, especially some species of garter snakes (*Thamnophis*) have evolved the ability to eat these poisonous salamanders with little or no ill effect (see Chapter 15).

Classification, distribution, and conservation 21 genera, 107 species. Newts inhabit eastern (*Notophthalmus*) and western (*Taricha*) North America; Europe, northwest Africa, western Asia (representative genera include *Lyciasalamandra, Mertensiella, Neurergus, Ommatotriton, Pleurodeles, Salamandra, Salamandrina, Triturus*); and eastern India to Japan (*Cynops, Echinotriton, Pachytriton, Paramesotriton, Tylototriton*) (**Figure 3.10C**). The IUCN lists 17 species as Critically Endangered or Endangered and 26 species as Near Threatened or Vulnerable.

Systematics references Carranza and Amat (2005), Weisrock et al. (2006), Steinfartz et al. (2007), Zhang et al. (2008), Themudo et al. (2009), Wiens et al. (2011), Gu et al. (2012), Wu et al. (2013), Vences et al. (2014).

Ambystomatidae • Mole Salamanders

Ambystomatids are robust salamanders, with adults measuring up to 30 cm in total length. Metamorphosis is either facultative or obligate in different species. For example, the Mexican axolotl (Ambystoma mexicanum) never completes metamorphosis and is a permanently aquatic, paedomorphic species that has been used in a wide variety of studies in developmental and experimental biology (Shaffer 1993; Kauer 2002). Adults of species that complete metamorphosis are terrestrial (Figure 3.11A). Most ambystomatids breed in early spring, and eggs are usually deposited in ponds or slow-moving streams. However, several species (e.g., Ambystoma opacum) breed during the fall and deposit eggs on land near water. The nest sites are flooded, and larvae develop in water. Hybridization among several species of Ambystoma has produced unisexual forms in parts of the midwestern and northeastern United States and southeastern Canada (see Chapter 8).

Classification, distribution, and conservation 1 genus (*Ambystoma*), 32 species. *Ambystoma* inhabit North America from southern Canada to the southern edge of the Mexican Plateau (**Figure 3.11B**). The IUCN lists 11 species as Critically Endangered or Endangered and 4 species are Near Threatened or Vulnerable. Although *A. mexicanum* is a common research animal and pet in captivity, as of 2014 it numbered fewer than 1,000 individuals in the wild

(A)

A CONTRACTOR

Figure 3.11 Ambystomatidae. (A) Barred tiger salamander, *Ambystoma mavortium*. (B) Distribution. (Photograph © Matt Jeppson/ Shutterstock.)

and will probably become extinct in the near future because of destruction of its restricted habitat around Mexico City.

Systematics references Shaffer (1993), Robertson et al. (2006), Weisrock et al. (2006), Bi et al. (2008), Bi and Bogart (2010), O'Neill et al. (2013), Williams et al. (2013).

Dicamptodontidae • Pacific Giant Salamanders

Dicamptodontids are moderate to large salamanders (up to 17 cm SVL or 34 cm total length in *Dicamptodon tenebrosus*) that superficially resemble their sister lineage, Ambystomatidae (**Figure 3.12A**). *Dicamptodon* inhabit damp coniferous forests with cold streams or cold mountain lakes. Except for rare individuals, *Dicamptodon copei* is permanently aquatic and paedomorphic and retains external gills. Metamorphosis is facultative in individuals or populations of the other species. Metamorphosed adults are terrestrial. Eggs are deposited in clusters under rocks or debris in cold streams and are guarded by the female. At hatching, all four limbs are well developed, an unusual character among salamander

(A)

Figure 3.12 Dicamptodontidae. California giant salamander, *Dicamptodon ensatus*. All four species in this family are morphologically similar. (B) Distribution. (Photograph © Design Pics Inc./Alamy.)



Canada

larvae (usually only the forelimbs are developed); this may be related to the fast-flowing streams in which the larvae hatch (Wake and Shubin 1998).

60°N

Dicamptodon tenebrosus breeds mainly during May, whereas *D. copei* may breed anytime except the winter months; the breeding season for other species is poorly documented. The larval period is 2–5 years. Both larvae and adults of *Dicamptodon* are opportunistic predators, and large individuals of *D. tenebrosus* consume small mammals such as shrews and voles, lizards, snakes and other salamanders (including other *Dicamptodon*). The four species of *Dicamptodon* are virtually indistinguishable morphologically but are differentiated genetically and in some life-history characters.

Classification, distribution, and conservation 1 genus (*Dicamptodon*), 4 species. *Dicamptodon* inhabit the Pacific



(B)

Northwest of North America from northern California to southern Canada and the Rocky Mountains of central Idaho and adjacent Montana (**Figure 3.12B**). The IUCN lists 1 species (*D. ensatus*) as Near Threatened.

Systematics references Good (1989), Carstens et al. (2005), Steele et al. (2005), Steele and Storfer (2006a,b).

Proteidae • Mudpuppies and Olms

Proteids are aquatic and paedomorphic, with large external gills and caudal fins. They are unusual among salamanders in that they lack maxillary bones (which are also absent in the sirenid *Pseudobranchus*), have two pairs of larval gill slits (other salamanders have three), and have a diploid chromosome count of 38 (compared with fewer than 30 in other Salamandroidea).

Necturus species inhabit lakes, streams, canals, and other permanent bodies of water in the eastern half of North America. The largest species, *N. maculosus*, grows to about 45 cm in total length (Figure 3.13A), but adults of other species are generally 20–30 cm in total length. Courtship and mating in *Necturus* occur from fall through winter or early spring, depending on the species and population. Oviposition occurs during spring or early summer. Females attach their eggs to the undersides of logs, rocks, or debris, and females of several species attend the clutches through hatching (Parzefall 2000). *Necturus* are generalized predators on aquatic invertebrates and vertebrates, including insect larvae, crayfish, molluscs, annelids, fish, tadpoles, and salamanders and their eggs. They construct burrows or waters (8–14°C) of limestone caves and crevices but may emerge into surface springs on dark nights or after heavy rains (Sket 1997). *Proteus* is similar to other cave-dwelling salamanders, such as *Eurycea* (Plethodontidae), in having a slender body and limbs and reduced eyes. Two forms of *Proteus* are known, a more common white form having whitish skin and extremely reduced eyes (**Figure 3.13B**) and a black form with blackish skin and less reduced eyes.

Fighting between reproductively active male *Proteus* has been observed in the laboratory. Chemical cues are apparently used to locate prey and by males to mark territories. *Proteus* reaches sexual maturity at about 7 years, and captive individuals 30–40 years old are still capable of reproduction.

Classification, distribution, and conservation 2 genera, 6 species. The distribution of Proteidae is disjunct (**Figure 3.13C**). *Necturus* (5 species) inhabits eastern North America; *Proteus anguinus* inhabits karst regions in northeastern Italy, Slovenia, Croatia, and parts of Bosnia and Hercegovina. Although more than 250 historical populations of *Proteus* are known, conservation concerns have emerged as habitats and hydrologic regimes are altered; water pollution has caused the disappearance of formerly dense populations. The IUCN lists 1 species as Endangered (*Necturus alabamensis*), 1 species as Near Threatened (*N. lewisi*), and 1 species as Vulnerable (*Proteus anguinus*).

Systematics references Tihen (1958), Hecht and Edwards (1976), Gorički and Trontelj (2006), Liu et al. (2006), Bonett et al. (2013).

use retreat sites under submerged logs or rocks during the day and are nocturnally active. *N. maculosus* has been trapped as deep as 27 m in lakes.

The olm (*Proteus an-guinus*) inhabits primarily the western Balkans in Europe and grows to a total length of about 25 cm, with females growing slightly larger than males. It lives in cold subterranean

Figure 3.13 Proteidae.

(A) North American mudpuppy, *Necturus maculosus*.
(B) The olm, *Proteus anguinus*, a cave-dwelling species from northern Italy. (C) Distribution. (Photographs: A, courtesy of Todd W. Pierson; B, © Hodalic/Nature Picture Library/Corbis.)





Figure 3.14 Rhyacotritonidae. (A) California mountain salamander, *Rhyacotriton variegatus*. (B) Distribution. (Photograph courtesy of Todd W. Pierson.)

Rhyacotritonidae • Torrent Salamanders

Rhyacotritonids comprise a single genus (*Rhyacotriton*) and are characterized by unique, squared-off glands posterior to the vent in adult males (Sever 1988). They are further distinguished from other salamanders by loss of the operculum and opercular muscle (otherwise lost in only a few hynobiids), and in having greatly reduced lungs and associated structures (also seen in plethodontids and some hynobiids). Larvae and adults of *Rhyacotriton* inhabit cold, well-shaded seepages and streams in humid old-growth conifer forests, although individuals are occasionally found away from water. Maximum adult sizes are up to about 60 mm SVL, but body size varies among populations.

Where known, breeding seasons in *Rhyacotriton* are lengthy, some as long as 10 months. Eggs are deposited singly and are hidden in crevices or among debris on stream bottoms. Larval periods are 3–5 years (Nussbaum and Tait 1977). Species of *Rhyacotriton* are morphologically similar but well differentiated genetically, suggesting a very old radiation. None of the species is sympatric with the others, although *R. variegatus* (**Figure 3.14A**) and *R. kezeri* are narrowly parapatric in northwestern Oregon, where competition may preclude their sympatry (Good and Wake 1992).

Classification, distribution, and conservation 1 genus (*Rhyacotriton*), 4 species. *Rhyacotriton* inhabit the coastal Pacific Northwest of the United States, from northern California to Washington and the Cascade Range of Oregon and Washington (**Figure 3.14B**). The IUCN lists all 4 species as Near Threatened or Vulnerable.

Systematics references Good and Wake (1992), Miller et al. (2006), Wagner et al. (2006).

Amphiumidae • Amphiumas

Like sirenids, amphiumids are elongate, paedomorphic, aquatic salamanders that lack eyelids. However, unlike sirenids, amphiumids retain both pairs of limbs and limb girdles, but they are severely reduced. Amphiumids also lack external gills (but retain one pair of gill slits) and have large pedicellate teeth on the upper and lower jaws. *Amphiuma means* (Figure 3.15A) and *A. tridactylum* are very large

salamanders and attain total lengths of approximately 1.1 m, but the maximum size of *A. pholeter* is only 35 cm. Amphiumids inhabit sluggish streams and rivers or swamps, occasionally moving overland during wet periods. Fertilization is internal, with males depositing spermatophores directly into the cloaca of females during courtship. Large, yolky eggs are laid in long strands on land, underneath or within logs, or in the nest mounds of alligators; they are attended by the female and may take 5 months to hatch (Fontenot 1999). *Amphiuma* prey actively on a wide variety of vertebrates and invertebrates, including insects, crayfish,



Figure 3.15 Amphiumidae. (A) Two-toed amphiuma, *Amphiuma means*. (B) Distribution. (Photograph © Suzanne L. and Joseph T. Collins/Science Source.) snails, amphibians, reptiles, and fish. Like the sympatric sirenid salamanders, *Amphiuma* survive drought periods by burrowing into mud and aestivating for up to 2 years or more (Knepton 1954).

Classification, distribution, and conservation 1 genus (*Amphiuma*), 3 species. The three species differ in the number of toes on both the fore- and hindlimbs—*A. tridactylum* has three toes, *A. means*, two, and *A. pholeter*, one. *Amphiuma* inhabit the coastal plain and lower Mississippi Valley of the southeastern United States (**Figure 3.15B**). The IUCN lists *A. pholeter* as Near Threatened.

Systematics references Rieppel and Grande (1998), Bonett et al. (2009, 2013).

Plethodontidae • Lungless Salamanders

The Plethodontidae are the most species-rich group of salamanders, accounting for two-thirds of all salamander species. They are also the only salamanders that have extensively radiated in the Neotropics. Plethodontids have offered a paradigm for studies of speciation (e.g., Jockusch et al. 2002; Kozak and Wiens 2010; Devitt et al. 2011) and of patterns and mechanisms of evolution in amphibians, especially those focusing on the role of heterochrony in generating morphological novelties (Hanken 1986; D. Wake 1991b, 1992; Parra-Olea and Wake 2001; Bonett et al. 2013). Much of the spectacular radiation of plethodontids is marked by adaptive transitions in locomotor and feeding structures (D. Wake and Larson 1987).

Given the potentially confusing taxonomy of plethodontids, we provide a more complete taxonomy of Plethodontidae in **Figure 3.16**. Because of quirks in the history of plethodontid taxonomy, many researchers use a tribe-level classification when discussing this group. Tribes are a Linnean rank below family, indicated in animals by names end in "–ini" (e.g., Bolitoglossini). As with all Linnean ranks, the name of the rank (tribe, subfamily, etc.) is relatively unimportant if the group is monophyletic and well defined.

All plethodontids lack lungs and rely solely on cutaneous respiration. Fully metamorphosed individuals are characterized by a nasolabial groove that aids in chemoreception. The origin of lunglessness among plethodontids is most often attributed to adaptation to moving water, a presumed ancestral environment (see contrasting views of Ruben and Boucot 1989; Ruben et al. 1993; Beachy and Bruce 1992). Lunglessness has also evolved in Hynobiidae (e.g., Onychodactylus, Ranodon) and Rhyacotritonidae (Rhyacotriton), and the salamandrids Chioglossa, Pachytriton, and Salmandrina have reduced lungs. All of these species live in or along fast-flowing streams. Major centers of diversity of plethodontids are the southern Appalachian mountains of eastern North America, the highlands of southern Mexico and Guatemala, and the highlands of eastern Costa Rica and western Panama.

Plethodontid body forms vary greatly, from relatively robust to elongate and slender. Plethodontids include the smallest (*Thorius*; 30 mm total length) and some of the largest (*Pseudoeurycea belli*; 32 cm total length) terrestrial salamanders. Many arboreal species, which are primarily tropical bolitoglossines, have webbed feet and prehensile tails. Some populations of *Ensatina* have bright aposematic coloration (see Figure 3.16F), and several species of plethodontids are involved in mimicry complexes (see Chapter 15).

The Desmognathini (Desmognathus and Phaeognathus) are characterized by a unique ligament extending from the atlas vertebrae over the skull to the lower jaw (the atlantomandibular ligament), and a suite of derived features associated with peculiar burrowing and feeding modes (D. Wake 1966; Schwenk and Wake 1993). Desmognathines are aquatic to terrestrial. Haideotriton, and some species of Eurycea and Gyrinophilus are permanently aquatic as adults, and most other Hemidactyliinae species are are semiaquatic. Species of Plethodontini are terrestrial to scansorial. Bolitoglossines are the most diversified clade of plethodontids in terms of species diversity and morphology, but only one is aquatic (D. Wake and Campbell 2001). Lowland species of bolitoglossines are fossorial or arboreal, whereas upland species are terrestrial to arboreal and many occupy specialized habitats such as moss mats.

Of all salamander families, Plethodontidae shows the greatest diversity of morphological specializations to particular habitats. Examples of plethodontid lifestyles include fossorial (*Batrachoseps, Oedipina, Phaeognathus*), aquatic or riparian (*Eurycea, Gyrinophilus, Stereochilus*), terrestrial (*Ensatina, Plethodon, Pseudoeurycea*), arboreal (*Bolitoglossa, Chiropterotriton*), cave-dwelling (*Eurycea, Haideotriton*), moss-mat specialists (*Nototriton*), and crevice-dwelling (*Hydromantes*). *Batrachoseps* and *Oedipina* have convergently evolved fossorial specializations, including body elongation, diminutive size, reduced hands and feet, and long tails; these specializations have permitted multiple independent invasions of lowland tropical environments (Parra-Olea and Wake 2001).

Plethodontids are ancestrally oviparous; females usually lay eggs in concealed sites and brood them until hatching, which may take 1 to several months, depending on species and location. However, direct development has evolved independently two times in Plethodontinae—once in the common ancestor of Plethodontinae and a second time in the ancestor to Batrachosepini and Bolitoglossini (Chippendale et al. 2004). Egg attendance behavior has been lost in some taxa (Jockusch and Mahoney 1997). Oviposition sites are usually not shared among individuals. However, communal nesting is known in *Desmognathus wrighti, Eurycea, Hemidactylium, Nototriton,* and some species of *Batrachoseps*.

Plethodontids are notable for the enormous size of their genomes. The human genome contains some 6 billion nucleotides, whereas the size of the plethodontid genome ranges from 14 to 120 billion nucleotides (Mueller et al. 2008; Sun et al. 2011). Consequently, plethodontids have



(B) Desmognathini



(E) Hydromantini



(H) Batrachosepini



Figure 3.16 Plethodontidae. (A) For this species-rich salamander family, a phylogeny of 2 subfamilies and 9 tribes is shown. The lineages Plenthodontinae and Hemidactylinae diverged about 75 mya. (B) Seal salamander, *Desmognathus monticola* (Desmognathini). (C) Arboreal salamander, *Aneides lugubris* (Aneidini). (D) Red-legged salamander, *Plethodon shermani* (Plethodontini). (E) Shasta salamander, *Hydromantes shastae* (Hydromantini). (F) Common ensatina, *Ensatina eschscholtzii*

(C) Aneidini



(F) Ensatinini







(D) Plethodontini



(G) Bolitoglossini



(J) Hemidactyliini



(Ensatinini). (G) Nimble long-limbed salamander, Nyctanolis pernix (Bolitoglossini). (H) California slender salamander, Batrachoseps attenuatus (Batrachosepini). (I) Red salamander, Pseudotriton ruber (Spelerpini). (J) Eastern four-toed salamander, Hemidactylium scutatum (Hemidactyliini). (Photographs: B–D, G–J, courtesy of Todd W. Pierson; E, courtesy of Daniel M. Portik; F, courtesy of L. Lee Grismer.)



Figure 3.17 Distribution of Plethodontidae. The range of this large family includes disjunct locations in Europe and the Americas, including the Neotropical range of Bolitoglossini.

larger nuclei and larger cells than other vertebrates simply because the genome takes up so much volume. These salamanders are also unique in that a large percentage of their red blood cells (RBCs) lack nuclei (Villolobos et al. 1988)—a very rare trait in non-mammalian vertebrates. One hypothesis for the evolution of enucleated RBCs is that nucleated RBCs would be very large cells because of the large genome, and would therefore inhibit blood flow in narrow capillaries (Mueller et al. 2008).

Classification, distribution, and conservation 27 genera, 443 species. Plethodontids were once thought to be exclusively European and American, but a plethodontid species (*Karsenia koreana*) was discovered in South Korea in 2005 (Min et al. 2005). Thus, the family has a disjunct distribution that includes North America, the Neotropics, South Korea, and southern Europe (**Figure 3.17**). Plethodontids are currently undergoing a conservation crisis. The tropical bolitoglossines have been devastated by chytrid fungus (Rovito et al. 2009; Cheng et al. 2011). The IUCN lists 132 species (30% of all plethodontids) as Critically Endangered or Endangered and 100 species (23%) as Near Threatened or Vulnerable.

Systematics references Dunn (1926), D. B. Wake (1966, 2012, 2013), Mueller et al. (2004), Min et al. (2005), Vietes et

Karsenia koreana (Hydromantini) was described in South Korea in 2005.

al. (2007, 2011), Kozak et al. (2009), Fisher-Reid and Wiens (2011), Rovito et al. (2012, 2013), Elmer et al. (2013), Bonnet et al. (2014).

3.3 Anura: Frogs and Toads

Anurans comprise the vast majority of amphibian diversity (~88% of species). Adult anurans are instantly recognizable by their lack of a tail, and most species possess muscular hindlimbs and mouths that are large relative to their bodies. Anura (from the Greek *an*, "without," + *ura*, "tail") is the node-based name for the ancestor of extant frog lineages, and Salientia (from the Latin *saliet*, "to leap") is the stembased name for all lineages more closely related to Anura than to other lissamphibians, including extinct lineages that diverged before modern frogs.

Skeletal morphology

Anurans share multiple morphological skeletal synapomorphies. Their skulls are extremely reduced, lacking many elements present in ancestral lissamphibians (compare Figures 2.13A and C). The frontals and parietal bone are fused to form a frontoparietal. The elements of the hyoid apparatus are fused into a hyoid plate, and several elements are absent



Figure 3.18 Skeletal morphology of frogs. Generalized skeleton of a modern frog with some major synapomorphies of Anura indicated.

from the skull. The tongue is attached in the front of the mouth in most frogs and has a free posterior edge. Most frogs protrude the tongue by flipping it out of the mouth using the attached anterior end as a pivot point (see Chapter 11), but Nasikabatrachidae and Rhinophrynidae have different tongue protrusion mechanisms, as described in the Rhinophrynidae family account on page 63.

Anurans have no more than 9 presacral vertebrae, and their caudal vertebrae are fused into a rod called the **urostyle** (Figure 3.18). Anatomical tails are absent; the tail of the tailed frogs (Ascaphidae) is actually an extension of the cloaca. Anurans have elongated hindlimbs and feet, and the astragalus and calcaneum of the ankle are elongate and at least partially fused. In the forelimb, the radius and ulna are fused, and the tibia and fibula of the hindlimb are fused. All of these features may be associated with saltation (jumping; see Section 10.3), the major mode of locomotion for most frogs.

SKULL Frog skulls have the appearance of being rather open and lightly built compared with the skulls of many other amphibians. This is due partially to the many skull bones that have been lost over evolutionary time, including the palatines, vomers, quadratojugals, and columellae. Most anurans have teeth, albeit often reduced in size. A notable exception is the Bufonidae, which lack teeth entirely. Only one species of frog, *Gastrotheca guentheri*, possesses teeth on the mandible (see Trueb 1973, Duellman and Trueb 1994). Phylogenetic evidence shows that mandibular teeth were lost in the common ancestor of frogs about 230 mya, but re-evolved in *G. guentheri* from a toothless-mandible ancestor between 17 and 5 mya (Wiens 2011). The dermal bones of the skull roof in frogs are fused with the overlying skin. In some frogs the dermal bones of the skull are elaborated into casques—heavily-ossified, helmet-like structures that project from the skull, most notably seen in *Hemiphractus* (Hemiphractidae; see Figure 3.43A) and the hylids *Triprion* and *Anotheca*.

VERTEBRAE Vertebral characters provide important clues to frog phylogenetic relationships. The number of presacral vertebrae in frogs varies from five to nine, with higher numbers present in the anuran lineages that diverged earliest. The shape of the vertebral centrum, the structure that encloses the notochord, varies among frogs and is often a synapomorphy at the family level. Although the specific developmental patterns are different, mature vertebrae fall into one of several patterns, of which three are common. Amphicoelous vertebrae are characterized by the convex shape of the anterior and posterior ends of the centrum (body). The centrum of amphicoelus vertebrae incompletely ossifies around the notochord and no movable joint exists between vertebrae (Figure 3.19A). This morphology is characteristic of Ascaphidae, Leiopelmatidae, Megophryidae, Myobatrachidae, Pelobatidae, and Scaphiopodidae. In opisthocoelous vertebrae, characteristic of Alytidae, Bombinatoridae, Discoglossidae, Pipidae, and Rhinophrynidae, the anterior end of the centrum is rounded and the posterior end is concave. In procoelous vertebrae, observed in all other frogs, the centrum is anteriorly concave and posteriorly rounded. The centrum in opisthocoelous and procoelous vertebrae completely obliterates the notochord, forming a movable joint between adjacent vertebrae (Figure 3.19B).

PECTORAL GIRDLE Pectoral girdles anchor the forelimbs to the body and exhibit a wide range of variation (e.g., degree of fusion and ossification of the various elements), most likely in relation to locomotor mode, burrowing, swimming, and feeding adaptations. The proximal limb element (humerus) articulates with the pectoral girdle at the glenoid fossa. Frog pectoral girdles consist of three elements above the glenoid fossa: the scapula, suprascapula, and cleithrum. Ventromedially below the glenoid fossa, the girdle elements include the omosternum and sternum along the midline, and the clavicles and coracoids extending from the midline to articulate with the scapula and forelimb at the glenoid fossa. A series of cartilaginous elements—the epicoracoid and procoracoid cartilages—lies between the clavicles and coracoids on either side.

Reproduction and life history

Anuran life history and reproductive modes are diverse and will be described in detail in Chapters 8 and 14. Most



anurans have external fertilization aided by close contact between the sexes in a distinctive grasp called **amplexus**.

AMPLEXUS Amplexus is a mating behavior in which a male frog grasps the female from behind to bring their cloacae into close proximity and thus aid fertilization. Three classes of amplectic behavior are recognized (Lynch 1973; Nussbaum 1980). In inguinal amplexus the male grasps the female around the inguinal (waist) region, whereas in axillary amplexus the female is grasped immediately behind her forelimbs (see Figure 8.6A, B). In cephalic amplexus the male is positioned far forward on the dorsum of the female and clasps her head (see Figure 8.6C). Inguinal amplexus is characteristic of most early diverging frog lineages (e.g., non-neobatrachians) but also of some Neobatrachia (Heleophrynidae, Myobatrachidae, Sooglossidae, Brachycephalidae, and some bufonids and Leptodactylidae sensu lato). Axillary amplexus is characteristic of most Neobatrachia. Thus, the direction of evolutionary change in this character within Neobatrachia is difficult to ascertain, and these amplexus behaviors may have evolved independently multiple times. Cephalic amplexus is known in Dendrobatidae, and an unusual variant is observed in mantellid frogs from Madagascar (see the family account for Mantellidae).

LARVAE Many frogs have a larval stage (tadpole) that is radically different from juvenile and adult frogs in morphology and ecology. Tadpoles lack true teeth, but most have keratinous jaw sheaths and toothlike **denticles** that they use to scrape plant matter or detritus, and most of them have a large branchial basket and internal gills. Water is taken in through the mouth, passes across the gills, and—except in Pipidae and Rhynophrynidae—exits through a single **spiracle**. Some free-living tadpoles do not feed and depend on yolk supplied in the eggs; these tadpoles usually metamorphose quickly. Metamorphosis of a tadpole into a juvenile frog results in profound changes in body organization internally and externally, and this process is a major difference between the **Figure 3.19 Vertebral morphology.** (A) No movable joint exists between amphicoelus vertebrae, and ossification is incomplete around the notochord. (B) In opisthocoelous and procoelous vertebrae, the centrum completely obliterates the notochord and there are movable joints between adjacent vertebrae. Procoelous vertebrae are rounded toward the animal's posterior, while opisthocoelous vertebra are rounded toward the anterior.

metamorphosis of frogs and that of salamanders and caecilians. The adult body form of salamanders and caecilians is similar to that of larvae and is acquired gradually during metamorphosis.

Tadpole body plans differ both within and among families, especially in relation to the structure of the mouthparts (presence and arrangement of papillae, jaw sheaths, and denticles), the branchial chambers, and the position of the spiracle, through which water leaves the chambers. The study of tadpole morphology has been greatly influenced by Orton's classification scheme (1953 and subsequent refinements), which classifies the morphological diversity of tadpoles into four general types (**Figure 3.20**). Although Orton's categories are useful shorthand for characterizing mouthparts and spiracle positions, they mask considerable functional and evolutionary diversity within each type, and additional types have been documented.

Fossil record

Two fossil salientians are known from the Early Triassic. Triadobatrachus massinoti (Figure 3.21) is known from a single nearly complete skeleton from Madagascar (~230 mya) (Rage and Roček 1989). It is about 5 million years older than Czatkobatrachus polonicus from Poland (Evans and Borsuk-Bialynicka 1998), which is known from a few isolated skeletal elements. These two fossils show that stem frogs are known from southern and northern parts of Pangaea at the very beginning of the Mesozoic. Molecular divergence analyses show that the split between frogs and salamanders occurred in the Early Carboniferous, and thus salientian history extends over 350 million years (Roelants et al. 2007). The structure of their limbs shows that these stem frogs were not jumpers, nor had they acquired the forelimb morphology required for shock absorption upon landing, as seen in crown group frogs (Anura) (Borsuk-Bialynicka and Evans 2002; Sigurdsen et al. 2012). About 40 million years lapsed between Triadobatrachus and the earliest anuran fossils in the Jurassic, and thus there remains an important gap in knowledge in the evolutionary history of frogs.

Several Jurassic fossils are either anurans or pre-anuran salientians. The earliest of these, *Prosalirus bitis* (Early Jurassic, ~190 mya; Shubin and Jenkins 1995), occurs in the

Figure 3.20 Orton's tadpole types.

For each larval type, ventral views of the oral disc and of the head-body are shown. Blue lines show the path of water flow, and arrowheads show where water exits through the spiracle. (A) Orton's Type 1 larvae are characteristic of Pipidae and Rhynophrynidae. They have wide, slitlike mouths without keratinized mouthparts and paired spiracles. (B) Type 2 larvae (Microhylidae) have a single midventral spiracle and more complex mouthparts than Type 1 but also lack keratinized mouthparts. (C) Type 3 larvae (Ascaphidae, Leiopelmatidae, Bombinatoridae, and Alytidae) have keratinized mouthparts and midventral spiracles. (D) Type 4 larvae, characteristic of all other frogs, differ from Type 3 in having sinistral spiracles (i.e., spiracles on the left side of the body). (After Orton 1953.)



same North American deposits as the earliest known caecilian (*Eocaecilia*). Two others occur later in the Jurassic (*Notobatrachus* and *Vieraella* from Argentina) (Báez and Basso 1996), but fossils assigned to the extant family Alytidae also appear in the Middle to Late Jurassic (Evans et al. 1990; Evans and Milner 1993; Roček 2000). Furthermore, stem pipids and perhaps rhinophrynids were probably already present by the Late Jurassic as well (Báez et al. 2000). This evidence suggests that several extant families of primitive frogs have an extremely ancient evolutionary history. The earliest fossil tadpoles are known from the Late Jurassic or Early Cretaceous in China (Yuan et al. 2003). Fossil pipid tadpoles are known from the Early Cretaceous (Estes et al. 1978), and well-preserved pelobatid tadpoles are known from the Miocene (Wassersug and Wake 1995). For general reviews of frog fossil history, see Báez (1996), Sanchiz and Roček (1996), Roček (2000, 2013), and Roček and Rage (2000).

Anatomical and functional studies of *Prosalirus* provide insight into the origin of saltation and the peculiar morphology of frogs, much of which was already established by the Jurassic. The carpal (wrist) torsion character of frogs is due to modifications in the joint structure of the wrists, and the urostyle, in conjunction with stabilizing muscles of the pelvis, assists in transmitting force from the ilia to the vertebral column during jumping. These characters were well developed in *Prosalirus* and already presaged in *Triadobatrachus* (Roček and Rage 2000).



Figure 3.21 A fossil salientian from the Early Triassic. Skeletal reconstruction of *Triadobatrachus massinoti*. The fossil record of the stem lineage of frogs goes back over 350 million years. (After Rage and Roček 1989.)
Systematics and Phylogeny of Frogs

Frog systematics is by far the most active field in herpetological systematics in terms of discovering new species. There has been considerable progress uncovering the phylogenetic history of anurans, especially in the relationships of Leptodactylidae *sensu lato* and Ranidae *sensu lato* (**Table 3.1**). It is an exciting time to be a frog biodiversity researcher, and because amphibian populations are declining worldwide, it is increasingly important to describe this diversity

It is precisely this vast amount of new information about frog diversity that makes frog taxonomy the area of greatest debate among amphibian systematists. The discovery of an enormous number of new species and clarification of previously ambiguous relationships with molecular phylogenetic data have led to a proliferation of frog family names. For example, the previous edition of this textbook (2004) recognized 30 frog families, while the current edition recognizes 52. This increase certainly reflects dedicated work, attention, and interest in phylogeny of frogs by modern amphibian evolutionary biologists. However, the difficulty in maintaining a cohesive concept of frog diversity increases as the number of families increases. The phylogeny in **Figure 3.22** largely follows AmphibiaWeb and Amphibian Species of the World, but we deviate from those authorities in some cases:

- 1. Craugastoridae and Strabomantidae were proposed as two new families of New World direct-developing frogs (clade Terrana) by Hedges et al. (2008), even though there was only weak clade support for the monophyly of Strabomantidae. Indeed, no publication has since supported Strabomantidae with a level of strong clade support (e.g., Heinicke et al. 2009; Pyron and Wiens 2011). We instead recognize a larger Craugastoridae that includes taxa formerly assigned to Strabomantidae (Pyron and Wiens 2011).
- 2. We do not recognize Odontobatrachidae for similar reasons in that its clade support is low in the study that proposes its name (contra Barej et al. 2014).
- 3. We do not recognize Aromobatidae as a separate family from Dendrobatidae (contra Grant et al. 2006). Although both names are valid in that they define monophyletic groups, we question the utility of this change.
- We recognize the sister taxa Ascaphidae and Leiopelmatidae as separate families given their long usage in herpetology (contra Frost et al. 2006).

The relationships among some families remain unclear, especially those currently part of Hyloidea, Ranoidea, and those formerly placed in Leptodactylidae *sensu lato*. The taxonomy of these groups will almost certainly change as more species of these clades are discovered and their phylogen becomes better supported with additional data.

TABLE 3.1 Comparison of anuran families recognized in the previous and current editions of this book

3rd Edition (2004)	4th Edition (2015)
Hylidae sensu lato	Hylidae sensu stricto
	Hemiphractidae
Leptodactylidae sensu lato	Leptodactylidae sensu stricto
	Alsodidae
	Batrachylidae
	Ceratobatrachidae
	Ceuthomantidae
	Craugastoridae
	Cycloramphidae
	Eleutherodactylidae
	Hylodidae
	Odontophrynidae
	Telmatobiidae
Microhylidae	Microhylidae sensu stricto
sensu lato	Brevicepitidae
Pelobatidae sensu lato	Pelobatidae sensu stricto
	Scaphiopodidae
Petropedetidae	Petropedetidae sensu stricto
sensu lato	[•] Phrynobatrachidae
Ranidae	Ranidae sensu stricto
sensu lato	Calyptocephalellidae
	Ceratophryidae
	Conrauidae
	Dicroglossidae
	Micrixalidae
	Nyctibatrachidae
	Ptychadenidae
	Pyxicephalidae
	Ranixalidae
Pseudidae	Placed in Hylidae sensu stricto
Discoglossidae	Placed in Alytidae
(none)	Nasikabatrachidae (new family)



Figure 3.22 Phylogeny of anuran families. These relationships are based on phylogenetic analysis of DNA data. (Data from Roelants and Bossuyt 2005, Roelants et al. 2007; Pyron and Wiens 2011; Kurabayashi and Sumida 2013; and Zhang et al. 2013.)

Classification, distribution, and conservation Approximately 539 genera and more than 6,400 extant species of frogs are known, and many new species are described each year. Frogs have a cosmopolitan distribution except where limited by extreme cold or dry climates. They are absent from many oceanic islands and are most diverse in tropical Central and South America, Africa, and Southeast Asia. Some notable comprehensive phylogenies of frog relationships and summaries of classification include Ford and Cannatella (1993), Haas (2003), Frost et al. (2006), Roelants et al. (2007), Blackburn and Wake (2011), Pyron and Wiens (2011), Wiens (2011), and Zhang et al. (2013).

Ascaphidae • Tailed Frogs

Ascaphidae is represented by the single extant genus Ascaphus (Figure 3.23A) These small frogs (25-50 mm SVL) are unique among frogs in having an intromittent organ that resembles a tail, giving rise to the common name. The tail is actually a highly vascularized extension of the cloaca that is supported by cartilaginous rods (the postpubis, or Nobelian rods) and attached to the ventral part of the pelvic girdle. During inguinal amplexus, the tail is bent forward by contraction of the rectus abdominis muscles and is inserted into the cloaca of the female. Ascaphus have nine presacral vertebrae, an ancestral character shared with Leiopelma that differs from the eight (or fewer) presacral vertebrae in other extant



Figure 3.23 Ascaphidae. (A) Tailed frog, *Ascaphus montanus*. (B) Distribution. (Photograph courtesy of Wayne Van Devender.)

frogs. Ascaphus, Leiopelma (Leiopelmatidae), and Xenopus and Pseudhymenochirus (Pipidae) also have a prepubic element, the epipubis, found in no other frogs.

Ascaphus inhabit cold torrential streams and are highly aquatic, even as adults. Tympana (eardrums) are absent; these frogs apparently do not call. Inguinal amplexus occurs underwater. Ascaphus lay a few large eggs under rocks in water, and the embryos develop very slowly (Brown 1989; Adams 1993). After hatching, the length of the larval period varies from 1 to 5 years, depending on altitude and geographic location (Wallace and Diller 1998). The tadpoles live in fast-flowing water and have reduced tail fins, but have well-developed suctorial oral discs that firmly attach the tadpole to the substrate (see Figure 11.4). They have been observed using these oral discs to climb out of streams in spray zones. Internal fertilization, absence of calls, and tadpole morphology are probably all specializations for the highly turbulent aquatic environments where Ascaphus live.

Classification, distribution, and conservation 1 genus, 2 species (*Ascaphus truei, A. montanus*). Ascaphids have a disjunct distribution in the northwestern United States and Canada (*A. truei*) and Rocky Mountains (*A. montanus*) (**Figure 3.23B**). Neither *Ascaphus* species is listed by the IUCN as an extinction risk. Frost et al. (2006) merged

Ascaphus into Leiopelmatidae, but we do not follow this taxonomic change.

Systematics references Nielsen et al. (2001, 2006), Conlon et al. (2007).

Leiopelmatidae • New Zealand Primitive Frogs

Leiopelmatid frogs are the only amphibians native to New Zealand. The four extant species of *Leiopelma* (Figure 3.24A) are nocturnal frogs with an SVL of up to 50 mm. Three species are terrestrial, and the other inhabits streamside habitats. They are unique among frogs in having inscriptional ribs embedded in the ventral body musculature (Green and Cannatella 1993). *Leiopelma* lack tympana, certain middle ear structures, and vocal sacs. Leiopelmatids are also long-lived frogs; mark–recapture studies have found males and females at least 34 years old (Bell and Pledger 2010).

Females lay small clutches (20–70 eggs) in moist terrestrial habitats (Stephenson and Stephenson 1957). Development is rapid, with the tadpoles developing neither jaw sheaths nor denticles (Bell 1978). Adult males of three of the four *Leiopelma* species attend the clutches, and after hatching, carry the tadpoles on their backs until development is complete. Male attendance does not occur in the more



Figure 3.24 Leiopelmatidae. (A) Archey's frog, *Leiopelma archeyi*. (B) Distribution. (Photograph courtesy of David M. Green.)

aquatic species, *L. hochstetteri*, in which free-living tadpoles move into water soon after hatching.

Classification, distribution, and conservation 1 genus (*Leiopelma*), 4 species. *Leiopelma* inhabit New Zealand (**Figure 3.24B**), where all four species are threatened by habitat degradation and introduced exotic species (Bell 2010). Chytrid fungus (see Chapter 17) was discovered in New Zealand in 1999 and is linked to the decline of *L. archeyi* (Bell et al. 2004), but *L. hochstetteri* seems to be resistant to infection (Moreno et al. 2011). *L. hamiltoni* is known only from a single population of fewer than 300 individuals. The IUCN lists 2 species as Critically Endangered or Endangered and the other 2 species as Vulnerable.

Systematics references Worthy (1987), Holyoake et al. (2001), Fouquet et al. (2010).

Bombinatoridae • Fire-Bellied Toads

Bombina and *Barbourula* form a clade characterized by derived features of the skull and hyoid (Ford and Cannatella 1993). Species of *Bombina* are small to medium size (40–80 mm SVL) and toadlike, whereas *Barbourula* are larger



(60–100 mm SVL) and fully aquatic. *Bombina* have bright orange or yellow aposematic coloration on the belly (**Figure 3.25A**) and emit toxic skin secretions (Bachmeyer et al. 1967). They adopt a defensive posture, the **unken reflex**, to display these colors when threatened (see Figure 15.25E). Very little is known about the natural history of *Barbourula*, although *B. kalimantanensis* is the only frog species known to lack lungs (Bickford et al. 2008). *Bombina* lay single eggs in ponds; the reproductive biology and tadpoles of *Barbourula* are unknown. Two species of *Bombina*, *B. bombina* and *B. variegata*, have been the subject of extensive studies of hybrid zone dynamics (Szymura 1993; Nurnberger et al. 1995; Hofman and Szymura 2007). The divergence between *Bombina* and *Barbourula* is very old (~50 mya; Blackburn et al. 2010).

Classification, distribution, and conservation 2 genera (*Bombina, Barbourula*), 10 species. *Bombina* have a disjunct distribution in Europe and Asia to China, Korea, and Vietnam; *Barbourula* inhabit Borneo and the Philippines (Figure 3.25B). The IUCN lists 2 species as Endangered and 2 as Vulnerable.

Systematics references Clarke (1987), Hofman et al. (2007), Yu et al. (2007), Pabjian et al. (2008), Zheng et al. (2009), Pabjian et al. (2013).

Alytidae • Disc-Tongued Frogs and Midwife Toads

Alytids are small to moderate-size frogs (30–70 mm SVL) with aquatic eggs and tadpoles. *Alytes* are fossorial, constructing tunnels in which they live, whereas *Discoglossus* and *Latonia* inhabit rivers and marshes as well as terrestrial habitats. Inguinal amplexus in *Alytes* takes place on land, and the male maneuvers the fertilized eggs onto his back and hindlimbs. Here they are carried and moistened



Figure 3.25 Bombinatoridae. (A) Oriental fire-bellied toad, *Bombina orientalis*. (B) Distribution. (Photograph © marima/Shutterstock.)

Figure 3.26 Alytidae. (A) Common midwife toad, *Alytes obstetricans*. This male is carrying a string of eggs wrapped around his hind legs. (B) Distribution. (Photograph © Paul Starosta/Corbis.)

(A)





when necessary until near hatching, at which time they are deposited in water. Because of this behavior, the common name for *Alytes* is midwife toads (**Figure 3.26A**). *Discoglossus* lay their eggs directly in water.

Latonia nigriventer was declared extinct by the IUCN in 1996 after no documentation of its existence since the 1950s, when its only known habitat, the marshes of Hula Valley, Israel, were drained. However, this species was rediscovered in 2011 at a wetland nature preserve in the Hula Valley (see Figure 17.30C) (Biton et al. 2013).

Classification, distribution, and conservation 3 genera (*Alytes, Discoglossus, Latonia*), 11 species. This family inhabits western Europe and the Middle East to northwestern Africa (**Figure 3.26B**). It has a confusing taxonomic history as some or all alytid species have been placed in the formerly recognized family Discoglossidae (not to be confused with Dicroglossidae). The IUCN lists 1 species (*Latonia nigriventer*) as Critically Endangered and 5 species as Near Threatened or Vulnerable.

Systematics references Martínez-Solano (2004), Martínez-Solano et al. (2004a), San Mauro et al. (2005), Zangari et al. (2006), Gonçalves et al. (2007), Velo-Antón et al. (2008), Pabjian et al. (2012), Biton et al. (2013).

Rhinophrynidae • Mexican Burrowing Toad

The single species in this family, *Rhinophrynus dorsalis* (Figure 3.27A), is highly modified for burrowing (Trueb and Gans 1983). Adult *Rhinophrynus* are 75–85 mm SVL with a somewhat bulbous body and short, powerful limbs with a well-developed spade on the inner metatarsal tubercle and first toe. The head is pointed and has thickened, cornified skin at its tip. The eyes are very small, and the tympanum is absent. The skull is reinforced and the pectoral girdle overlaps it. *Rhinophrynus* lacks teeth, and the entire feeding apparatus, including buccal, pharyngeal, esophageal, and hyoid structures, is highly modified to feed on ants and termites underground. Rather than being flipped out of the mouth as in other frogs, the tongue is protruded from a groove in the front of the mouth, similar to the action in ant-eating mammals.

Rhinophrynus inhabits subhumid areas and is active aboveground only after heavy rains. It is an explosive breeder, laying eggs in temporary pools. The tadpoles exhibit schooling behavior. Several unusual features of the chondrocranium of *Rhinophrynus* are shared with Pipidae (Swart and De Sá 1999). For example, the lower jaw develops earlier in these two clades than in other frogs, and permits switching from a filter feeding to a macrophagous feeding tadpole. Swart and De Sá (1999) reported conspecific larvae in guts of some tadpoles. Many characters of *Rhinophrynus* convergently evolved in a distantly related frog family, Nasikabatrachidae.

Classification, distribution, and conservation 1 species, *Rhinophrynus dorsalis*. It inhabits extreme southern Texas to Costa Rica (**Figure 3.27C**). It is not listed as an extinction risk by the IUCN.

Systematics references Fouquette (1969).

Pipidae • African Clawed Frogs and Suriname Toads Pipids are unique among frogs in lacking tongues. *Xenopus* and some species of *Pipa* are also unusual in having nonpedicellate teeth on the maxillae and premaxillae. The size range of pipids is 40–170 mm SVL. *Xenopus* (Figure 3.27B) is one of the most widely used animals in experimental and developmental biology (Tinsley and Kobel 1996). Most species of *Xenopus* are **polyploids**, with some species having 4 sets of chromosomes (tetraploids) and others up to 12 sets (dodecaploids) (Evans 2003). Pipids also have an extensive fossil record (e.g., Báez 1996; Trueb and Báez 2006).

Xenopus deposit eggs in water and the tadpoles are filter feeders, whereas tadpoles of *Hymenochirus* (and possibly *Pseudhymenochirus*) are carnivorous. *Hymenochirus* tadpoles actively pursue prey using visual orientation and suction feeding and are therefore convergent functionally and behaviorally with teleost fishes (Deban and Olson 2002). Species of *Pipa*, *Hymenochirus*, and *Pseudhymenochirus* undergo an elaborate and lengthy courtship ritual in which amplectic pairs swim in vertical loops. (A) Rhinophrynidae



The subsequent reproductive behavior of *Pipa* is truly bizarre. At the top of a loop, when the frogs' ventral sides are up and the female is above the male, the female releases eggs that fall onto the male's ventral surface. The male releases sperm that fertilize the eggs, and at the bottom of the loop, when the frogs' dorsal sides are up and the male is above the female, he presses the fertilized eggs onto her back. The sticky fertilized eggs adhere to the female's back, and each egg becomes enveloped by swelling of the skin (see Figure 8.18C) (Rabb and Rabb 1963a,b). Further development in P. pipa and P. arrabali is direct and takes place within these depressions. After the embryos in these two species fully develop, they burst out of the mother's skin, but in several other species of Pipa, free-swimming tadpoles emerge and complete their development in water.

Some unusual features of pipids are associated with their aquatic existence (Trueb 1996). The bodies are dorsoventrally compressed, and the limbs are splayed laterally. Lateral line systems are present, and the feet are large and fully webbed. Hands bear long fingers and are not webbed except in *Hymenochirus* and *Pseudhymenochirus*. The toes have distinct keratinous, clawlike tips (hence the name clawed frogs). All pipids call underwater and have highly modified ears and laryngeal apparatuses to accommodate the properties of sound production and transduction through water (Yager 1992a,b; Elepfandt 1996). These sounds are not produced by moving air between the lungs and throat as in other frogs. Rather, pipids make a clicking sound using their highly modified hyoid bones. One exception is Pseudhymenochirus which have re-evolved the ability to call using

air movement, yet they retain the ancestral hyoid morphology shared with other pipids (Irisarri et al. 2011).

Classification, distribution, and conservation 4 genera (Hymenochirus, Pipa, Pseudhymenochirus, Xenopus), 33 species. Pipa inhabit Panama and tropical South America; all other genera inhabit sub-Saharan Africa (Figure 3.27C). Xenopus is sometimes split into two genera, Xenopus and Silurana, a taxonomy we do not use. The IUCN lists 3 species as Critically Endangered or Endangered and 1 species as Near Threatened.

Systematics references Trueb and Cannatella (1986), Cannatella and Trueb (1988a,b), Evans et al. (2004), Irisarri et al. (2011), Bewick et al. (2012).

Scaphiopodidae • North American Spadefoot Toads

Scaphiopodids are medium-size frogs, between 50 and 80 mm SVL. They are burrowers and have hindfeet with a well-developed keratinous, spadelike metatarsal tubercle, internally supported by a well-ossified prehallux that is used for digging. Scaphiopodids typically remain buried in sand or soil and emerge infrequently except during heavy rains. They dig their own burrows or use burrows of other animals. Species of Scaphiopus (Figure 3.28A) and Spea are explosive breeders that breed in ephemeral ponds. Some species in desert regions have exceedingly rapid development times, with as little as 8 days from egg laying to metamorphosis in Scaphiopus couchii (Newman 1992). A cannibal morph of Spea tadpoles develops in response to environmental conditions (see Section 8.9).



Figure 3.28 Scaphiopodidae. (A) Couch's spadefoot toad, *Scaphiopus couchii*. (B) Distribution. (Photograph courtesy of Todd W. Pierson.)

Classification, distribution, and conservation 2 genera (*Scaphiopus, Spea*), 7 species. They inhabit North America (**Figure 3.28B**). The IUCN lists *Spea hammondii* as Near Threatened.

Systematics references Sage et al. (1983), Wiens and Titus (1991), Henrici (1994), Maglia (1998, 1999), García-París et al. (2003).

Pelodytidae • Parsley Frogs

Pelodytes are small (~50 mm SVL) terrestrial frogs. They are nocturnal except during the breeding season when they become conspicuously diurnal. Eggs are laid in ponds, usually attached to vegetation. Pelodytidae was traditionally included as a subfamily within Pelobatidae. However, the astragalus and calcaneum are entirely fused in *Pelodytes*, unlike any pelobatid species (Ford and Cannatella 1993), and molecular data show that pelodytids and pelobatids do not form an exclusive clade. The frogs' common name derives from their body coloration, which resembles sprigs of parsley (**Figure 3.29A**).

Classification, distribution, and conservation 1 genus, 3 species (*Pelodytes ibericus, P. punctatus, P. caucasicus*). Pelodytids have a disjunct distribution in



Figure 3.29 Pelodytidae. (A) Parsley frog, *Pelodytes punctatus*. (B) Distribution. (Photograph © AGE Fotostock/Alamy.)

western Europe and the Caucasus Mountains of western Asia (**Figure 3.29B**). The IUCN lists *P. caucasicus* as Near Threatened.

Systematics references Henrici (1994), García-París et al. (2003), Veith et al. (2006).

Pelobatidae • Old World Spadefoot Toads

Pelobatids (Figure 3.30A) are medium-size frogs with a maximum length of 100 mm. Their biology is strikingly similar to that of Scaphiopodidae that inhabit North America; indeed, both families were previously considered part of Pelobatidae, but phylogenetic analysis shows that pelobatids are more closely related to Mygophryidae than to Scaphiopodidae (see Figure 3.22). Pelobatids have a well-developed keratinous, spadelike metatarsal tubercle on the hind feet, internally supported by a wellossified prehallux. This structure is used in burrowing. Many pelobatids have glandular, tuberculate skin, including enlarged parotoid glands on the dorsum. Pelobatids are fossorial and emerge infrequently except during heavy rains. They dig their own burrows or use burrows of other animals. Because eggs are laid in temporary water sources,



Figure 3.30 Pelobatidae. (A) The common European spadefoot toad, *Pelobates fuscus.* (B) Distribution. (Photograph © iliuta goean/Shutterstock.)

there has been strong natural selection for rapid development times (approximately 2 weeks) and even cannibalism (see Section 8.9). When disturbed, *Pelobates fuscus* emits a foul odor.

Classification, distribution, and conservation 1 genus (*Pelobates*), 4 species. *Pelobates* inhabit western Eurasia and northwestern Africa (**Figure 3.30B**). Pelobatidae formerly contained genera now placed in Scaphiopodidae. The IUCN lists *P. varaldii* as Endangered and *P. cultripes* as Near Threatened.

Systematics references Henrici (1994), García-París et al. (2003), Veith et al. (2006).

Megophryidae • Asian Toads

Most megophryids inhabit the rainforest floor or stream edges. Like pelobatids, megophryids have very glandular skin, and unusual clusters of granular glands are found in the axillary, pectoral, and femoral regions in both sexes of various species (Inger 1966; Jacobs et al. 1985). The function of these glands is unknown. Megophryids also vary considerably in body size, ranging from 15 to 120 mm SVL.

Megophryids deposit eggs in streams. Larvae vary greatly in morphology and natural history. Many have reduced mouthparts. Tadpoles of Megophrys live in quiet waters of streams, whereas other megophryid larvae live in swifter currents or in the substrate. The entire body of the tadpole is translucent. Leptobrachium boringii is notable for the series of sharp keratinous nuptial spines that line the upper lip of males during the breeding season. Males both construct nests and make advertisement calls underwater to attract females. They violently defend nesting territory from other males using the nuptial spines in combat (Zheng et al. 2011; Hudson and Fu 2013). The spines fall off at the end of the breeding season. Tadpoles of Leptobrachella mjobergi are wormlike with an elongate body and little distinction between the size of the head and body (Haas et al. 2006). This body form is probably a specialization for burrowing in sand or gravel, which is an unusual mode of life for tadpoles.

Classification, distribution, and conservation 11 genera, 187 species. Representative genera include *Leptobrachella*, *Leptobrachium* (**Figure 3.31A**), *Leptolalax, Megophrys, Oreola*-



(B)



Figure 3.31 Megophryidae. (A) Thai spadefoot toad, *Leptobrachium hendricksoni* of the Malay Peninsula. (B) Distribution. (Photograph courtesy of L. Lee Grismer.)

lax, Scutiger, and *Xenophrys.* Asian toads inhabit Bangladesh and northern India to China, Southeast Asia, Philippines, and numerous Indonesian islands (Figure 3.31B). The IUCN lists 17 species as Critically Endangered or Endangered and 40 species as Near Threatened or Vulnerable.

Systematics references Lathrop (1997), Zheng et al. (2004, 2008), Fu et al. (2007), Rao and Wilkinson (2008), Brown et al. (2009), Matsui et al. (2010).

NEOBATRACHIA

Neobatrachia comprises about 96% of all identified frog species, with representatives inhabiting every temperate and tropical continent. Neobatrachians share multiple skeletal synapomorphies (loss of parahyoid bones, fusion of the third distal carpals to other carpals) and limb muscles (separation of the sartorius and semitendinosus muscles of the hindlimbs) (Duellman and Trueb 1986). Most neobatrachians also have axillary amplexus, although numerous counterexamples exist. Molecular phylogenetic analyses support a monophyletic Neobatrachia as well as the monophyly of two subclades—Ranoidea and Hyloidea—that account for a vast majority of neobatrachian diversity. The non-ranoid neobatrachians primarily inhabit sub-Saharan Africa, although the Hyperoliidae have dispersed to Madagascar and surrounding islands.





Figure 3.32 Heleophrynidae. (A) Royal ghost frog, *Heleophryne regis.* (B) Distribution. (Photograph courtesy of Miguel Vences and Frank Glaw.)

Heleophrynidae • Ghost Frogs

Heleophrynids live along torrential mountain streams. They have fully webbed feet and expanded toe discs (**Fig-ure 3.32A**) and range in size from 35 to 65 mm SVL. Some 100–200 eggs are laid under rocks in shallow pools (Branch 1991). Orton's Type 4 tadpoles are unique in having a large suctorial oral disc with many rows of denticles but lacking jaw sheaths (see Figure 3.20). The tadpoles use the suctorial oral disc to cling to rocks in swift currents, and even to climb up wet rock faces; they graze on algae (Wager 1965). Metamorphosis occurs after 1–2 years.

Classification, distribution, and conservation 1 genus (*Heleophryne*), 6 species. *Heleophryne* inhabit high mountains of southern South Africa (**Figure 3.32B**). The IUCN lists *H. rosei* as Critically Endangered and *H. hewitti* as Endangered, both due to habitat loss and urban development.

Systematics references Poynton (1964), Boycott (1988).

Sooglossidae • Seychelles Frogs

Sooglossids are an ancient, species-poor lineage that became isolated on the Seychelles during the breakup of Gondwana in the Cretaceous (see Chapter 5). These small terrestrial frogs (~40 mm SVL) inhabit moss forests. *Sooglossus gardineri* (Figure 3.33A) is one of the smallest frogs, 10–12 mm SVL. Amplexus is inguinal and the eggs are laid terrestrially (Nussbaum 1980). Direct development occurs in *S. gardineri*, but in other species the eggs hatch into nonfeeding tadpoles that are carried on the back of the female.

Classification, distribution, and conservation 2 genera (*Sooglossus, Sechellophryne*), 4 species. They inhabit the Seychelles Islands (**Figure 3.33C**). The IUCN lists all 4 species as Endangered or Critically Endangered.

Systematics references Nussbaum and Wu (2007), Van der Meijden et al. (2007), Taylor et al. (2012).

Nasikabatrachidae • Purple Pig-nosed Frogs

This family of frogs contains only one species (*Nasikaba-trachus sahyadrensis*; **Figure 3.33B**) and was not formally described until 2003 (Biju and Bossyut 2003). It is not only significant to find a new vertebrate lineage that split with its closest living ancestor (Sooglossidae) over 100 mya (Roel-ants et al. 2007), but *Nasikabatrachus* is also an interesting biogeographical history story. Sooglossids and nasikabatrachids are the living ancestors of a lineage that arose in east-ern Gondwana in the Jurassic about 170 mya. As Madagascar, the Seychelles, and India each became isolated during the breakup of Gondwana (see Chapter 5), the ancestor of Sooglossidae was isolated in the Seychelles, while the ancestor of *Nasikabatrachus* remained in India as it collided with Asia. The species inhabits forests in the Western Ghats of India (a biodiversity hotspot for amphibians; see Chapter 5).

(A) Sooglossidae



(B) Nasikabatrachidae



Figure 3.33 Sooglossidae and Nasikabatrachidae. (A) Gardiner's frog, *Sooglossus gardineri* (Sooglossidae). (B) Purple pig-nosed frog, *Nasikabatrachus sahyadrensis* (Nasikabatrachidae). (C) Distribution. (Photographs: A © PhotoAlto/ Alamy; B courtesy of S. D. Biju.)

Nasikabatrachus and Rhinophrynus (Rhinophrynidae) have convergently evolved a remarkably similar morphology and ecology. The body is bloated with a small head with a prominent tip. Like Rhinophrynus, Nasikabatrachus spends a vast majority of its life underground foraging for termites, and is an explosive breeder that emerges only after heavy rains to lay eggs in water (Radhakrishnan et al. 2007; Zachariah et al. 2012). Adults reach about 90 mm SVL.

Classification, distribution, and conservation 1 species, *Nasikabatrachus sahyadrensis.* It inhabits the Western Ghats of India (**Figure 3.33C**). The IUCN lists it as Endangered, due primarily to habitat loss when land is cleared for coffee and spice plantations.

Systematics references Biju and Bossuyt (2003), Radhakrishnan et al. (2007), Roelants et al. (2007), and Zachariah et al. (2012).

Hyloidea

Hyloidea is one of two extremely diverse neobatrachian clades (Ranoidea is the other) and contains about 57% of all named frog species. Many hyloid families are probably well known to readers, including true toads (Bufonidae), dart poison frogs (Dendrobatidae), and Amero-Australian



treefrogs (Hylidae). No morphological synapomorphies define Hyloidea; indeed, an outdated informal definition of Hyloidea is "neobatrachians that are not Ranoidea." However, numerous phylogenetic studies of DNA data support Hyloidea monophyly. As with Ranoidea, determining the phylogenetic interrelationships of hyloid families has proven difficult (note the hyloid polytomy in Figure 3.22).

Myobatrachidae

Myobatrachids vary in size from about 20 mm to more than 110 mm SVL. Digital discs are usually small or absent. Life histories of myobatrachids are varied. Most species are terrestrial, but some are fossorial, and species of *Taudactylus* and *Rheobatrachus* live along or in torrential mountain streams. Males of *Adelotus brevis* are larger than females with more robust heads (nearly half the total body length) with tusklike teeth projecting from their lower jaw. Males use these tusks in combat for access to females. *Arenophryne* (two species) and *Myobatrachus gouldii* (Figure 3.34A) are burrowing species that inhabit arid and semiarid regions of western Australia. *M. gouldii* bears a remarkable resemblance to other termite-eating burrowing ecomorphs (e.g., Rhinophrynidae, Nakisabatrachidae) with a large body, robust limbs, and a small, pointed mouth.

Many myobatrachids deposit eggs in water and have typical aquatic tadpoles. However, eggs may be laid on land and undergo either direct development or have aquatic tadpoles, which may be feeding or nonfeeding. Foam nests are constructed by some limnodynastines. Eggs of *Arenophryne* and *Myobatrachus gouldii* directly develop into froglets in nests dug by the mother (Anstis et al. 2007).

Two unusual forms of egg brooding occur in myobatrachids. Eggs and tadpoles are brooded in a pair of inguinal pouches in males of *Assa darlingtoni* (Ingram et al. 1975). The eggs are laid on the ground and attended by the male. At hatching, the tadpoles wriggle up into the pouches, where development through metamorphosis takes place. Two remarkable frogs in the genus *Rheobatrachus* have unique specializations for brooding their eggs (Tyler 1983). After egg laying and external fertilization, the female par(A) Myobatrachinae





(B) Limnodynastinae

Figure 3.34 Myobatrachidae.

(A) Turtle frog, Myobatrachus gouldii (Myobatrachinae)
(B) Striped marsh frog, Limnodynastes peronii (Limnodynastinae). (C) Distribution.
(Photographs: A, courtesy of Harvey Pough; B, © Doug Steley/Alamy.)



ent swallows the eggs, and development and metamorphosis occur in the stomach. *Rheobatrachus silus* and *R. vitellinus* have not been seen in the field since 1981 and 1985, respectively, and both species have been declared extinct by the *IUCN. Rheobatrachus* and *Taudactylus diurnus* are some of the first known victims of the chytrid fungus epidemic that spread among Australian anurans during the early 1980s (Laurance et al. 1996). Populations of many other myobatrachid frogs have also declined drastically, primarily due to chytrid infection.

Classification, distribution, and conservation 21 extant genera, 133 species. 2 subfamilies: Myobatrachinae (representative genera include *Crinia*, *Geocrinia*, *Myobatrachus*, *Rheobatrachus*, *Taudactylus*, *Uperoleia*); and Limnodynastinae (representative genera include *Heleioporus*, *Limnodynastes* (**Figure 3.34B**), *Mixophyes*, *Neobatrachus*, *Notaden*, *Philoria*, *Pseudophryne*). They inhabit Australia and New Guinea (**Figure 3.34C**). Limnodynastinae is sometimes considered a separate family, Limnodynastidae. The IUCN lists 16 species as Critically Endangered or Endangered and 10 species as Near Threatened or Vulnerable.

Systematics references Schäuble et al. (2000), Read et al. (2001), Morgan et al. (2007), Catullo et al. (2011, 2014).

Calyptocephalellidae • Chilean Toads

Calyptocephalellids have a restricted distribution in the mountains of central Chile. Fossil remains attributed to *Calyptocephalella* exist from Eocene deposits in the same region, suggesting the clade has inhabited the area for at least 45 mya (Gómez et al. 2011). *Calyptocephalella* are very large with significant sexual size dimorphism. Females may grow up to 320 mm and males up to 120 mm SVL. *Telmatobufo* (Figure 3.35A) are smaller frogs that inhabit



(A)



Figure 3.35 Calyptocephalellidae.

(A) Bullock's false toad, *Telma-tobufo bullock*. (B) Distribution. (Photograph © Dant ©Fenolio/ Science Source.) fast-moving streams. Their tadpoles have large oral suckers that allow them to attach firmly to rocks. They are powerful swimmers and can swim upstream if disturbed (Formas 1972).

Classification, distribution, and conservation 2 genera (*Calyptocephalella, Telmatobufo*), 4 species. They inhabit the mountains of central Chile (**Figure 3.35B**). Calyptocephallelids were previously placed in Leptodactylidae *sensu lato*. The IUCN lists 2 species as Critically Endangered or Endangered, and the other 2 species as Vulnerable.

Systematics references Formas et al. (2001), Aguilar and Pacheco (2005), Correa et al. (2006), Aguilar and Valencia (2009).

Eleutherodactylidae • New World Rainfrogs

Eleutherodactylidae is a species-rich family of primarily forest-dwelling frogs with diverse body sizes ranging from 10

(A) Eleutherodactylidae



(C) Brachycephalidae



Figure 3.36 Eleutherodactylidae, Ceuthomantidae, Brachycephalidae. (A) Greenhouse frog, *Eleutherodactylus planirostris* (Eleutherodactylinae). (B) *Ceuthomantis smaragdinus*. Described in 2009, this species has no English common name. (C) The pumpkin toadlet, *Brachycephalus nodoterga*, a recently described species once considered synonymous with *B. epihippium*. (D) Distribution. (Photographs: A, courtesy of Todd W. Pierson; B, courtesy of Bruce Means; C, © Pedro Bernardo/Shutterstock.) to 90 mm SVL (Figure 3.36A). Eggs are direct developing. *Eleutherodactylus coqui, E. jasperi,* and possibly many more species have internal fertilization. *Eleutherodactylus jasperi* is viviparous, with three to five young per brood that are maintained in the fused posterior portions of the oviducts (M. H. Wake 1993); this species has not been seen since 1981 and is probably now extinct. *Eleutherodactylus coqui* is native to Puerto Rico but is a notorious invasive species on many islands, most famously those of Hawaii. Almost nothing is known about the natural history for *Adelophryne* and *Phyzelaphryne*, as most species have a restricted distribution and have rarely been collected.

Classification, distribution, and conservation 4 genera, 207 species. 2 subfamilies: Eleutherodactylinae (*Diasporus, Eleutherodactylus*) and Phyzelaphryninae (*Adelophryne, Phyzelaphryne*). They inhabit central Texas through northern South America and the Caribbean (**Figure 3.36D**). Eleutherodactylids were previously placed in Leptodactylidae



sensu lato. The IUCN lists 118 species (57%) as Critically Endangered or Endangered and 28 species as Near Threatened or Vulnerable.

Systematics references Lynch (1986), Lynch and Duellman (1997), Crawford and Smith (2005), Lehr et al. (2005), Heinicke et al. (2007), Padial et al. (2007, 2008), Hedges et al. (2008), Canedo and Haddad (2012), Fouquet et al. (2012b).

Ceuthomantidae

Ceuthomantids are small (18–32 mm SVL) and are restricted to montane forests and tepuis from elevations of approximately 500 to 1,500 m in and around the Guiana Highlands in South America. Ceuthomantidae was described in 2009 (Heinicke et al. 2009) to accommodate a new species, *Ceuthomantis smaragdinus* (Figure 3.36B). The family includes two other species previously placed in the genus *Pristimantis* (Craugastoridae). A fourth species was described in 2010 (Barrio-Amorós 2010). Almost nothing is known of their life history. Although embryonic development has never been documented, ceuthomantids are probably direct developers like their phylogenetic relatives.

Classification, distribution, and conservation 1 genus (*Ceuthomantis*), 4 species. They inhabit southern and eastern parts of the Guiana Highlands in South America (**Figure 3.36D**). Ceuthomantids were previously placed in Lepto-dactylidae *sensu lato*. The IUCN lists *C. aracamuni* as Near Threatened.

Systematics references Heinicke et al. (2009).

Brachycephalidae

Brachycephalids range in size from 10 mm SVL (*Brachycephalus didactylus*, one of the smallest tetrapods known) to 54 mm SVL (*Ischnocnema guentheri*). Species have reduced digits (2 digits on the hands, 3 or 4 on the feet) and lack a sternum. Osteoderms are present middorsally in *Brachycephalus*. Amplexus is initially inguinal during courtship, later shifting to a more axillary position as eggs are laid (Pombal et al. 1994). Eggs are laid terrestrially, and direct development occurs in *Brachycephalus ephippium* and probably in the other species. After eggs are deposited, females coat them with soil particles, which may serve both as camouflage and to prevent desiccation. At least two species of *Ischnocnema (I. guentheri* and *I. parva*) are direct developmers.

Brachycephalids are diurnal inhabitants of leaf litter of humid forests. *Brachycephalus ephippium, B. nodoterga,* and *B. pitanga* are bright orange (Figure 3.36C). *B. ephippium* and *B. pernix* secrete tetrodotoxin, a potent neurotoxin (Pires et al. 2005). Other species are cryptically colored.

Classification, distribution, and conservation 2 genera (*Brachycephalus, Ischnocnema*), 54 species. They inhabit southeastern Brazil (**Figure 3.36D**). The IUCN lists 3 species as Near Threatened.

Systematics references McDiarmid (1971), Cannatella and Trueb (1988), Clemente-Carvalho et al. (2011), Canedo and Haddad (2012).

Craugastoridae

Craugastorids are extremely diverse in terms of body size (13–105 mm SVL), coloration, and number of species (more than 700). Species may be brightly colored or cryptic (**Figure 3.37A**) and primarily inhabit lowland and montane forest leaf litter, but some are stream dwelling. All species have direct-developing offspring. Most craugastorid diversity is in the genus *Pristimantis*, which has almost 450 species. Three *Pristimantis* species emit a foul-smelling fluid when handled (Means and Savage 2007). Most *Craugastor* are found in leaf litter, but *C. augustus*, which occurs from the southwestern United States to central Mexico, inhabits rocky outcrops and crevices where it is camouflaged by its gray coloration.







Classification, distribution, and conservation 21 genera, 717 species. Representative genera include *Craugastor, Hypodactylus, Oreobates, Phrynopus, Pristimantis, Psychrophrynella,* and *Strabomantis*. Craugastorids inhabit southern Arizona and central Texas south through central South America (**Figure 3.37B**). Our definition of Craugastoridae includes Strabomantidae. Craugastorids were previously placed in Leptodacylidae *sensu lato.* The IUCN lists 175 species as Critically Endangered or Endangered and 134 species as Near Threatened or Vulnerable.

Systematics references Crawford and Smith (2005), Heinicke et al. (2007), Hedges et al. (2008), Canedo and Haddad (2012), Padial et al. (2012), Pinto-Sánchez et al. (2012).

Centrolenidae • Glass Frogs

Most species of centrolenids are recognizable by their transparent ventral skin (**Figure 3.38A**). They also possess a unique medial process on the third metacarpal. The astragalus and calcaneum are completely fused, the terminal phalanges are T-shaped, and expanded toe discs are present. Most centrolenids are small (<30 mm), but some *Centrolene* reach nearly 80 mm.



(B) Allophrynidae



Centrolenids lay small clutches of eggs attached to vegetation or rocks above flowing water. Clutches are attended by the males in many species (e.g., Lynch et al. 1983; Villa 1984). At hatching, the tadpoles drop into the water below and burrow into mud, gravel, or detritus on the bottom of streams. Centrolenid tadpoles living in oxygen-poor substrates have a respiratory specialization for these environments, in that blood circulates close to the surface of the skin. This phenomenon also causes their otherwise unpigmented skin to be bright red (Villa and Valerio 1982). Males of *Centrolene* have a prominent bony process on the humerus that is used in intraspecific aggressive interactions. Centrolenids are most diverse in wet montane forests.

Classification, distribution, and conservation 12 genera, 151 species. 2 subfamilies: Centroleninae (representative genera include *Centrolene, Cochranella, Nymphargus*) and Hyalinobatrachinae (*Celsiella, Hyalinobatrachium*). They inhabit southern Mexico to Bolivia and Argentina, southeastern Brazil, and Paraguay (**Figure 3.38C**). The IUCN lists 21 species as Critically Endangered or Endangered and 38 species as Near Threatened or Vulnerable.

Systematics references Cisneros-Heredia and McDiarmid (2007), Guayasamin et al. (2008, 2009), Castroviejo-Fisher et al. (2014).

Figure 3.38 Centrolenidae and Allophrynidae. (A) Yuruani glass frog, *Hyalinobatrachium iaspidense*. The transparent ventral skin of Centrolenidae leads to their common name of glass frogs. (B) Tukeit Hill frog, *Allophryne ruthveni*. (C) Distribution; orange indicates regions of overlap. (Photographs: A, © Morley Read/Shutterstock; B, © Piotr Naskrecki/Minden Pictures/Corbis.)



Allophrynidae

Allophrynids are small frogs (20–30 mm SVL). The skull is unusual in having a strongly ossified cranial roof but reduced maxillae, pterygoids, squamosals, and palatines, and teeth are absent entirely. Species of *Allophyrne* are arboreal and inhabit open forests, where they are are found in bromeliads. *Allophryne ruthveni* (Figure 3.38B) forms breeding aggregations in trees, after which females deposit fertilized eggs in water.

Classification, **distribution**, **and conservation** 1 genus (*Allophryne*), 3 species. *Allophryne* inhabit the Guayanan region of South America as well as northeastern and western Brazil (**Figure 3.38C**). No allophrynid species are listed by the IUCN as an extinction risk.

(A) Telmatobiidae



(B) Rhinodermatidae



(C) Odontophrynidae



Systematics references Austin et al. (2002), Guayasamin et al. (2009), Castroviejo-Fisher et al. (2012).

Telmatobiidae

Telmatobiids are large (up to 14 cm for Telmatobius coleus), highly aquatic frogs that inhabit high elevations in the Andes Mountains (Figure 3.39A). These frogs live in deep, cold lake waters and eat primarily aquatic arthropods. They have many morphological and physiological specializations for an aquatic existence. Foot webbing is extensive, as it is in most fully aquatic frogs, and baggy dermal flaps similar to those seen in Cryptobranchus salamanders (Cryptobranchidae) increase the surface area for integumentary respiration (see Figure 7.1). As in Cryptobranchus, capillaries penetrate to the epidermis of T. culeus, and the lungs are reduced, and both species use a swaying motion to disrupt the waterskin boundary layer (Hutchison et al. 1976). Reproductive information about telmatobiids is scarce. Telmatobius culeus breeds at the shoreline of shallow water bodies and lavs a clutch of about 500 eggs (Pérez 1996).

Classification, distribution, and conservation 2 genera (*Batrachophrynus, Telmatobius*), 62 species. They inhabit the Andes Mountains of South America (**Figure 3.39D**). Tel-

Figure 3.39 Telmatobiidae, Rhinodermatidae, Odontophrynidae. (A) *Telmatobius dankoi*. Telmatobidae are highly aquatic, inhabiting deep lakes high in the Andes Mountains (B) Darwin's frog, *Rhinoderma darwini* (Rhinodermatidae). (C) Brazilian cerrado toad, *Proceratophrys moratoi* (Odontophyrnidae). (D) Distribution. (Photographs: A, courtesy of Marco Méndez; B, © Danita Delimont/Alamy; C, © Fabio Maffei/Shutterstock.)



matobiids were previously placed in Leptodactylidae *sensu lato*. The IUCN lists 22 species as Critically Endangered or Endangered (35% of telmatobiids) and 15 species as Near Threatened or Vulnerable.

Systematics references Lynch (1978), Aguilar and Pacheco (2005), Córdova et al. (2005), Sinsch et al. (2005), Correa et al. (2006), de la Riva et al. (2010), Sáez et al. (2014).

Rhinodermatidae • Darwin's Frogs

Rhinoderma (mouth-brooding frogs) are small frogs (<33 mm SVL) with a fleshy proboscis at the tip of the rostrum (snout) (**Figure 3.39B**). These frogs inhabit riparian habitats along cold streams and temperate rainforests. Females lay eggs on the land and the male attends to them. After some embryonic development, the male picks up the tadpoles and broods them in his vocal sac (see Figure 8.18D). *Rhinoderma rufum* males brood the tadpoles in the vocal sac for about 14 days and then release them into pools of water, whereas *R. darwinii* broods the tadpoles for their entire development. *Insuetophrynus acarpicus* is larger (~45–55 mm SVL) than *Rhinoderma* and both breeds and lays eggs in water.

Classification, distribution, and conservation 2 genera (*Insuetophrynus, Rhinoderma*), 3 species. They inhabit wet temperate southern beech (*Nothofagus*) forests of southern Argentina and Chile (**Figure 3.39D**). Rhinodermatids were previously placed in Leptodactylidae *sensu lato.* The IUCN lists *Insuetophrynus acarpicus* and *Rhinoderma rufum* as Critically Endangered, although the latter species has not been seen in the wild for more than 30 years. *Rhinoderma darwinii* is listed as Vulnerable. *Rhinoderma* populations have declined largely due to chytrid infection (Soto-Azat et al. 2013) and habitat destruction (Bourke et al. 2012).

Systematics references Cei (1962, 1980), Méndez et al. (2006), Rabanal and Formas (2009), Formas (2013).

Odontophrynidae

Odontophrynids are small to medium size (28–85 mm SVL) and inhabit ponds and streams in the South American Atlantic rainforest, as well as drier cerrado and caatinga habitats of Brazil. *Odontophrynus* resemble *Bufo* (Bufonidae) in having rotund bodies and numerous body tubercles. Some *Proceratophrys* species have hornlike structures that originate from the tissue covering the dorsal side of the eye socket (palpebral region) and the tip of the rostrum. Other species lack these horns or have palpebral tubercles or swellings (**Figure 3.39C**). If disturbed, some species of *Proceratophrys* stretch their legs posteriorly and keep the body extremely rigid. How this behavior functions as an antipredator defense has not been recorded (de Amorim Peixoto et al. 2013).

Life-history data are lacking for most species of odontophryids except *Odontophrynus cordobae* (Grenat et al. 2012). Odontophrynus males call from rocks and vegetation surrounding streams or ponds, and unlike most frogs, the female chooses the partner with which to mate. Amplexus occurs in the water, and females deposit eggs at the bottom of the stream or pond (Grenat et al. 2012). Odontophrynus americanus is tetraploid with both male and female sexes (Beçak et al. 1966). Macrogenioglottus is rarely observed, and little is known about its natural history.

Classification, distribution, and conservation 3 genera (*Macrogenioglottus, Odontophrynus, Proceratophrys*), 48 species. They inhabit southern and eastern South America (**Figure 3.39D**). Odontophrynids were previously placed in Leptodactylidae *sensu lato.* The IUCN lists 1 species (*Proceratophrys moratoi*) as Critically Endangered and 2 species as Near Threatened or Vulnerable.

Systematics references Rosset et al. (2007), Amaro et al. (2009), Caramaschi and Napoli (2012), Dias et al. (2013).

Leptodactylidae

Leptodactylidae sensu stricto (Figure 3.40A) includes insectivorous frogs that are mostly semiterrestrial/aquatic except for *Hydrolaetare*, which is highly aquatic. Leptodactylids vary considerably in body size, ranging from approximately 20 to 185 mm SVL. This group contains the Túngara frog (*Engystomops* [formerly *Physalaemus*] *pustulosus*), a model organism in studying evolutionary trade-offs between mating success and threat from predation. Leptodactylid reproductive behavior and physiology are diverse (Prado et al. 2012). Adults of most *Engystomops*, *Leptodactylus*, and *Pleurodema* species construct aquatic or terrestrial foam nests (see Figure 8.16).

Leptodactylus fallax reproduction is notable (Gibson and Buley 2004). Males call females to their burrows. After constructing a foam nest of fertilized eggs, the female remains in the burrow and aggressively defends the clutch until the end of larval development, while the male defends the entrance to the burrow. Moreover, the female deposits as many as 25,000 unfertilized eggs to feed the tadpoles during the larval period. *Adenomera* construct terrestrial foam nests, and the tadpoles may develop in the nest or go through an aquatic stage (Angulo et al. 2003).

Leptodactylidae *sensu lato* was once a very large family with more than 50 genera and 1,100 species. However, it was long known that this group of primarily Central and South American stream- and litter-dwelling frogs was not monophyletic, but there was insufficient evidence to clarify these phylogenetic relationships. Recent phylogenetic analyses have improved this situation by identifying some major "leptodactylid" clades. Leptodactylidae *sensu lato* has been split into 11 families: Alsodidae, Batrachylidae, Ceratophryidae, Ceuthomantidae, Craugastoridae, Cycloramphidae, Eleutherodactylidae, Hylodidae, Odontophrynidae, Telmatobiidae and Leptodactylidae *sensu stricto*, the latter **Figure 3.40 Leptodactylidae.** (A) Bolivian white-lipped frog, *Leptodactylus bolivianus*. (B) Distribution. (Photograph courtesy of Todd W. Pierson.)



restricted to only 14 genera. The phylogenetic relationships among these former "leptodactylid" clades remain largely unknown, and further taxonomic changes are expected.

Classification, distribution, and conservation 14 genera, 200 species. Representative genera include Adenomera, Engystomops, Leptodactylus, Paratelmatobius, Physalaemus, Pleurodema, and Pseudopaludicola. Leptodactylids are found from extreme southern Texas through southern South America (Figure 3.40B). The IUCN lists 5 species as Critically Endangered or Endangered and 8 species as Near Threatened or Vulnerable.

Systematics references Heyer (1974, 1978), Angulo et al. (2003), Correa et al. (2006), Hedges and Heinicke (2007), Lourenço et al. (2008), Ponssa et al. (2010), Faivovich et al. (2012), Fouquet et al. (2013).

Hylodidae

Hylodids are typically small (<35 mm SVL) diurnal frogs that are sometimes called torrent frogs for their preferred stream and streamside habitat (Figure 3.41A). During courtship season, *Hylodes dactylocinus* males battle over territory, beginning with a series of visual displays including a foot-flagging behavior in which the males laterally extend their legs and toes away from their body (Narvaes and Rodrigues 2005) (a similar behavior to that seen in the distantly related Micrixalidae; see Figure 13.21). Females deposit eggs in water, where tadpoles remain until metamorphosis.

Classification, distribution, and conservation 3 genera (*Crossodactylus, Hylodes, Megalosia*), 42 species. They inhabit southwestern Brazil to northern Argentina (**Figure 3.41B**). Hylodids were previously placed in Leptodactylidae *sensu lato.* The IUCN lists 1 species (*Crossodactylus schmidti*) as Near Threatened; however, the conservation status of Hylodidae is no doubt similar to that of Cycloramphidae, another inhabitant of South American Atlantic rainforest.



Systematics references Pavan et al. (2001), Nuin and do Val (2005), Grant et al. (2006).

Hylidae • American and Australian Treefrogs

Hylids are diverse in terms of both species and morphology. They range from <30 to 150 mm SVL. Most are arboreal with well-developed toe discs and claw-shaped terminal phalanges. However, some are fossorial (Cyclorana and some Smilisca), and others live in tree holes (Triprion). Like some other fossorial frogs, fossorial hylids often live in rather arid areas and form cocoons to protect themselves from desiccation during unfavorable periods. Hylids in dry environments often have unusual modifications of skull morphology, including extensive co-ossification and casques. Most hylids are strong jumpers, but members of the Phyllomedusinae are primarily arboreal walkers and make slow, deliberate movements. Adult Pseudis are aquatic frogs that inhabit ponds, lakes, ditches, and other still or slow-moving water. Their feet have elongate ossified intercalary elements that enhance the expansive webbing. Lysapsus often live in floating vegetation in a manner similar to hylids of the genus Acris in North America.

Although most hylids do not have extensive macroscopic glands, many phyllomedusines have conspicuous glands on the dorsum. These produce peptides that, in one instance, are used in hunting magic rituals by indigenous Figure 3.41 Hylodidae. (A) Brazilian torrent frog, *Hylodes asper.* (B) Distribution. (Photograph courtesy of Mauro Teixeira Junior.)





(A) Hylinae



Figure 3.42 Hylidae. (A) North American barking treefrog, *Hyla gratiosa* (Hylinae). (B) Waxy monkey treefrog of Central America, *Phyllomedusa sauvagii* (Phyllomedusinae). (C) Australian orange-thighed treefrog, *Litoria xanthomera* (Pelodryadinae). (Photographs: A, courtesy of Todd W. Pierson; B, courtesy of David McIntyre; C, courtesy of Stephen Zozaya.)

(B)



(B) Phyllomedusinae

populations in South America (Daly et al. 1992). Hunters introduce secretions of *Phyllomedusa bicolor* into burns in their skin, thereby inducing violent physiological reactions, including vomiting, incontinence, and rapid heart rate, followed by euphoria, which is thought to improve the hunters' skills.

Hylid reproductive modes are diverse. Amplexus is axillary. Most hylines lay eggs in water and have aquaticfeeding tadpoles. Phyllomedusines are arboreal except for one species (*Phyllomedusa atelopoides*) and lay their eggs on vegetation over pools or streams. The tadpoles complete their development in water after hatching. *Pseudus* lay their eggs among aquatic vegetation in shallow water or floating vegetation. The tadpoles of *Pseudis paradoxa* are the largest of any frog, reaching almost 22 cm SVL, yet they metamorphose into relatively small juvenile froglets (5 cm) (Emerson 1988).

Classification, distribution, and conservation 50 genera, 947 species. 3 subfamilies: Hylinae (**Figure 3.42A**; representative genera include *Acris, Duellmanohyla, Hyla, Hyloscirtus, Hypsiboas, Plectrohyla, Pseudacris, Pseudis, Scinax, Smilisca*) inhabit North and South America, West Indies, extreme northern Africa, and temperate Eurasia to Japan; Phyllomedusinae (**Figure 3.42B**; genera are *Agalychnis, Cruziohyla, Pachymedusa, Phasmahyla, Phrynomedusa, Phyllomedusa*) inhabit tropical Mexico to Argentina; Pelodryadinae (**Figure 3.42C**; genera are *Cyclorana, Litoria, Nycimystes*) inhabit the Australo-Papuan region. The IUCN lists 128 species as Critically Endangered or Endangered and 54 species as Near Threatened or Vulnerable. *Pseudis* was previously recognized as its own family, Pseudidae.

Systematics references Gallardo (1961), Duellman (2001), Faivovich et al. (2005, 2010), Salducci et al. (2005),

Wiens et al. (2005, 2010a), Garda and Cannatella (2007), Hua et al. (2009).

Hemiphractidae • Horned and Marsupial Frogs

Hemiphractids range in body size from less than 20 mm to 80 mm SVL. *Hemiphractus* species are terrestrial and have robust bodies and heads with prominent, sharp projections on the rostrum, above the eyes, at the corners of the mouth, and on the back and sides (Figure 3.43A). Other hemiphractids have a more typical frog appearance. Hemiphractids are notable for reproductive specializations associated with transporting tadpoles (Del Pino 1989; Weygoldt et al. 1991). Depending on the species, the eggs, tadpoles, or young frogs are carried on the backs of the females, either exposed on the dorsum (*Cryptobatrachus, Hemiphractus, Stefania*) or in a special dorsal pouch (*Flectonotus, Fritziana, Gastrotheca*) that may be relatively open or completely closed except for a small aperture (hence the name marsupial frogs).

Classification, distribution, and conservation 6 genera (*Cryptobatrachus, Flectonotus, Fritziana, Gastrotheca, Hemiphractus, Stefania*), 102 species. They inhabit Central America to the Andes region of South America, as well as the islands of Trinidad and Tobago (**Figure 3.43B**). Hemiphractids were previously placed in Hylidae. The IUCN lists 20 species as Critically Endangered or Endangered and 16 species as Near Threatened or Vulnerable.

Systematics references Duellman and Fritts (1972), Mendelson et al. (2000), Sheil et al. (2001), Faivovich et al. (2005), Wiens et al. (2007), Schmid et al. (2013), Blackburn and Duellman (2013).



Figure 3.43 Hemiphractidae. (A) Horned frog, *Hemiphractus* sp., in Amazonian rain forest, Peru. (B) Distribution. (Photograph © Michael and Patricia Fogden/Corbis.)



(A)

(A) Colostethinae







Figure 3.44 Dendrobatidae.

(A) Ruby poison frog, Ameerega paroula (Colostethinae). (B)
Mimic poison frog, Ranitomeya imitator (Dendrobatinae). (C)
Distribution. (Photographs: A,
© Morley Read/Shutterstock; B,
© Dirk Ercken/Shutterstock.)



Dendrobatidae • Dart Poison Frogs

Dendrobatids are generally small frogs (<50 mm SVL) and are recognizable by a pair of dermal scutes on the dorsal surfaces of the fingers—a character otherwise observed only in a few leptodactylids and myobatrachids. Dendrobatids are famous in the popular literature as dart poison frogs (or simply poison frogs) because several South American indigenous cultures use the toxic skin secretions of three species of *Phyllobates* to poison blowgun darts. Indeed, *Phyllobates* skin contains some of the most potent naturally occurring alkaloids known, which act irreversibly on synapses and neuromuscular junctions.

The alkaloids of dendrobatids are lipophilic batrachotoxins, as contrasted with water-soluble alkaloids such as tetrodotoxin found in the skin of some other amphibians (e.g., some salamandrids). Dendrobatids that harbor these compounds have bright aposematic (warning) colors (**Figure 3.44A,B**), and mimicry systems involving several species of toxic dendrobatids have evolved in Amazonia (Symula et al. 2001; dendrobatid skin toxins are reviewed by Daly et al. 1987, Daly 1995, and Saporito et al. 2012).

Skin alkaloids and aposematic coloration are derived characters in dendrobatids, and some species of Aromobates

and *Colostethus* are nontoxic and cryptically colored. Toxin and aposomatic colors are present in *Epipedobates, Minyobates, Phyllobates,* and *Dendrobates.* Experimental and circumstantial evidence indicates that the sources of dendrobatid alkaloids are from a diet of beetles, ants, and perhaps millipedes (see Saporito et al. 2012 for a review).

Amplexus is cephalic where known, but many species do not amplex. All dendrobatids except *Aromobates* are diurnal and terrestrial, and small clutches of eggs are deposited in terrestrial or arboreal locations and attended by a parent. The tadpoles adhere to the backs of the parent and are carried for a variable period of time before being deposited in water. Females of some species of *Dendrobates* deposit their tadpoles individually in arboreal sites, returning occasionally to deposit unfertilized eggs, which serve as a food source for the tadpoles. Complex parental care occurs in dendrobatids, and it may involve either parent or both, depending on the species.

One remarkable species, *Aromobates nocturnus*, differs from other frogs in this family. It is 25–40% larger than any other dendrobatid (about 60 mm SVL), nocturnal, fully aquatic, and probably lays eggs in streams. *Aromobates* is not highly toxic but emits a foul odor that gives this genus its name.

Classification, distribution, and conservation 18 genera, 299 species. 4 subfamilies: Aromobatinae (Allobates, Anomaloglossus, Aromobates, Mannophryne, Rheobates), Colostethinae (Ameerega, Colostethus, Epipedobates, Silverstoneia), Dendrobatinae (Adelphobates, Andinobates, Dendrobates, Excidobates, Minyobates, Oophaga, Phyllobates, Ranitomeya), and Hyloxalinae (Hyloxalus). They inhabit an area from coastal Nicaragua to the Amazon basin of northwest South America in the Amazon basin (**Figure 3.44C**).

Systematics references Santos et al. (2003), Vences et al. (2003), Grant et al. (2006), Verdade and Rodrigues (2007), Manzanilla et al. (2009), Santos et al. (2009), Santos and Cannatella (2011), Barrio-Amorós and Santos (2012).

Cycloramphidae

Cycloramphids are relatively large frogs that inhabit the Atlantic rainforest in Brazil and have semiterrestrial or terrestrial tadpoles. *Cycloramphus* achieve an adult body size of approximately 55 mm SVL, and species have a distinct aquatic or terrestrial ecomorph (Brasiliero et al. 2007). Aquatic species inhabit stream splash zones and have dorsally compressed bodies and webbed feet. These species lay eggs under rocks, and after hatching, the tadpoles forage on the banks of the stream. Species that inhabit the forest litter have relatively shorter legs and no webbing on their feet (**Figure 3.45A**). They lay eggs in moist terrestrial areas, and tadpoles feed only on yolk. Males of cycloramphid species have glands in their inguinal region that secrete a mucuslike fluid with no known function (Gonçalves and de Brito-Gitirana 2008).



Figure 3.45 Cycloramphidae. (A) Large-eared rock frog, *Thoropa megatympanum*. (B) Distribution. (Photograph courtesy of Mauro Teixeira Junior.)

Classification, distribution, and conservation 2 genera (*Cycloramphus, Thoropa*), 34 species. They inhabit southeastern Brazil (**Figure 3.45B**). Cycloramphids were previously placed in Leptodactylidae *sensu lato.* The IUCN lists 2 species as Critically Endangered or Endangered and 5 species as Near Threatened or Vulnerable. This is almost certainly an underestimate as data are not available for most species. Cycloramphid populations are expected to decline further due to logging of the Brazilian Atlantic rainforest (Myers et al. 2000).

Systematics references Maxon et al. (1981), Heyer (1983), Heyer and Maxon (1983), Noleto et al. (2011).

Ceratobatrachidae

Ceratobatrachids are generally small to medium-size frogs (25–60 mm SVL), although *Discodeles guppyi* may grow to about 165 mm SVL. All species are direct developing. The genus *Platymantis* forms the bulk of the ceratobatrachid species diversity (72 of 87 described species; **Figure 3.46A**), and new species are continually being described. Although a majority of *Platymantis* diversity is in the Philippines and the Solomon-Bismarck-Admiralty archipelago off the coast of New Guinea, two species also inhabit the remote oce-







Figure 3.46 Ceratobatrachidae. (A) Schmidt's wrinkled ground frog, *Platymantis schmidti*. (B) Distribution. (Photograph © Daniel L. Geiger/SNAP/Alamy.)

anic islands of Fiji—a remarkable distribution given that amphibians are generally poor overwater dispersers (see Chapter 5). *Platymantis* contains both terrestrial and arboreal species, and this is reflected in their overall morphology (e.g., arboreal species have expanded toe pads). *Ceratobatrachus guentheri* is a camouflaged, terrestrial ambush predator with fanglike bony projections on its mandible. It eats other frogs and small reptiles, in addition to insects and arachnids.

Classification, distribution, and conservation 6 genera, 87 species. Genera are *Batrachylodes, Ceratobatrachus, Discodeles, Palmatorappia, Platymantis,* and Southeast Asian species formerly of the genus *Ingerana*. They inhabit the Philippines, Malaysian and Indonesian portions of the island of Borneo, New Guinea (and nearby islands), eastern Indonesia, the Solomon Islands, and Fiji (**Figure 3.46B**). A new phylogeny-based classification for the family proposes the recognition of only 3 genera (Brown et al. 2015). Ceratobatrachids were previously placed in Ranidae *sensu lato*. The IUCN lists 7 species of *Platymantis* as Critically Endangered or Endangered and 12 species as Near Threatened or Vulnerable.

Systematics references Köhler et al. (2008), Wiens et al. (2009), Brown et al. (2015).

Bufonidae • True Toads and Harlequin Frogs

Bufonids represent the extremes of anuran body size, ranging from 20 mm to 23 cm SVL. Most species are terrestrial, but some (e.g., Ansonia from Southeast Asia) are semiaquatic stream frogs, and a few (Pedostibes from Southeast Asia) are arboreal. Bufonids are unique among anurans in having a Bidder's organ, a rudimentary ovary that develops on the anterior end of the larval testes of males (Roessler et al. 1990). Experimental evidence in Rhinella arenarum indicates that the Bidder's organ produces estrogen, and it may have additional functions (Scaia et al. 2011, 2013). The persistence of Bidder's organs in many adult bufonids is considered a paedomorphic trait. Bufonid skulls are instantly recognizable because teeth are entirely absent, a rare condition among frogs. The skulls are also heavily ossified and usually co-ossified with the overlying skin. Da Silva and Mendelson (1999) reported the presence of unusual inguinal fat bodies in Bufonidae, which have been independently lost several times; their function is unknown.

Prominent cutaneous glands, such as the conspicuous parotoid glands located on the posterodorsal portion of the head, are characteristic of many species of bufonids (**Figure 3.47A**). Species of the diverse Neotropical genus *Atelopus* have bright aposematic colors (**Figure 3.47B**) and potent skin toxins. The skin toxins of most bufonids are primarily peptides, but tetrodotoxin, a water-soluble alkaloid, is found in some species of *Atelopus*. Lipid-soluble alkaloids similar to those of dendrobatids have been found in the bufonid *Melanophryniscus*.

, Reproductive modes in bufonids span the range observed within frogs as a whole. Among three African bufonid genera (Altiphrynoides, Nectophrynoides, and Nimbaphrynoides), reproductive modes vary from oviparity with free-swimming larvae to direct terrestrial development and viviparity (M. H. Wake 1993; Graybeal and Cannatella 1995). Most bufonids deposit strings of eggs in ponds or streams that hatch into Type 4 larvae. However, some bufonids, such as the Philippine Pelophryne, deposit eggs in leaf axils several meters aboveground. The tadpoles of *Mertensophryne* have an unusual fleshy crown completely encircling the eyes and nostrils (Channing 1978; Grandison 1980). The crown probably facilitates respiration at the surface film in their arboreal sites. The tadpoles of Ansonia, Atelopus, and Rhinella veraguensis occur in torrential streams and have well-developed suckers on the belly, which they use to attach themselves to the substrate. This modification has evolved convergently in other tadpoles occurring in torrents, for example, in the ranid Staurois.

Taxonomy of the genus *Bufo* is contentious. In their large-scale phylogenetic analysis of amphibians, Frost et al. (2006) partitioned the large paraphyletic genus *Bufo* into 14 new or resurrected genera. For example, the name *Bufo* was restricted to only three species (including *Bufo bufo*), the North American *Bufo* were renamed *Anaxyrus*, and the clade containing the cane toad was named *Chaunus*, later synonymized with *Rhinella* (Chaparro et al. 2007). Debates on these taxonomic changes continue to this day. Pauly et al. (2009) argued that these changes were not warranted because of methodological flaws in Frost et al. (2006), and cautioned against the needlessly disruptive consequences of

TABLE 3.2 Currently recognized genera formerly placed in the genus *Bufo*

Genus	Geographic Distribution
Amietophrynus	Sub-Saharan Africa
Anaxyrus	North America, from Alaska and southern Canada to the highlands of Mexico
Bufo	Eurasia and Japan, south to the Middle East and North Africa
Capensibufo	Southern and western South Africa
Mertensophryne	Central and East Africa
Incilius	Gulf Coast of North America to western Ecuador
Rhinella	Lower Rio Grande Valley of North America to southern South America ^a
Vandijkophrynus	Southern Africa

After Frost et al. 2006 and Frost 2014.

^aThe cane toad (*Rhinella marina*) has been introduced to the Antilles, Hawaii, Fiji, Philippines, Taiwan, Ryukyu Islands (Japan), New Guinea, Australia, and many Pacific islands.



taxonomic changes to this iconic genus of toads (see Frost et al. 2009 for a response).

This debate highlights the different philosophies regarding higher-level classification in practice. On the one hand, expanding the number of families, genera, and so on results in a taxonomy that reflects the evolutionary history of the group with more detail. For example, recognizing a larger Bufo genus masks the fact that Anaxyrus form a clade separate from *Rhinella*. On the other hand, other researchers emphasize that classification should be conservative and should involve the fewest genus-species couplet changes possible (see also the discussion of Anolis in Chapter 4). In this textbook, we adopt a modified taxonomy of Frost et al. (2006) because it is becoming increasingly used in the literature regardless of this debate. Table 3.2 compares the old and new taxonomies. We emphasize that a resolution of this taxonomic debate awaits additional phylogenetic data and that Bufo taxonomy will likely remain in flux for some years.

Classification, distribution, and conservation 47 genera, 590 species. Representative genera include *Anaxyrus, Ansonia, Atelopus, Bufo, Dendrophryniscus, Melanophryniscus, Nectophrynoides, Oreophrynella, Peltophryne, Rhamphophryne,* and *Rhinella.* The distribution of bufonids is cosmopolitan in temperate and tropical regions except the Australo-Papuan region, Madagascar, and oceanic islands (see Figure 3.47). The IUCN lists 162 species as Critically Endangered or Endangered, 80 species as Near Threatened or Vulnerable, and 8 species as recently extinct.

Systematics references Blair (1972), Pauly et al. (2004, 2009), Pramuk (2006), Pramuk et al. (2008), Van Bocxlaer et al. (2009, 2010), Dubois and Bour (2010), Lötters et al. (2010), Fontenot et al. (2011).

Alsodidae

Alsodids range in size from about 25 to 70 mm SVL and are restricted to forests and some arid regions of Patagonia and the Andes of South America (**Figure 3.48A**). The larvae of *Alsodes gargola* inhabit slow-moving streams and consume

(A) Alsodidae



(B) Batrachylidae





Figure 3.48 Alsodidae and Batrachylidae. (A) Alsodes igneus (Alsodidae), endemic to the southern beech (Nothofagus) forests of southern Chile. (B) Emerald forest frog, Hylorina sylvatica (Batrachylidae), a treefrog of southern Chile. (C) Distribution. (Photographs: A, © Danté Fenolio/ Science Source; B, © Danita Delimont/Alamy.

primarily algae and plant material (Baffico and Úbeda 2006). They have a prolonged larval period that may exceed 2 years and can overwinter in ice-covered water (Logares and Úbeda 2004).

Classification, distribution, and conservation 2 genera (*Alsodes, Eupsophus*), 29 species. They inhabit eastern and central South America (**Figure 3.48C**). Alsodids were previously placed in Leptodactylidae *sensu lato*. The IUCN lists 7 species as Critically Endangered or Endangered and 4 species as Near Threatened or Vulnerable. Some of the reduction in alsodid populations is due to the introduction of non-native salmonid fish that consume the tadpoles (Pascual et al. 2002).

Systematics references Lynch (1978), Blotto et al. (2013).

Batrachylidae

Batrachylids are medium-size frogs (~50–60 mm SVL) that inhabit Patagonia and the Andes slopes of South America (Figure 3.48B). Batrachylids have axillary amplexus. After fertilization, *Chaltenobatrachus grandisonae* females lay eggs in ponds, attaching egg clusters to rocks or branches underwater (Cisternas et al. 2013). *Atelognathus patagonicus* has two types of tadpoles: The aquatic type lives in shallow water at the edges of ponds, typically beneath rocks, and has skin folds that presumably increase cutaneous respiration. The littoral type inhabits deeper portions of ponds and lacks cutaneous folds (Cuello et al. 2006). (*Atelognathus, Batrachyla, Chaltenobatrachus, Hylorina*), 15 species. They inhabit southern Chile and southwestern Argentina (**Figure 3.48C**). Batrachylids were previously placed in Leptodactylidae *sensu lato*. The IUCN lists 3 species as Endangered and 5 species as Near Threatened or Vulnerable.

Classification, distribution, and conservation 4 genera

Systematics references Cuevas and Formas (2008), Basso et al. (2011).

Ranoidea

Ranoidea is one of two extremely diverse neobatrachian clades (Hyloidea is the other), containing about 37% of all named frog species. Among other families, Ranoidea includes popularly known frogs such as "true frogs" (Ranidae), colorful Madagascan mantellids (Mantellidae), and Asian and African treefrogs, including the "flying frogs" of the genus Rhacophorus (Rhacophoridae). At least one morphological synapomorphy-complete fusion of the epicoracoid cartilages in the pectoral girdle—supports the monophyly of Ranoidea. This morphological character is sometimes described as a firmisternal pectoral girdle, although that category masks the morphological variation seen in some ranoid species. The monophyly of Ranoidea is also supported by molecular phylogenetic data, but determining the phylogenetic interrelationships of ranoid families has proven difficult; note the polytomies in Figure 3.22. Few morphological characters unite ranoid families into larger clades and, as in Hyloidea, even state-of-the-art modern molecular phylogenetics analyses have yet to converge on a strongly supported, fully resolved ranoid phylogeny.

Hyperoliidae • Reed Frogs

Hyperoliids are small to medium-size frogs (15–80 mm SVL), many of which are arboreal, have toe discs, and are brightly colored (Figure 3.49A). However, *Kassina* and a few other species are terrestrial. Amplexus is axillary in most species. Many hyperoliids deposit eggs in ponds, but some attach clutches to vegetation above water. *Afrixalus* lay their eggs on a leaf and then fold the edges of the leaf together, gluing them with oviductal secretions. A few species use tree holes for egg deposition. *Tachycnemis* lay large eggs in soil or depressions near water. After hatching, the fusiform tadpoles wriggle along the surface of the ground into water to complete development (Kaminsky et al. 1999).

Afrixalus fomasini is the only terrestrial frog definitely known to prey on the egg clutches of other anuran species, although this behavior has also been reported for aquatic



Figure 3.49 Hyperoliidae. (A) Golden-eyed reed frog, *Hyperolius ocellatus*. (B) Distribution. (Photograph courtesy of Daniel M. Portik.)

pipids (Drewes and Altig 1996). *Phlyctimantis boulengeri* has an interesting defensive behavior in which it hides its head between its forelimbs, raises its rump to expose bright red on its hindlimbs, and exudes a viscous secretion onto its dorsum (Rödel and Ernst 2001).

Classification, distribution, and conservation 18 genera, 223 species. Representative genera include *Afrixalus, Heterixalus, Hyperolius, Kassina, Phlyctimantis,* and *Tachycnemis.* They inhabit sub-Saharan Africa, Madagascar, and the Seychelles (**Figure 3.49B**). The IUCN lists 21 species as Critically Endangered or Endangered and 34 species as Near Threatened or Vulnerable.

Systematics references Drewes (1984), Wieczorek et al. (2000), Vences et al. (2003), Rödel et al. (2009), Veith et al. (2009), Conradie et al. (2012).

Arthroleptidae • Squeaker Frogs

Arthroleptids are leaf-litter frogs of African rainforests (**Figure 3.50A**). They are typically small (<50 mm SVL) with the exception of *Leptopelis palmatus* (>80 mm SVL). Males of most *Arthroleptis* and *Cardioglossa* species are notable for their elongate third fingers, sometimes approaching 40% of SVL, although this trait has been secondarily lost in some species (Blackburn 2009). The function of the long fingers is unknown, but they are almost certainly involved with some aspect of reproduction. Although most arthroleptids are insectivores, *Leptopelis brevirostris* eats mainly snails.

During the breeding season, small clutches of large eggs are laid in leaf litter or in burrows in the ground (Branch 1991; Kaminsky et al. 1999). Eggs of *Arthroleptis* develop directly into froglets whereas all other arthroleptid species have free-swimming tadpoles. *Trichobatrachus robustus*, commonly called the hairy frog, lays eggs in streams. During the breeding season, males develop long, hairlike, highly vascularized projections on the posterior flanks and thighs, giving them a shaggy appearance (see Figure 7.2A). Males sit on their clutches of eggs, and the hairs are thought to aid in cutaneous respiration or in aeration of the eggs. *Leptopelis brevirostris* may undergo direct development (Schiøtz 1999).

Astylosternus, Scotobleps, and Trichobatrachus possess a sharp keratinous claw embedded in the skin of two or more toes on the hindlimb. These claws are used for defense—if the frog is picked up, the claws break through the skin and the frog rakes the claws against the predator, sometimes causing bleeding gashes (Blackburn et al. 2008).

Classification, distribution, and conservation 8 genera, 148 species. Genera are *Arthroleptis, Astylosternus, Cardioglossa, Leptodactylodon, Leptopelis, Nyctibates, Scotobleps,* and *Trichobatrachus.* They inhabit sub-Saharan Africa (Figure 3.50B). The IUCN lists 29 species as Critically Endangered or Endangered and 26 species as Near Threatened or Vulnerable.



Figure 3.50 Arthroleptidae. (A) Victoria forest treefrog, *Leptopelis boulengeri*. (B) Distribution. (Photograph courtesy of Daniel M. Portik.)

Systematics references Poynton and Broadley (1985), Blackburn (2008), Zimkus and Blackburn (2008, 2009).

Hemisotidae • Shovel-Nosed Frogs

Hemisus species are burrowers ranging in size from approximately 20 to 75 mm SVL that inhabit savanna regions of sub-Saharan Africa. They resemble other burrowing frogs such as Nasikabatrachidae and Rhinophrynidae, having small, pointed heads posteriorly delimited by a transverse skin fold (**Figure 3.51A**). Hemisotids use their snout to dig headfirst into soil rather than digging hindfirst with the hindlimbs as seen in all other burrowing frogs (Emerson 1976). Shared derived characters of Hemisotidae include the absence of a sternum (also observed in Rhinophrynidae and Brachycephalidae) and a skull highly modified for headfirst burrowing. *Hemisus marmoratus* females lay eggs in terrestrial breeding chambers. The female attends the eggs until hatching, after which she assists the tadpoles to



Figure 3.51 Hemisotidae. (A) Pig-nosed frog, *Hemisus marmoratus*. The snout is used for burrowing. (B) Distribution. (Photograph courtesy of Daniel M. Portik.)

exit the chamber, sometimes carrying tadpoles on her back (Kaminsky et al. 1999).

Classification, distribution, and conservation 1 genus (*Hemisus*), 9 species. They inhabit savanna regions of sub-Saharan Africa (**Figure 3.51B**). The IUCN lists 1 species (*H. guttatus*) as Vulnerable.

Systematics references Laurent (1972).

Brevicipitidae • Rainfrogs

Brevicipitids resemble inflated bags, with short limbs and no distinction between head and body (**Figure 3.52A**). Species range in size from about 30 to 50 mm SVL. All species are endemic to Africa and are restricted to high-elevation montane forests. All genera are fossorial, with the exception of *Callulina*, which are partially arboreal. When disturbed, brevicipitids inflate their bodies and release copi-



Figure 3.52 Brevicipitidae. (A) Krefft's secret frog, *Callulina kreffti*. (B) Distribution. (Photograph courtesy of Stephen Zozaya.)

ous amounts of defensive chemicals that coat their dorsum. Some *Callulina* also have massively expanded defensive glands on the limbs and feet.

Brevicipitids are similar to other rotund burrowing frogs such as pelobatids, scaphiopodids, and *Notaden* (Myobatrachidae) in that they live primarily underground and emerge after heavy rains to breed. In the genus *Breviceps*, the bodies are so rotund and the limbs so short that the male cannot grasp the female during amplexus. Instead, he uses secretions of mucus glands on his ventral surface to glue himself to the dorsum of the female. Amplectant pairs of *Breviceps* construct underground nest chambers into which eggs are laid. In some cases, the female covers the fertile egg mass with a layer of infertile egg capsules that help protect the eggs from desiccation. Females of *Probreviceps macrodactylus* guard their egg masses until hatching (Müller et al. 2007).

Classification, distribution, and conservation 5 genera, 34 species. Genera are *Balebreviceps, Breviceps, Callulina, Probreviceps,* and *Spelaeophryne*. They inhabit eastern and southern Africa (**Figure 3.52B**). Brevicipitids were previously placed in Microhylidae *sensu lato.* The IUCN lists 5 species as Critically Endangered or Endangered and 7 species as Near Threatened or Vulnerable.

Systematics references Loader et al. (2004, 2006, 2010, 2014), De Sá et al. (2012).

Microhylidae • Narrow-Mouthed Frogs

Microhylidae is an extremely diverse family. Some species are relatively small, reaching only 10–15 mm SVL (e.g., some species of *Stumpffia* from Madagascar). Others (e.g., males of *Plethodontohyla inguinalis*) may reach 100 mm SVL. Microhylids may be fossorial, terrestrial, or arboreal, and body forms are highly variable. For example, expanded toe discs are present in arboreal species, and fossorial species



often have flattened bodies and pointed snouts. Microhylids live in habitats ranging from arid deserts to extremely wet rainforests.

The life histories of microhylids are extremely varied. Most microhylines and phrynomerines lay eggs in ponds and have free-swimming, feeding tadpoles. Many scaphiophrynines (e.g., Plethodontohyla) lay eggs in tree holes, and males of some, such as species of Plethodontohyla, are known to guard the clutches. Other scaphiophrynines (Paradoxophyla, Scaphiophryne) are explosive breeders that lay eggs in ponds. Direct development occurs in asterophrynines and some microhylines. All New Guinea microhylids are thought to have direct development, and males of two species, Liophryne schlaginhaufeni and Sphenophryne cornuta, transport the eggs and froglets on their backs-the only known cases of male transport of froglets among anurans (Bickford 2002). The tadpole of Otophryne (northern South America) is highly unusual in having a sinistral spiracle at the tip of a long siphon projecting from the body wall. These tadpoles burrow into the substrate at the bottom of streams (Wassersug and Pyburn 1987).

Two species of microhylids (*Chiasmocleis ventrimaculatus* and *Gastrophryne olivacea*) form facultative commensal associations with tarantula spiders, using the same burrows and foraging areas as the spiders (Cocroft and Hambler 1989). The spiders apparently recognize these frogs through chemosensory cues and do not attack them, even though the spiders readily eat other frogs within the foraging territories.

Classification, distribution, and conservation 63 genera, 557 species. Given the diversity of microhylids, 11 subclades are recognized as subfamilies: Asterophryinae (**Figure 3.53A**; representative genera include *Albericus, Austrocha*- perina, Callulops, Cophixalus, Oreophryne, Xenorhina) inhabit southern peninsular Malaysia, Borneo, Indonesia, southern Philippines, Indonesia, New Guinea, and extreme northern Australia; Gastrophryninae (Figure 3.53B; representative genera include Chiasmocleis, Ctenophryne, Elachistocleis, Gastophryne, Hypopachis, Stereocyclops, Syncope) inhabit North and South America; Hoplophryninae (Hoplophryne, Parhoplophryne) inhabit Tanzania; Kalophryninae (Kalophrynus) inhabit southern China to Java, Philippines, and India; Melanobatrachinae (Melanobatrachus) inhabit southern India; Microhylinae (Figure 3.53C; representative genera include Calluella, Kaloula, Microhyla, Ramanella) inhabit East Asia, India, Korea, and Greater Sunda Islands; Otophryninae (*Otophryne, Synapturanus*) inhabit northern South America; Phrynomerinae (*Phrynomantis*) inhabit sub-Saharan Africa; Cophylinae (*Anodonthyla, Cophyla, Madecassophryne, Platypelis, Plethodontohyla, Rhombophryne, Stumpffia*), Dyscophinae (*Dyscophus*), and Scaphiophryninae (*Paradoxophyla, Scaphiophryne*) inhabit Madagascar. Although there is strong phylogenetic support for the monophyly of microhylids, the interrelationships of its subfamilies remains largely unknown. The IUCN lists 32 species as Critically Endangered or Endangered and 48 species as Near Threatened or Vulnerable.



Figure 3.53 Microhylidae. (A) *Paedophryne dekot* (Asterophryinae) from New Guinea. At the size of a dime or even smaller, members of this genus are among the smallest known frogs. (B) The Eastern narrow-mouthed toad, *Gastrophryne carolinensis* (Gastrophryninae) of North America is

fossorial. (C) Taiwan rice frog, *Microhyla hemonsi* (Microhylinae) breeds in temporary ponds, slow streams, and the rice paddies of eastern Asia. (D) Distribution. (Photographs: A, courtesy of Fred Kraus; B, courtesy of Todd W. Pierson; C, courtesy of Kentwood D. Wells.)

Systematics references Parker (1934), Zweifel (1962, 1972, 1986), Grosjean et al. (2007), Lehr and Trueb (2007), Roelants et al. (2007), Van der Meijden et al. (2007), Köhler and Günther (2008), Wollenberg et al. (2008), Kurabayashi et al. (2011), Matsui et al. (2011), de Sá et al. (2012), Blackburn et al. (2013).

Rhacophoridae • African and Asian Treefrogs

Most rhacophorids are arboreal and have enlarged toe discs, often with extensive webbing (**Figure 3.54A,B**). Body sizes vary from about 25 to 100 mm SVL. Rhacophorid and hylid frogs are remarkably similar in morphology and ecology, but these characters convergently evolved in both groups. The "flying frogs" *Rhacophorus helenae* and *R. nigropalmatus* of Southeast Asia use webbing and a flattened body to parachute (see Figure 10.26; Emerson et al. 1999).

The reproductive biology of rhacophorids varies greatly. Some species lay eggs in water and have aquatic tadpoles, whereas others (e.g., *Chiromantis, Polypedates, Rhacophorus*) construct foam nests either in water or on vegetation above water. Some *Chiromantis* species (e.g., *C. petersii, C. rufescens, C. xerampelina*) build their nests on tree branches, and a nest may be communally constructed by a female in conjunction with several males (see Figure 14.24). The foam hardens, thus protecting the eggs from desiccation until hatching, whereupon the larvae drop into the water below. Still other species place their eggs in tree holes and have nonfeeding or feeding tadpoles (Wassersug et al. 1981). Some species of *Philautus* lay small clutches in arboreal sites and have direct development (Alcala and Brown 1982). The Asian rhacophorid *Kurixalus eiffingeri* lays small clutches of eggs in water collected in bamboo stalks; the tadpoles are obligately oophagous (egg-eating), and periodically the female supplies the developing tadpoles with eggs (Kam et al. 1998). Similar behavior is known in *Leptodactylus fallax* (Leptodacylidae) and some dendrobatids.

Classification, distribution, and conservation 19 genera, 374 species. 2 subfamilies: Buergeriinae (*Buergeria*) inhabit Taiwan and Hainan Island (China) to the Ryukyu and main islands of Japan; Rhacophorinae (representative genera include *Chiromantis, Philautus, Polypedates, Pseudophilautus, Raorchestes, Rhacophorus, Theloderma*) inhabit Africa, Madagascar, southern India, Sri Lanka, China and Japan, and the islands of Southeast Asia and the Sunda Shelf (**Figure 3.54C**). The IUCN lists 69 species as Critically Endangered or Endangered, 59 species as Near Threatened or Vulnerable, and 20 species as recently extinct.



Systematics references Liem (1970), Biju et al. (2008), Li et al. (2008, 2009, 2011, 2012, 2013), Yu et al. (2008, 2009, 2010, 2013), Hertwig et al. (2011, 2013).

Mantellidae

Mantellids have undergone an extraordinary radiation in lifestyles and ecomorphology on the island of Madagascar (Bossuyt and Milinkovitch 2000). Mantidactylus (approximately 70 species) have radiated into terrestrial, arboreal, and aquatic niches. Species of Boophis (55 species; Figure 3.55A) inhabit trees and are similar to hylines (Hylidae) of tropical America. Laliostoma (1 species; Figure 3.55B) and Aglyptodactylus (3 species) are semifossorial and terrestrial, respectively. Species of Mantella have evolved bright aposematic colorations and lipophilic skin alkaloids like those of some Neotropical dendrobatid frogs (Figure 3.55C; also see Figure 2.3) (Daly et al. 1996); they are primarily terrestrial (one species is semiarboreal). Body sizes in Mantidactylus range from about 15 to more than 100 mm SVL; most species in the other genera are small to medium size (30-60 mm SVL), although Boophis albilabris and B. opisthodon can reach 85 mm or more SVL (Cadle 1995).

Mantellids are diverse in their reproductive biology. Many *Mantidactylus* lay their eggs on leaves or other vegetation above water and the tadpoles develop in streams or ponds, while others have terrestrial nests and the tadpoles wash into streams to complete development. However, the reproductive biology of many species of *Mantidactylus* is unknown. Several species have direct development of terrestrial or arboreal eggs, and at least one aquatic species deposits eggs on rocks or in rock crevices in streams. Both males and females have been observed guarding clutches in several species. *Aglyptodactylus* and *Laliostoma* are explosive breeders that deposit their eggs in temporary ponds. Most species of *Boophis* attach eggs to vegetation or debris in streams, although a few species breed in ponds; species that breed in fast-moving currents attach eggs to bedrock and the tadpoles often have suctorial oral discs. Most species of *Mantella* deposit eggs in terrestrial nests and the tadpoles are washed into adjacent ponds or streams. However, the semiarboreal species *Mantella laevigata* attaches its eggs singly above pools in tree holes and the tadpoles develop in the collected water.

Unusual mating behavior with minimal contact between partners takes place in *Mantidactylus* and *Mantella* (Blommers-Schlosser 1975). During mating the male places his thighs directly over the head of the female. Sperm are deposited onto the female's back and trickle over the extruded eggs, thus fertilizing them. Males may leave the female before the completion of egg laying. The stimulus that induces egg laying in *Mantidactylus* is unknown but may be mediated through secretions of the femoral glands present on the ventral surface of the thighs in males. The mating posture would bring these glands into direct contact with the head and body of the female.

Classification, distribution, and conservation 12 genera, 206 species. 3 subfamilies: Boophinae (*Boophis*), Laliosto-

(A) Boophinae



(B) Laliostominae



Figure 3.55 Mantellidae.

(A) Forest bright-eyed frog, Boophis erythrodactylus
(Boophinae). (B) Madagascar bullfrog, Laliostoma labrosum
(Laliostominae). (C) Madagascar golden frog, Mantella aurantiaca (Mantellinae). (D)
Distribution. (Photographs courtesy of Miguel Vences and Frank Glaw.)

(C) Mantellinae



(D)



minae (Aglyptodactylus, Laliostoma), and Mantellinae (Blommersia, Boehmantis, Gephyromantis, Guibemantis, Mantella, Mantidactylus, Spinomantis, Tsingymantis, Wakea). They inhabit Madagascar and Mayotte Island (Comoros) (Figure 3.55D). The IUCN lists 22 species as Critically Endangered or Endangered and 35 species as Near Threatened or Vulnerable.

Systematics references Glaw and Vences (2006), Glaw et al. (2006), Raharivololoniaina et al. (2006), Vences et al. (2007), Kurabayashi et al. (2008), Wollenberg et al. (2011), Kaffenberger et al. (2012), Amat et al. (2013).

Ranidae • True Frogs

Ranidae *sensu stricto* (see systematics discussion below) are highly aquatic frogs with powerful hindlimbs and extensive toe webbing (Figure 3.56A,B). They are relatively large (up to 180 mm SVL). Ranids are some of the best known frogs in North America, and the family includes *Rana catesbeiana* (American bullfrog), *R. pipiens* (leopard frog), and *R. sylvatica* (wood frog).

As the generic name suggests, frogs in the Asian genus *Odorrana* emit a foul-smelling, toxic secretion if disturbed. Although most *Odorrana* are highly aquatic, inhabiting streams, one unidentified species of Chinese *Odorrana* has been observed perching on ledges in flooded caves (M. C. Brandley, personal observation). *Odorrana tormota* and *Huia cavitympanum* are unique among frogs in that their tympanic membrane is recessed within an auditory canal (as in mammals) instead of flush with the skin as in most other frogs. Both species can communicate using ultrasonic sound, and the unusual morphology of the tympanic mem-



brane may improve detection of these frequencies (Arch et al. 2008).

Ranidae *sensu lato* was historically a much larger family containing more than 600 species, but it was not defined by any morphological synapomorphies and was widely thought to be polyphyletic. Recent molecular phylogenetic analyses have clarified some relationships, especially recognizing subclades that have been promoted to family status (see Table 3.1). However, the phylogenetic interrelationships among these Ranoidea families are still largely unknown (see Figure 3.22).

As with *Bufo* (Bufonidae), the taxonomy of *Rana* is debated. Most notably for the North American ranid fauna, Frost et al. (2006) proposed using the name *Aquarana* (later synonymized with *Lithobates*) for the clade of *Rana* that included New World species such as *R. catesbeiana* and *R. pipiens*. However, we do not adopt this taxonomy, for the reasons outlined in Pauly et al. (2009).

Classification, distribution, and conservation 14 genera, 365 species. Representative genera include *Amolops, Babina, Huia, Hylarana, Lithobates, Odorrana, Pelophylax, Rana,* and *Staurois.* Ranids have a cosmopolitan distribution except in extreme southern South America and South Africa, Madagascar, West Indies, and most of Australia (**Figure 3.56C**). The IUCN lists 35 species as Critically Endangered or Endangered and 67 species as Near Threatened or Vulnerable.

Systematics references Chen et al. (2005), Hillis and Wilcox (2005), Matsui et al. (2005, 2006), Scott (2005), Van der Meijden et al. (2005), Bossuyt et al. (2006), Cai et al. (2007), Che et al. (2007), Wiens et al. (2009), Stuart et al. (2010), Arifin et al. (2011), Chen et al. (2013).

Ranixalidae • Dancing Frogs

Ranixalids comprise a single genus (*Indirana*) of smallbodied frogs (<40 mm SVL) that inhabit the Western Ghats of India (**Figure 3.57A**). Little is known about their natural history. The tadpoles of *Indirana beddomii* are semiterrestrial and have unusually long tails. Tadpoles that have not yet developed limbs use the tail to propel themselves on land (Veeranagoudar et al. 2009). Neither behavior is known in other frogs with semiterrestrial tadpoles, and it is not

 known whether this behavior is shared by all species. Males have femoral glands, but the function is not known.

Classification, distribution, and conservation 1 genus (*Indirana*), 10 species. They inhabit central and southern India (**Figure 3.57B**). Ranixalids were previously placed in Ranidae *sensu lato.* The IUCN lists 5 species as Critically Endangered or Endangered and 1 species (*Indirana leithii*) as Vulnerable.

Systematics references Vences et al. (2000), Nair et al. (2012a,b).

Pyxicephalidae Box-Headed Frogs and African Bullfrogs

Pyxicephalids include terrestrial, semiarboreal, and aquatic species. Body sizes range from 15 to about 250 mm SVL. Some genera are explosive breeders, while Anhydrophryne and Arthroleptella independently evolved direct development (Van der Meijden et al. 2011). The African bullfrog, Pyxicephalus adspersus (Figure 3.58A), superficially resembles Ceratophrys (Ceratophryidae), and is the best-known pyxicephalid because of its enormous size-up to 25 cm SVL and weighing up to 1 kg. It is a voracious sit-andwait predator with sharp teeth and two prominent bony pseudoteeth, and it will eat any animal that fits into its large mouth, including small mammals, birds, lizards, and snakes. These frogs spend a majority of the year underground encased in a cocoon formed by layers of keratinized skin that retards water loss (see Figure 6.4A; Loveridge and Withers 1981).

Pyxicephalus adspersus is an explosive breeder, and adults emerge during the rainy sason to breed in temporary pools. Males of this species have a unique and fascinating form of parental care. After the tadpoles hatch, the males dig a channel to a larger body of water, thereby allowing the tadpoles to escape the temporary pond into a larger water body (see Chapter 8). *Anhydrophryne* is a direct-developing species that constructs a nest chamber in moist soil or leaf litter. *Pyxicephalus delalandii* is rare in that it has sexually reproducing tetraploid populations. Some species of *Arthro*-





Figure 3.57 Ranixalidae. (A) Amboli leaping frog, *Indirana chiravasi*. (B) Distribution. (Photograph courtesy of S. D. Biju.)

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(A) Pyxicephalidae
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(B) Phrynobatrachidae





Endangered or Endangered and 10 species as Near Threatened or Vulnerable.

Systematics references Bossuyt et al. (2006), Wiens et al. (2009), Van der Meijden et al. (2011), Channing et al. (2013), Wasonga and Channing (2013).

Phrynobatrachidae • Puddle Frogs

Phrynobatrachids are small (12–40 mm SVL), typically brown or drab-colored frogs that occupy a wide variety of habitats, including lowland savannas and rainforests to montane regions in Africa (**Figure 3.58B**). Their common name refers to their habit of breeding in temporary water bodies, including agricultural areas (Zimkus et al. 2010). Females lay large clutches of eggs (up to several thousand) that float at the surface of the water. Exceptions include *Phrynobatrachus guineensis*, which breeds in tree holes, and *P. alticola* and *P. phyllophilus*, which attach their eggs to dead leaves (Rödel and Ernst 2002a,b). Rival males of *P. krefftii* inflate their bright yellow throat sac as an antagonistic display (Hirschman and Hödl 2006).

Classification, distribution, and conservation 1 genus (*Phrynobatrachus*), 88 species. They inhabit sub-Saharan Africa (**Figure 3.58C**). Phrynobatrachids were previously placed in Cycloramphidae *sensu lato* or Ranidae *sensu lato*. The IUCN lists 6 species as Endangered and 11 species as Near Threatened or Vulnerable.

Systematics references Zimkus and Blackburn (2008), Zimkus (2009), Schick et al. (2010), Zimkus and Schick (2010), Zimkus et al. (2010, 2012), Zimkus and Gvozdik (2013).

Ptychadenidae • Grassland Frogs

Ptychadenids are medium-size frogs (40–60 mm SVL). All but two species inhabit African savannas and grasslands. The genus *Ptychadena* includes the majority of ptychadenid diversity and is the best-studied genus in the family (**Figure 3.59A**). Most *Ptychadena* breed in temporary water bodies. Because amphibians are generally intolerant of seawater's salinity, transoceanic dispersal is extremely rare. Yet, two



Figure 3.58 Pyxicephalidae and Phrynobatrachidae.

(A) African giant bullfrog, *Pyxicephalus adspersus* (Pyxicephalidae). (B) Coast river frog, *Phrynobatrachus plicatus* (Phrynobatrachidae). (C) The distribution of the two families covers essentially the same area of sub-Saharan Africa. (Photographs: A, © EcoPrint/Shutterstock; B, courtesy of Daniel M. Portik.)

leptella (e.g., *A. bicolor*, *A. drewesii*, *A. rugosa*, *A. subvoce*) lay eggs in moss or other moist areas, often associated with waterfalls; their tadpoles are nonfeeding and metamorphose rapidly into tiny froglets.

Classification, distribution, and conservation 13 genera, 80 species. 2 subfamilies: Cacosterninae (representative genera include *Amietia, Androphryne, Arthroleptella, Cacosternum, Strongylopus, Tomopterna*) and Pyxicephalinae (*Aubria, Pyxicephalus*). All pyxicephalids inhabit sub-Saharan Africa (**Figure 3.58C**). Pyxicephalids were previously placed in Ranidae *sensu lato*. The IUCN lists 9 species as Critically (A)





Figure 3.59 Ptychadenidae. (A) Mascarene ridge frog, *Ptychadena mascareniensis*. (B) Distribution. (Photograph courtesy of Miguel Vences and Frank Glaw.)

species of *Ptychadena* have independently colonized Madagascar and surrounding islands (*P. mascareniensis*) and São Tomé and Príncipe off the coast of West Africa (*P. newtoni*). These colonizations are a result of natural overwater dispersal rather than introduction by humans (Vences et al. 2004; Measey et al. 2007).

Classification, distribution, and conservation 3 genera (*Hildebrandtia, Lanzarana, Ptychadena*), 52 species. They inhabit sub-Saharan Africa, Egypt, Ethiopia, and Madagascar (**Figure 3.59B**). Ptychadenids were previously placed in Ranidae *sensu lato*. The IUCN lists 2 species as Endangered and 3 species as Near Threatened.

Systematics references Vences et al. (2004), Measey et al. (2007), Wiens et al. (2009), Dehling and Sinsch (2013a,b), Freilich et al. (2014).

Petropedetidae • African Torrent Frogs

Petropedetids are small to medium-size frogs (~40-70 mm SVL) that inhabit spray zones of streams in African forests and savannas. Activity of many savanna species is strongly tied to the rainy season, when the frogs emerge to feed and reproduce. Males of most species of Petropedetes (Figure 3.60A) have femoral glands and develop a fleshy protrusion on the tympanum called a tympanic papilla. Several functions have been proposed for this papilla (Narins et al. 2001). The papilla contains structures that resemble exocrine glands and may secrete an unknown substance, perhaps pheromones. When the papilla is removed, the peak amplitude of the male's advertisement call decreases, suggesting that the tympanum both projects and receives auditory information. Finally, the papilla moves conspicuously when a frog calls and may convey information visually. Males also have a carpal spike on their hands that they use





(A) Nyctibatrachidae



(B) Micrixalidae



(C) 20°N India Nyctibatrachidae Micrixalidae

for aggressive territorial behavior (Sanderson 1936; Barej et al. 2010). Petropedetids have free-swimming tadpoles.

Classification, distribution, and conservation 3 genera (*Arthroleptides, Odontobatrachus, Petropedetes*), 13 species. They inhabit four disjunct regions in sub-Saharan Africa (**Figure 3.60B**). The IUCN lists 5 species as Critically Endangered or Endangered and 3 species as Near Threatened.

Systematics references Wiens et al. (2009), Barej et al. (2010, 2014), Loader et al. (2013).

Nyctibatrachidae • Night Frogs

The two nyctibatrachid lineages are very old, sharing a common ancestor in the Late Cretaceous more than 65 mya. They differ markedly in body size and preferred habitat. *Nyctibatrachus* species (**Figure 3.61A**) are small (<20 mm SVL) and inhabit terrestrial, marsh, or rocky montane torrents in the Western Ghats of India, whereas *Lankanectes* are large (~85 mm SVL) aquatic species that inhabits forested regions. Female *N. humayuni* lay eggs on vegetation overhanging the water, into which the tadpoles drop after hatching (Kunte 2004). Males *Nyctibatrachus* have femoral glands and possess mandibular fangs.

Classification, distribution, and conservation 2 genera (*Lankanectes, Nyctibatrachus*), 28 species. They inhabit Sri Lanka and the Western Ghats of India (**Figure 3.61C**). Nyctibatrachids were previously placed in Ranidae *sensu lato*. The IUCN lists 6 species as Endangered and 3 species as Vulnerable.

Systematics references Delorme et al. (2004), Biju et al. (2011), Van Bocxlaer et al. (2012).

Micrixalidae

Micrixalids are small to medium-size frogs (13–35 mm SVL) that, like Nyctibatrachidae, inhabit the Western Ghats of India (Figure 3.61B). Most of the natural history information about micrixalids is based on observations of *Micrixalus saxicola*. When *M. saxicola* males fight for control of a nesting site, they engage in a foot-flagging display

Figure 3.61 Nyctibatrachidae and Micrixalidae. (A) *Nyctibatrachus* sp. (Nyctibatrachidae). (B) Nelliyampathi dancing frog, *Micrixalus nelliyampathi* (Micrixalidae), a recently discovered species. (C) Distribution. (Photographs: A, courtesy of Vishal Prassad; B, courtesy of S. D. Biju.)

(see Figure 13.21), extending their leg laterally and splaying their toes (Preininger 2013a,b). *M. saxicola* females excavate a cavity, oviposit, and then conceal the eggs (Guruaja 2010).

Classification, distribution, and conservation 1 genus (*Micrixalus*), 24 species. They inhabit the Western Ghats of India (**Figure 3.61C**). Micrixalids were previously placed in Ranidae *sensu lato*. The IUCN lists 2 species as Critically Endangered or Endangered and 4 species as Near Threat-ened or Vulnerable.

Systematics references Biju et al. (2014).

Dicroglossidae • Forked-Tongue Frogs

Dicroglossids have diverse body forms and range in size from 20 to 145 mm SVL (**Figure 3.62A**). They occur in terrestrial and aquatic habitats and have diverse reproductive modes, including both tadpoles and direct development. The crab-eating frog *Fejervarya cancrivora* is unusual because crabs comprise a large portion of its diet and it is also tolerant of seawater—a specialization for living in mangrove swamps. *Limnonectes* species have prominent fanglike bony projections on the tip of the mandible, and some species have lost the ability to vocalize or vocalize infrequently.

Reproduction in *Occidozyga sumatrana* is unusual in that amplexus is inguinal (rare among neobatrachians) and the female attaches the egg mass to the ceilings of holes or hollows (Eto and Matsui 2012). The tadpole of *O. baluensis* is an obligate carnivore with numerous specializations, including an anterior-opening mouth, anterior-directed eyes that may permit stereoscopic vision, hypertrophied jaw musculature, and a large stomach (Haas et al. 2014).



Figure 3.62 Dicroglossidae. (A) African crowned frog, *Hoplobatrachus occipitalis*. (B) Distribution. (Photograph courtesy of Daniel M. Portik.)



Conrauidae

Classification, distribution, and conservation 13 genera, 187 species. 2 subfamilies: Dicroglossinae (representative genera include *Euphlyctis, Fejervarya, Hoplobatrachus, Limnonectes, Nanorana, Quasipaa, Sphaerotheca*) and Occidozyginae (*Ingerana, Occidozygus*); the placement of *Ombrana* remains unknown. They inhabit northwestern and sub-Saharan Africa east through the Middle East to Southeast Asia, Indonesia, New Guinea, Philippines, and Japan (**Figure 3.62B**). Dicroglossids were previously placed in Ranidae *sensu lato.* The IUCN lists 16 species as Critically Endangered or Endangered and 37 species as Near Threatened or Vulnerable.

Systematics references Kosuch et al. (2001), Grosjean et al. (2004), Roelants et al. (2004), Jiang et al. (2005), Kurabayashi et al. (2005), Ohler and Dubois (2006), Che et al. (2009, 2010), Inger and Stuart (2010), Kotaki et al. (2010), McLeod (2010), Setiadi et al. (2011), Evans et al. (2003).

Conrauids are most notable for the Goliath frog (*Conraua goliath*). Reaching more than 30 cm SVL and weighing up to 3.3 kg, it is the largest extant species of frog (**Figure 3.63A**) Most natural history information about conrauids comes from a single study of *C. goliath* (Sabater-Pi 1985). This frog is primarily nocturnal and inhabits riverine rapids and cascades. Females attach clutches of a few hundred eggs to underwater vegetation. *C. goliath* lacks a vocal sac, and its courtship behavior is unknown.

Classification, distribution, and conservation 1 genus (*Conraua*), 6 species. Conrauids have a disjunct distribution in West and East Africa (**Figure 3.63B**). Conrauids were previously placed in Ranidae *sensu lato*. The IUCN lists 2 species, including *C. goliath*, as Critically Endangered or Endangered and 2 species as Vulnerable, primarily due to hunting by humans for food.



Figure 3.63 Conrauidae. (A) Goliath frog, *Conraua* goliath, held by two boys in Ghana. (B) Distribution. (Photograph © Mark Moffett/Minden Pictures/ Corbis.)
Systematics references Wiens et al. (2009), Barej et al. (2014).

Ceratophryidae • Horned Frogs

Ceratophryids are large, nocturnal, terrestrial frogs of lowland forests in South America (**Figure 3.64A**). These frogs are cryptic sit-and-wait predators that consume a wide variety of organisms, but are unusual in that more than 50% of their prey by volume is vertebrates (frogs, snakes, lizards, and rodents) (Duellman and Lizana 1994). *Ceratophrys* are typically large frogs (up to 15 cm SVL) with very large heads and sharp teeth. The heads of juveniles makes up almost 50% of the body. Large adults may be so rotund that they resemble a partially deflated balloon with a mouth, giving rise to their common name Pac-Man frogs after the 1980s computer game character.

The tadpoles of *Ceratophrys* and *Lepidobatrachus* are primarily carnivorous with strong, keratinous jaw sheaths, hypertrophied jaw muscles, and a shortened digestive tract



Figure 3.64 Ceratophryidae. (A) Paraguay horned frog, Lepidobatrachus asper, Paraguay. (B) Distribution. (Photograph © Danita Delimont/Alamy.) (Vera Candioti 2005). *Lepidobatrachus laevis* consumes tadpoles, and adaptations to this predatory mode include a very large head, a buccopharyngeal cavity up to 4 times the volume of tadpoles of similar SVL, and a stomach capable of distending to accommodate the large size of the prey (Quinzio et al. 2006). *Chacophrys* have the typical Ortons' type 4 tadpole morphology (see Figure 3.20) and eat plant matter and detritus (Quinzio et al. 2006). When threatened by predators, especially cannibalistic conspecifics, *Ceratophrys* tadpoles emit a metallic sound that has an antipredatory effect (Natale et al. 2011; Salgado Costa et al. 2013).

Classification, distribution, and conservation 3 genera (*Ceratophrys, Chacophrys, Lepidobatrachus*), 12 species. Ceratophryids were previously placed in Leptodacylidae *sensu lato*. They inhabit South America (**Figure 3.64B**). The IUCN lists 3 species as Near Threatened or Vulnerable.

Systematics references Lynch (1982), Fabrezi (2006), Fabrezi and Quinzio (2008), Faivovich et al. (2014).

3.4 Gymnophiona: Caecilians

Caecilians are elongate, limbless, burrowing amphibians with distinctly annulated bodies that inhabit both terrestrial and aquatic environments. They represent the smallest of the three extant amphibian lineages in terms of species (3% of total). Apoda (from the Greek a, "without," + podos, "foot") is the node-based name for the ancestor of extant caecilian lineages, and Gymnophiona (from the Greek gymnos, "naked," + ophi, "snake") is the stem-based name for all lineages more closely related to Apoda than to other amphibians, including extinct lineages that diverged before extant caecilians. Although we use node-based names for frogs and salamanders (Anura, Caudata), we instead use the stem-based name Gymnophiona, even when referring to only extant caecilians. Although both Apoda and Gymnophiona are used in current literature, use of the latter is becoming more common.

Morphology

Many morphological structures of caecilians are reduced, as is true in other elongate or burrowing tetrapods. Tails are greatly reduced or absent altogether. No extant caecilian species has limbs or pectoral/pelvic girdles, but these structures are present in the earliest known fossil form, *Eocaecilia* (Figure 3.65). The eyes of caecilians are greatly reduced and often covered by a layer of skin or bone. The left lung may be reduced or absent, and one aquatic species lacks lungs. Dermal scales are present in some species of caecilians, lying within the annular grooves that delimit the body segments, or **annuli**.

All caecilians have a specialized chemosensory organ the **tentacle**—that opens to the surface of the head through an aperture in the skull located between the eyes and nos-





Figure 3.65 The oldest known caecilian. *Eocaecilia micropodia,* from the Early Jurassic, retains ancestral characters such as limbs (A) and skull bones (B) that are not present in extant caecilians (see Figure 3.67). (After Jenkins and Walsh 1993.)

trils (**Figure 3.66**). The tentacle is a complex of muscles, glands, and ducts and may include both olfactory and visual receptors, depending on the family (Billo and Wake 1987; O'Reilly et al. 1996). The position of the aperture varies considerably and is useful in identifying species. A portion

of the tentacular structures is protrusible through the aperture to varying degrees in different taxa.

The annuli ringing the body of caecilians are one of the group's most characteristic features. All caecilians have a series of primary annuli that are probably homologous



(B)



Figure 3.66 Paired tentacles and annuli are characteristic of caecilians. (A) Annular grooves and tentacles of an Asian caecilian (*Ichthyophis*, Ichthyophiidae). The tentacles are sensory structures derived from the tear ducts, eye muscles, and some parts of the eye. They have a direct connection to the vomeronasal organ and are probably employed in chemosensation. (B) In a unique adaptation, the eyes of African scolecomorphid caecilians, such as this banded caecilian (*Scolecomorphus vittatus*), are located within the tentacle. When the tentacle is retracted (left) the eye lies beneath the bones of the skull. The extended tentacle (right) carries the eye with it, making these caecilians the only vertebrates with protrusible eyes. (Photographs: A © kamnuan/Shutterstock; B courtesy of John Measey.)



with the costal grooves of salamanders. Each primary annulus is associated with one vertebra along most of the trunk. In many species of caecilians, primary annuli may become subdivided by secondary annuli, which in turn may become subdivided by tertiary annuli. In each case the appearance of the annuli follows a definite ontogenetic pattern: primaries appear first, followed by secondaries, which form in a wave beginning posteriorly and spreading anteriorly. Finally, the tertiaries form in the same way as the secondaries (Nussbaum and Wilkinson 1989).

Caecilian skulls are well ossified, which reflects their burrowing lifestyle. The skulls of most groups are relatively akinetic and completely roofed in bone except for sensory openings for the eyes, nares, and tentacles, a condition called **stegokrotaphy** (**Figure 3.67A**). However, rhinatrematids, scolecomorphids, and typhlonectids have a partially open temporal region and more kinetic skulls, called **zygokrotaphy** (**Figure 3.67B**). Some of the strength of the caecilian skull is due to the fusion of bones into compound elements, including a maxillopalatine (maxilla + palatine) and a large element termed the os basale (otic and occipital bones + parasphenoid) that forms most of the posteroventral and posterior portions of the skull. Teeth are present on the maxillopalatines, premaxillae, vomers, and pseudodentaries.

The physical demands of burrowing head-first places strong selection pressure for a robust skull, but also one with a small diameter to tunnel through the soil (Wake 1993; O'Reilly 2000; Kleinteich et al. 2012). Such a compact skull constrains the size of prev that can fit in the mouth. Caecilians overcome this limitation with modifications of the skeletal and muscular structures of the jaw (see Figure 11.6). The long retroarticular process acts as a lever to increase the force produced by the jaw muscles that attach to it (Summers and Wake 2005). Caecilians also produce greater bite force via a dual jaw adduction mechanism, unique among tetrapods, consisting of joint action of the mandibular adductor and interhyoideus muscles (Bemis et al. 1983; Nussbaum 1983). Finally, at least two species, Boulengerula taitanus (Herpelidae) and Schistometopum thomense (Dermophiidae) have a behavioral adaptation that allows them to eat prey that exceed their gape size. After grasping the prey with their jaws, these species rotate their bodies circularly, generating sufficient torque to tear off bite-sized pieces (Measey and Herrel 2006).

The scales of caecilian skin are composed of layers of collagenous fibers topped with mineralized nodules called **squamulae** (Zylberberg and Wake 1990). Several scales are aligned, much like an oblique stack of coins, in a pouch located in the dermis below the annular grooves. Scale pouches partly or completely encircle the body along each groove and are nestled among the mucus and poison glands of the dermis. Scales are unknown in extant amphibians other than caecilians, although mineralized osteoderms are present in some frogs and in many fossil amphibians.



Figure 3.67 Skull morphology of caecilians. (A) Stegokrotaphic skull of *Dermophis mexicanus* (Dermophiidae), dorsal view. (B) Zygokrotaphic skull of *Epicrionops petersi* (Rhinatrematidae), dorsal view. (After Wake and Hanken 1982.)

Most caecilians exhibit little sexual dimorphism. However, in some species the head, cloacal glands, and the area around the cloacal opening are larger in males. The number of primary annuli and vertebrae, as well as overall body size, are sometimes greater in females (Nussbaum and Pfrender 1998). The presence of bite scars on many specimens, sexual size dimorphism in some characters, and the density of many natural populations suggest complexity in caecilian social behaviors. However, the burrowing, secretive habits of most species preclude easy observation of this aspect of their life history.

Reproduction and life history

Fertilization in caecilians is internal and effected by a **phallodeum** (the male's protrusible copulatory organ) formed by a portion of the cloacal wall. Data for caecilian reproductive modes are sparse compared with other amphibians, but an estimated 50–80% of species are oviparous (M. H. Wake 1992; Wilkinson and Nussbaum 1998; Exbrayat 2006). Clutch size of oviparous species varies considerably, from 5 to 100 eggs. Eggs are laid in a continuous string and females remain with the eggs until hatching (Himstedt 2000; Gomes et al. 2012).

Viviparity evolved independently in Scolecomorphidae, Typhlonectidae, and Dermophiidae. Further life-history research may reveal additional evolutionary transitions to viviparity. The developing young of viviparous caecilians are nourished by secretions of cells in the oviductal epithelium, which the fetuses stimulate using specialized, multicuspate larval teeth (M. H. Wake 1977, 1993). At least three oviparous caecilian species-Boulengerula taitana (Herpelidae), and Siphonops annulatus and Microcaecilia dermatophaga (Siphonopidae)-have a unique form of parental care, dermophagy, not found in any other tetrapod group. After the offspring hatch the mother begins a modified sloughing process whereby the epidermal skin cells become engorged with lipids. The offspring writhe over the mother and consume her entire outer layer of lipid-rich skin (Kupfer et al. 2006). All of the skin of S. annulatus is consumed within 7 minutes, after which the mother's skin regenerates and is then consumed by the offspring again after approximately 64 hours (Wilkinson et al. 2008). Although documented for only these three distantly related species, this behavior may be much more widespread among caecilians.

Another mode of fetal nutrition is **oophagy**, or egg-eating. The gravid oviduct typically contains many unfertilized eggs early in gestation. Moreover, the number of offspring born to viviparous species is lower than the number of embryos present in the oviduct early in gestation. These observations suggest that developing embryos may consume both unfertilized eggs and other embryos. Indeed, in *Typhlonectes compressicaudus*, embryos have been found in the mouth and gut of other developing embryos (Exbrayat and Hraoui-Bloquet 1992).

The ancestral reproductive strategy of caecilians is to lay eggs in moist environments. Eggs hatch into free-living larvae. Larval caecilians are elongate, with gill openings and gill rudiments, caudal fins, and a lateral line system. Recently hatched larvae lack tentacles, but lungs are present from hatching. Larvae may be diurnal or nocturnal, depending on the species. In the latter case, larvae spend the daylight hours burrowed into mud or underneath surface objects or vegetation above the water line. Metamorphosis is a gradual process: larvae lose the caudal fins and lateral line system, the gill slits close, and the tentacle appears. Color changes at metamorphosis in some species. Rhinatrematids and ichthyophiids retain the ancestral characters



Figure 3.68 A phylogeny of caecilians based on life-

history trait analysis. The ancestral reproductive strategy of caecilians is to lay eggs (O, yellow squares) that hatch into free-living larvae (blue squares). A shift to direct development (green squares) is seen early in the group's evolutionary history, and viviparity (V, red squares) evolved independently in three lineages. However, the situation among three genera of indotyphlids that inhabit the Seychelles Islands (*Grandisonia, Hypogeophis*, and *Praslinia*) is more complicated. *Grandisonia*

and *Praslinia* have the ancestral free-living state. That they are nested in an otherwise direct-developing clade (Indotyphlidae) but are not each other's closest living relative suggests two possible scenarios: either free-living larvae re-evolved independently in both *Grandisonia* and *Praslinia*, or free-living larvae re-evolved only once—in the common ancestor of all three genera—and direct development subsequently re-evolved in *Hypogeophis*. (After San Mauro et al. 2014.) of oviparity and free-living larvae. However, a shift from free-living larvae to direct development evolved in the ancestor of all other caecilian lineages, with viviparity evolving in Scolecomorphidae, and appearing later in both Typhlonectidae and Dermophidae (**Figure 3.68**).

Fossil record

Caecilians are known from the Early Jurassic of Arizona in the United States (~190 mva), the Early Cretaceous of Morocco, the Late Cretaceous of Bolivia and Sudan, and the Paleocene (Brazil and Bolivia) through the Pleistocene (Rage 1991; Jenkins and Walsh 1993; Evans et al. 1996; Evans and Sigogneau-Russell 2001). The Late Cretaceous and Paleocene specimens are isolated vertebrae and shed little light on caecilian evolution, whereas the Early Cretaceous material from Morocco includes skull, dental, and vertebral elements. The Jurassic fossils are spectacularly preserved skulls and postcrania of Eocaecilia micropodia (see Figure 3.65). Aside from being the earliest and best-preserved caecilian fossil, Eocaecilia retains reduced but well-developed limbs and girdles. The skull is stegokrotaphic and therefore characterized by extensive fusion of the skull bones (Carroll 2000; Jenkins et al. 2007; Maddin et al. 2012). Eocaecilia shares with extant caecilians the os basale, a large bone in the skull formed from the fusion of multiple smaller bones that forms the posterior part of the braincase. The lower jaw of Eocaecilia is composed of only two elements and has an extremely long retroarticular process.





Systematics and Phylogeny of Caecilians

The monophyly of Gymnophiona includes most of the unusual morphological features mentioned above and is supported by countless molecular phylogenies. The past 40 years have seen a tremendous growth in knowledge of caecilian systematics (see Wilkinson 2011 for a review). Until recently, caecilians were classified into five or six families with the acknowledgement that Caeciliidae sensu lato was not monophyletic and there was insufficient morphological and molecular data to resolve the phylogenetic relationships (Nussbaum and Wilkinson 1989). However, recent molecular phylogenetic analyses have resolved these relationships with strong support. Most notably, Caeciliidae sensu lato has been split into Caeciliidae sensu stricto, Dermophiidae, Herpelidae, Indophiidae, and Siphonopidae (Figure 3.69). The divergence times among families are old, typically Cretaceous or older, and some of these old groups have very restricted, often disjunct ranges. For example, Indotyphlidae inhabits only the Seychelles and Western Ghats in India, two landmasses that preserve numerous other old Gondwanan vertebrate lineages (see Chapter 5). The family Chikilidae, a lineage that diverged from its sister lineage (Herpelidae) approximately 150 mya, was discovered in 2012 and is restricted to areas in northeastern India (Kamei et al. 2012).

> Classification, distribution, and conservation 35 genera, 200 species. Our taxonomy follows Wilkinson et al. (2011). Because of the strong support for congruent caecilian phylogenies across multiple data sets, this taxonomy is uncontroversial. The distribution of caecilians is largely pantropical except for Madagascar and land east of Wallace's Line (Papuan-Australian region; see Chapter 5). Caecilians have not been found in central Africa, although they are present in East and West Africa. Caecilians are restricted to moist, friable forest soils, or more open country such as agricultural land that were previously forested. They do not occur on islands except on near-continental islands, São Tomé, and the granitic Sevchelles Islands. The IUCN lists 2 species of caecilians as Critically Endangered or Endangered and 4 species as Vulnerable. However, even basic ecological and population data are totally lacking for a majority of species. Given this and the documented cases of chytrid infection, caecilians are probably facing the same

(A)



Figure 3.70 Rhinatrematidae. (A) Bicolored caecilian, *Epicrionops bicolor.* (B) Distribution. (Photograph courtesy of Luis A. Coloma.)

conservation crises as other amphibians, and the number of species at risk of extinction is likely to be far higher than currently documented (Gower and Wilkinson 2005).

Systematics references Some notable comprehensive phylogenetic systematic analyses of caecilians include Taylor (1968), Nussbaum and Wilkinson (1989), Wilkinson (1997), Frost et al. (2006), Wilkinson and Nussbaum (2006), Loader et al. (2007), San Mauro et al. (2009, 2012, 2014), Zhang and Wake (2009), Maciel and Hoogmoed (2011), Pyron and Wiens (2011), Wilkinson et al. (2011), Kamei et al. (2012), Maddin et al. (2012a,b).

Rhinatrematidae • Tailed Caecilians

Rhinatrematids (**Figure 3.70A**) reach a length of 33 cm SVL and retain several ancestral caecilian characters. They possess a true tail containing vertebrae with downward projecting arches (haemal arches) and associated musculature. The mouth is at the tip of the snout, unlike most other caecilians, in which the snout projects over the mouth. The tentacular opening is adjacent to the anterior edge of the eye, which is considered an ancestral condition relative to its more anterior position in other caecilians (Nussbaum 1977). Rhinatrematids are the most annular caecilians, with primary, secondary, and tertiary annulations. The skulls are zygokrotaphic.

Very little is known of the natural history of rhinatrematids, although the zygokrotaphic skulls and terminal mouths do not suggest extreme specialization for burrowing. Rhinatrematids may be cryptic surface forms. They are oviparous with free-living larvae. Larvae of *Epicrionops petersi* have been found in mud at the edge of streams (Duellman and Trueb 1986).

Classification, distribution, and conservation 2 genera (*Epicrionops, Rhinatrema*), 11 species. They inhabit northern South America (**Figure 3.70B**). No species are listed by the IUCN as an extinction risk.

Systematics references Nussbaum (1977).



Ichthyophiidae

Like rhinatrematids, ichthyophiids (Figure 3.71A) have a true tail and primary, secondary, and tertiary annuli (except in *Uraeotyphlus*, in which the secondary and tertiary annuli are present but not complete), but their skulls are solidly roofed (stegokrotaphic). The mouth may be nearly terminal or subterminal. Scales are present. The tentacle is closer to the eye than to the nostril, except in *Uraeotyphlus* where it is far forward in the skull, underneath the nostril. Ichthyophiids attain lengths up to about 50 cm SVL.

Ichthyophiids are oviparous, and observations of Ichthyophis kohtaoensis have provided most of the reproductive information about this family. Mating and oviposition occur at the beginning of the rainy season, and larvae metamorphose by the end of the following dry season (Kupfer et al. 2005). I. glutinosus lays clusters of 25-40 eggs in moist soil or a burrow near ponds or streams (Breckenridge and Jayasinghe 1979). Up to 100 eggs have been found in clutches of I. malabarensis and nearly 50 eggs in clutches of I. kohtaoensis (Himstedt 2000). Females attend clutches in all known cases. I. kohtaoensis females do not feed while attending eggs except to consume decaying eggs. The eggs are regularly rotated as the female repositions her body, and unattended eggs quickly succumb to fungi; possibly skin secretions of the female are required to prevent egg degradation. Hatching takes place in 70-80 days in Ichthyophis, and larvae have been found in mud or under leaves or rocks at the water's edge. The period of larval development in I. kohaoensis and some other species is about 1 year.

Classification, distribution, and conservation 3 genera (*Caudacaecilia, Ichthyophis, Uraeotyphlus*), 55 species. They



Figure 3.71 Ichthyophiidae (A) Striped caecilian, *Ichthyophis* sp. (B) Distribution. (Photography courtesy of L. Lee Grismer.)

inhabit India, Sri Lanka, Southeast Asia, Philippines, mainland Malaysia, Sumatra, and Borneo (Figure 3.71B). The IUCN lists 2 species as Vulnerable.

Systematics references Nussbaum (1979b), Bossuyt et al. (2004), Gower and Wilkinson (2007), Nishikawa et al. (2012).

Scolecomorphidae

Scolecomorphids (Figure 3.72A) range in length from 20 to 45 cm SVL and have several unusual, sometimes bizarre, characters. Their zygokrotaphic skulls lack several bony elements, including postfrontals, pterygoids, and stapes. The skull also lacks orbits; instead, scolecomorphs have a feature unknown in any other vertebrate—their vestigial eyes are attached to the end of the extended tentacles (see Figure 3.66; O'Reilly et al. 1996). Calcified spines, otherwise unknown among caecilians, are present on the phallodea in some species of *Scolecomorphus*. Scolecomorphids have only primary annuli. *Crotaphotrema* is probably oviparous, whereas species of *Scolecomorphus* are thought to be viviparous since intraoviductal fetuses are known for several species (Nussbaum and Wilkinson 1989).



Figure 3.72 Scolecomorphidae. (A) Banded caecilian, *Scolecomorphus vittatus.* (B) Distribution. (Photograph courtesy of John Measey.)

Classification, distribution, and conservation 2 genera (*Crotaphatrema, Scolecomorphus*), 6 species. Scolecomorphs have a disjunct distribution in West (Cameroon) and East (Malawi and Tanzania) Africa (**Figure 3.72B**). No species are listed by the IUCN as an extinction risk.

Systematics references Nussbaum (1985), Wilkinson et al. (2013).

Herpelidae • African Caecilians

Much of the natural history information about herpelids comes from studies of *Boulengerula* (Figure 3.73A), and specifically from *B. taitana*. This species eats primarily termites and earthworms (Gaborieau and Measey 2004). When encountering larger soft prey such as earthworms, *B. taitana* bites the worm and then spins around the long axis of its body, creating sufficient torque to tear off pieces of the worm to consume (Measey and Herrel 2006). That this mode of feeding also occurs in another family (Dermophiidae) suggests that this is a common behavior in caecilians, and is probably an adaptation that compensates for their limited gape size. Herpelids reach SVLs of 35 cm or less.



Figure 3.73 Herpelidae. (A) Usambara bluish-gray caecilian, *Boulengerula boulengeri*. (B) Distribution. (Photograph courtesy of John Measey.)

At the beginning of the autumn rainy season, *Bouleng-erula taitana* males and females mate in the soil. The female constructs a nest chamber into which she lays approximately 5 eggs that she attends until after hatching (Malonza and Measey 2005). *B. taitana* are dermatophagic and mothers grow layers of lipid-rich skin that the hatchlings subsequently consume. Hatchlings take 2 years to mature into adults.

Classification, distribution, and conservation 2 genera (*Boulengerula, Herpele*), 9 species. Herpelids have a disjunct distribution in tropical West (*Herpele*) and East (*Boulengerula*) Africa (**Figure 3.73B**). Herpelids were previously placed in Caeciliidae *sensu lato*. The IUCN lists 3 species of *Boulengerula* as Endangered.

Systematics references Nussbaum and Hinkel (1994), Wilkinson et al. (2004), Gower et al. (2011), Loader et al. (2011).

Chikilidae

Chikilidae (Figure 3.74A) was described in 2012 from specimens collected in northeastern India. There is little



Figure 3.74 Chikilidae. (A) *Chikila gaiduwani.* (B) Distribution. (Photograph courtesy of S. D. Biju.)

information about the natural history of these four species except that they are oviparous with direct-developing offspring. Chikilids have both primary and secondary annuli.

Classification, distribution, and conservation 1 genus (*Chikila*), 4 species. They inhabit northeastern India (**Figure 3.74B**). No species are listed by the IUCN as an extinction risk, but baseline natural history and population data are lacking.

Systematics references Kamei et al. (2012, 2013).

Caeciliidae • Common Caecilians

Caeciliidae *sensu stricto* species are typically large, with *Caecilia thompsoni* being the largest caecilian at 1.5 m in total length. The eyes are covered by bone in *Oscaecilia*. There are few natural history data for caeciliids. For example, it is not known if all caeciliids are oviparous or viviparous, although field research has shown that *Caecilia orientalis* is oviparous (Funk et al. 2004).

Classification, distribution, and conservation 2 genera (*Caecilia*, **Figure 3.75A**; and *Oscaecilia*), 42 species. They inhabit Costa Rica to central South America (**Figure 3.75B**). Caeciliidae *sensu lato* was once the largest family of caecilians in terms of number of species but was recently split into Caeciliidae *sensu stricto*, Dermophiidae, Herpelidae, Indophiidae, and Siphonopidae. No species are listed by the IUCN as an extinction risk.

Systematics references Funk et al. (2004).

Typhlonectidae • Aquatic Caecilians

Typhlonectids are highly aquatic and range in size from 20 cm to 1 m SVL. All species are viviparous and give birth to juveniles that quickly shed their gills and acquire adult morphology. *Chthonerpeton* has been found in water and in terrestrial burrows. Species of *Typhlonectes* (Figure 3.76A) and *Potomotyphlus* are fully aquatic and often burrow into the substrate. *Nectocaecilia* is probably semiaquatic because it has been collected in water-filled artificial pits far from



Figure 3.75 Caeciliidae. (A) Undescribed *Caecilia* sp., Peruvian Amazon Basin. (B) Distribution. (Photograph © Dant– Fenolio/Science Source.)



Figure 3.76 Typhlonectidae. (A) Striped caecilian, *Typhlonectes natans*. (B) Distribution. (Photograph © ephotocorp/ Alamy.)

natural water courses. The fully aquatic species have compressed bodies and well-developed dorsal fins on the posterior body. *Typhlonectes compressicauda* construct burrows 30–60 cm in length at the water level; individuals spend the day in their tunnels and emerge at night to forage in shallow water (Moodie 1978).

Litter sizes of *Typhlonectes natans* are 2 to 11 offspring, and the gestation period is 6–7 months. Birth occurs over a period of several days, with the young emerging headfirst from the mother. Massive voiding of the intestine in the neonates occurs soon after birth, reflecting the intrauterine feeding of the fetuses during gestation (Himstedt 2000). In *T. compressicauda*, the female gestates five embryos early in pregnancy, but only one of these embryos is viable at the end of gestation (Exbrayat 2006).

The trachea of typhlonectids is expanded into an accessory gas exchange organ called the tracheal lung. Typh-

lonectids also possess primary annuli and have zygokrotaphic skulls. Phylogenetic analyses suggest that ancestral typhlonectids were semiaquatic and that the evolution of a fully aquatic lifestyle entailed many changes in external morphology, skull and vertebral structure, and the respiratory system (Wilkinson and Nussbaum 1999). *Typhlonectes* is nocturnal and uses chemical cues to locate conspecifics (Warbeck et al. 1996).

A remarkable South American species, Atretochoana *eiselti*, is the largest lungless tetrapod (>80 cm total length) (Nussbaum and Wilkinson 1996; Hoogmoed et al. 2011). Additionally, it is the only known choanate (lungfish + tetrapod) in which the internal nares are sealed off from the buccal cavity by fusion of the choanal valves, thereby separating the nasal cavity from the buccal cavity (effectively, a secondary palate). The function of this morphological condition is speculative, but because typhlonectids possess chemosensory structures in their nasal cavity (M. H. Wake and Schwenk 1986), this secondary palate may more efficiently direct water in and out of the nasal passages, bypassing the buccal cavity (Wilkinson and Nussbaum 1997). Other unusual features occur in the skull, cranial musculature, and circulatory system. The left lung in Potomotyphlus is modified into a hydrostatic organ, and other parts of the respiratory and pulmonary circulatory systems are reduced (Wilkinson and Nussbaum 1999). In Typhlonectes both lungs are well developed.

Classification, distribution, and conservation 5 genera (*Atretochoana, Chthonerpeton, Nectocaecilia, Potomotyphlus, Typhlonectes*), 13 species. They inhabit primarily the northern Amazon and Guiana Highlands, but there are disjunct populations throughout central and northern South America (**Figure 3.76B**). No species are listed by the IUCN as an extinction risk.

Systematics references Wilkinson (1989, 1996), Wilkinson and Nussbaum (1999).

Indotyphlidae • Indo-African Caecilians

Indotyphlids are small (10–20 cm in total length). Some *Grandisonia* from the Seychelles and *Sylvacaecilia* from Ethiopia produce aquatic larvae, whereas *Hypogeophis*, *Gegneophis*, and *Idiocranium* lay terrestrial eggs with direct-developing larvae. *Idiocranium russeli* have been found coiled about their eggs on a small mound in a nest cavity under a dense grass mat. Almost all species have primary and secondary annuli.

Classification, distribution, and conservation 7 genera, 21 species. Genera are *Gegeneophis* (**Figure 3.77A**), *Grandisonia, Hypogeophis, Idiocranium, Indotyphlus, Praslinia,* and *Sylvacaecilia*. Indotyphlids were previously placed in Caeciliidae *sensu lato*. Indotyphlids have a bizarre, patchy distribution that includes small areas in Cameroon, Ethi-



Figure 3.77 Indotyphlidae. (A) Paresh's caecilian, *Gegeneophis pareshi*. (B) Distribution. (Photograph courtesy of K. P. Dinesh.)

opia, Seychelles, and southwestern and northeastern India (**Figure 3.77B**). The IUCN lists *Grandisonia brevis* as Endangered.

Systematics references Gower et al. (2011).

Siphonopidae

Siphonopids are typical caecilians in that they burrow in moist forest floors, where they feed on invertebrates. All species are also oviparous, but they show some morphological diversity in terms of size (~11 to >50 cm SVL), the presence of an external eye, and placement of the tentacle. The clutch size of *Siphonops annulatus* (Figure 3.78A) is small (~6 eggs), and the mother guards the eggs until after hatching. *S. annulatus* and *Microcaecilia dermatophaga* feed their young via dermatophagy (Wilkinson et al. 2013). Siphonopids have primary annuli that are grooved, thereby giving the appearance of secondary annuli.

Classification, distribution, and conservation 7 genera, 25 species. Genera are *Brasilotyphlus, Caecilita, Luetkenotyphlus, Microcaecilia, Mimosiphonops, Parvicaecilia,* and *Siphonops.* Siphonopids were previously placed in Caeciliidae *sensu lato.* They inhabit northern and central South America (**Figure 3.78B**). No species are listed by the IUCN as an extinction risk.

South America

(B)

Equator

30°S

Siphonopidae

Figure 3.78 Siphonopidae. (A) Ringed caecilian, Siphonops annulatus. (B) Distribution. (Photograph © Danita Delimont/Alamy.)



Systematics references No comprehensive phylogeny of siphonopids is available, but some taxa are included in higher-level phylogenetic analyses of caecilians.

Dermophiidae

Neotropical and Tropical African Caecilians

Dermophiids are viviparous, medium to large (20–60 cm SVL) caecilians. Litter sizes range from 2–7 in *Schistome-topum thomense* (Nussbaum and Pfrender 1998) to 4–16 in the Central American species *Dermophis mexicanus* (M. H. Wake 1980). *Geotrypetes seraphini* females have been found coiled around neonates in a nest chamber (Sanderson 1937). The gestation period is unknown for most viviparous species but is approximately 11 months in *D. mexicanus* (M. H. Wake 1980). Dermophiids have primary and secondary annuli.

Schistometopum species and D. mexicanus thrive in disturbed habitats such as agricultural lands and villages as long as pesticides and synthetic fertilizers are not used (M. Wake 1980; Nussbaum and Pfrender 1998). This preference for disturbed habitats apparently results from the abundant soil organic matter and prey (e.g., earthworms) frequently associated with disturbance.

Schistometopum thomense (Figure 3.79A) has the distinction of being the only terrestrial caecilian species to date subject to a population genetics analysis (Stoelting et al. 2014). The study found large genetic divergences among populations despite their close geographic proximities. These data suggest that this species has very limited dispersal ability thereby inhibiting gene flow (see Chapter 5). The fact that the dispersal-limiting, burrowing life history of *S. thomense* is similar to many other families suggests that this pattern of low dispersal and deep genetic structuring is a common phenomenon among terrestrial caecilians.

Classification, distribution, and conservation 4 genera (*Dermophis, Geotrypetes, Gymnopis, Schistometopum*), 14 species. Dermophiids have a disjunct distribution, inhabiting southern Mexico to northwestern Colombia, tropical West Africa, São Tomé, Tanzania, and Kenya (Figure 3.79B). Dermophids were previously placed in Caeciliidae *sensu lato*. The IUCN lists *Dermophis mexicanus* as Vulnerable.

Systematics references Nussbaum and Pfrender (1998), Wilkinson et al. (2011), Kamei et al. (2012), San Mauro et al. (2012).

Figure 3.79 Dermophiidae. (A) São Tomé caecilian, *Schistometopum thomense*. (B) Distribution. (Photograph courtesy of John Measey.)



(A)

Summary

■ There are more than 7,300 species of extant amphibians in three lineages: Caudata (salamanders), Anura (frogs), and Gymnophiona (caecilians). They are the living representatives of the clade Lissamphibia that arose in the Early Carboniferous.

Much of the global amphibian diversity is undescribed, especially from tropical areas; 25% of known frog species were discovered in the past 15 years.

Amphibian populations worldwide have been devastated by the introduction of the chytrid fungus, as well as habitat loss, pollution, and poaching or harvesting.

Amphibian skin plays important roles in respiration, defense, courtship, locomotion, and reproduction.

The thin, moist skin is the site of gas exchange in all amphibians, and the only source in lungless salamanders (Plethodontidae) and a few other species that lack lungs.

Cutaneous mucus glands provide a moist coating over the skin to prevent desiccation. Cutaneous granular (poison) glands produce a diversity of defensive chemicals in almost all species of amphibians; the most famous of these chemicals are the powerful alkaloids of dendrobatid frogs.

Amphibians display spectacular color diversity, and these colors are produced by the presence, absence, or interactions of chromatophores in the dermis. Xanthophores reflect red, yellow, and orange colors. Iridophores reflect white, silver, and blue colors. Melanophores produce melanin, which gives rise to brown or black coloration.

Extant salamanders occur in North America, temperate Eurasia, northern Africa, and tropical Central and South America.

Salamanders are most phylogenetically diverse in North America, which has a representative of every family except Hynobiidae.

Plethodontidae is the most species-rich salamander family, with extensive species radiations in the eastern United States, Mexico, and the Neotropics.

Species of cryptobranchids, hynobiids, and sirenids are paedomorphic and reproduce via external fertilization, but all other salamanders (Salamandroidea) transfer sperm via spermatophores (internal fertilization).

Salamander larvae are aquatic with external gills, gill slits, and tail fins but otherwise superficially resemble adults. Species in some families, most notably Ambystomatidae, are obligately or facultatively paedomorphic.

The phylogeny of salamanders has remained relatively stable in recent years as accumulating DNA phylogenetic studies support the tree in Figure 3.6, with the exception of Sirenidae, whose placement is still not strongly supported (although most phylogenetic evidence supports it as the sister lineage to Salamandroidea).

Extant frog lineages are distributed worldwide except in the most extreme cold and dry habitats. A majority of these species are in the clade Neobatrachia.

Frogs have numerous characteristic skeletal features, including a reduced number of vertebrae, the fusion of caudal vertebrae into a urostyle, and hindlegs modified for jumping.

Frog larvae (tadpoles) have keratinous mouthparts, usually used to scrape algae or detritus, and spiracles by which water exits after crossing the internal gills. The morphology of both of these features varies among clades of frogs and ecological habitat.

Frogs have evolved a spectacular array of reproductive courtship and reproductive strategies, including laying their eggs in terrestrial environments and extensive parental care such as carrying eggs or young on or in the body.

During mating in most frog species, the male grasps the female in the inguinal, axillary, or cephalic region in a hold called amplexus. The amplexus position is an identifying character of major clades of frogs.

The taxonomy of frogs has undergone extensive revision in the past decade due to the proliferation of DNA nucleotide data. New families have been recognized, many of them the result of increased phylogenetic resolution of the hyloid and ranoid frogs.

Extant caecilians inhabit the American and African tropics, India, Seychelles, Southeast Asia, and islands of the Sunda Shelf and Philippines.

Caecilians are characterized by their lack of limbs, presence of body annulations, and highly modified skulls used for burrowing. They also possess a unique sensory structure called the tentacle. The tentacle is a complex of muscles, glands, and ducts that develops in close association with the eyes. The tentacle may have both olfactory and visual sensory cells, depending on the family.

Given the secretive nature of caecilians, many aspects of their natural history are unknown.

At least three caecilian species feed their offspring via dermophagy. The mother grows layers of lipid-rich skin that the offspring consume.

The most notable recent phylogenetic progress in caecilians has been to clarify the relationships of taxa formerly placed in Caeciliidae *sensu lato*. Caeciliidae has now been split into five families with high phylogenetic support.



Systematics and Diversity of Extant Reptiles

xtant reptiles, including Testudines (turtles), Rhynchocephalia (tuatara), Squamata (lizards and snakes), Crocodylia (alligators, crocodiles, and gharials), and Aves (birds), include more than 20,000 extant species and countless fossil forms. About half of these species are birds, and the other half are reptiles in the herpetological sense.

Squamata is by far the largest lineage of reptiles, containing more than 6,000 species of lizards and more than 3,400 species of snakes. Large families of lizards include the Scincidae (>1,550 species) and Gekkonidae (nearly 1,000 species). Colubridae (about 1,800 species) is the largest clade of snakes. Testudines, the largest of the non-squamate reptile clades, contains only about 340 species but is substantially more numerous than Crocodylia (25 species) and Rhynchocephalia (1 species).

This chapter describes the systematics, characteristics, distribution, and conservation status of all families of reptiles, as well as subfamilies of some diverse groups. As in Chapter 3, we include references for studies published since 2004, and some classic systematics papers. Herpetologists colloquially refer to most clades by the anglicized form of their scientific name (e.g., dibamids, colubrids, geomydids), although there are exceptions (e.g., softshells, skinks, vipers), and we include widely used common names.

4.1 Characteristics of Reptiles

The amniotic egg that distinguishes reptiles from amphibians opened new ecological niches that led to the evolution of different and distinctive morphologies. No longer dependent on the presence of water in order to reproduce, reptiles inhabit virtually all of Earth's tropical, temperate, and alpine habitats. Several species are marine, many are arboreal or fossorial, and many inhabit arid regions, including hot deserts. This section describes the major characteristics of reptile skin and sensory systems. Major specializations among the squamates—including limb reduction and the evolution of venom and venom-delivering systems—are discussed in Section 4.3, and unique specializations of the turtles are described in Section 4.7.

Reptile skin

The skin of all amniotes consists of an outer layer—the **stratum corneum**—made up of dead epidermal cells or cell derivatives produced by living cells of the deep epidermal layer, or **stratum germinativum**. All reptiles, including birds, retain **scales**, which are folded areas of the epidermis (**Figure 4.1**). The scaly skin of reptiles distinguishes them at a glance from the smooth-skinned amphibians. Paleozoic tetrapods were scaly, and the absence of scales in Lissamphibia is a derived condition that is probably associated with the importance of skin in amphibian gas exchange (see Section 3.1 and Chapter 6). Resistance to abrasion is the most general function of reptilian skin, and protection from predation is added when scales are elaborated into spines.

Two types of keratin proteins, α -keratin and β -keratin, lend strength and rigidity to the epidermis of reptiles. Alphakeratins are present in the skins of amphibians and mammals as well, but β -keratin is found only in reptiles. Betakeratins form pleated sheets that lend strength and rigidity to reptilian skin, preventing disruption of the permeability barriers that are formed by mixtures of long-chain lipid molecules. The β -keratins of turtles are chemically more similar to the β -keratins of crocodylians and birds than to those of lizards and snakes (Valle et al. 2009; Li et al. 2013).

Popular treatments of reptiles often emphasize the impermeability of their skin, but that view is oversimplified. The resistance of the skin to water movement is measured as the number of seconds required for water vapor to pass through 1 centimeter of skin. Values for reptiles range from 100 to 300 s/cm for species in aquatic and moist habitats to over 1,500 s/cm for desert species (Lillywhite 2006).



Figure 4.1 Reptile skin is characterized by scales, scutes, and osteoderms. (A) The scales of lizards often have different shapes in different parts of the body. Here a triple row of spines (center) separates a mosaic of small rounded scales on the dorsal surface of a bearded dragon (*Pogona vitticeps*) from overlapping scales on the ventral surface (venter). (B,C) The scutes of turtle shells are modified scales. Some species of turtles, such as the painted turtle (*Chrysemys picta*) replace their

Values for birds and mammals lie between 10 and 300 s/ cm, whereas those for many amphibians range from near zero for species from mesic habitats to 200–300 s/cm for waterproof arboreal frogs (see Chapter 6). Thus, reptiles in general have skin permeabilities similar to those of other amniotes, and (contrary to popular opinion) resistance to water loss is the result of lipids in the skin and is not a function of the scales (Lillywhite 2006).

Underlying the epidermis is the dermis, which contains nerves and blood vessels supplying the epidermis. In many lizards, turtles, and crocodylians, bone deposited in the dermal layer gives the skin added rigidity. In lizards, these **osteoderms** are thin slivers of bone, wheras the osteoderms of crocodylians are thick and rugose (see Figure 4.1D). Snakes lack osteoderms.

Skin colors are produced by dermal chromatophore units, which are similar in amphibians and reptiles (see Figscutes annually (B), shedding the old scute to reveal the smooth surface of the new scute. Tortoises retain the old scutes (C), which accumulate to give the pyramidal appearance seen in the carapace of this African spurred tortoise (*Geochelone sulcata*). (D) The skin of crocodylians such as the Siamese crocodile (*Croco-dylus siamensis*) contains bony osteoderms. (Photographs: A, © Image Quest Marine/Alamy; B, © Alberthep/istock; C, courtesy of David McIntyre; D, © luamduan/istock.)

ure 3.3). Some squamates have mosaic chromatophores in which a single cell contains all three chromatophore types (Sherbrooke and Frost 1989). Physiological color change is common among lizards and occurs in a few snakes (Hedges et al. 1989).

SCALES Scales are thickened layers of epidermal and dermal tissues that form by folding of the integument during embryogenesis. The outer keratin layer of scales, the Oberhäutchen, is ornamented with microscopic ridges and processes. The irridescence of indigo snakes (*Drymarchon corais*) and the intense black patches in the patterns of rhinoceros vipers (*Bitis rhinoceros*) are produced by micro- and nanoscale ridges on the Oberhäutchen (Monroe and Monroe 1968; Spinner et al. 2013). Certain forms of ornamentation are associated with particular microhabitats. For example, fossorial (burrowing) snakes usually have ex-

ceptionally smooth scale surfaces compared with terrestrial species. Scale numbers and arrangements, the patterns on the Oberhäutchen, and osteoderm structure are important characters in species identification.

The **scutes** of turtles (see Figure 4.1B,C) differ from the epidermal scales of other reptilian groups in that the embryonic development of scutes is coordinated with the development of the underlying bone (Zangerl 1969; Mousta-kas-Verho et al. 2014).

SHEDDING Crocodylians and turtles (as well as birds and mammals) shed their outermost layers of skin cells individually or in small groups (dandruff is groups of epidermal cells shed from the human scalp). In contrast, a defining characteristic of the skin of lepidosaurs (squamates and tuatara) is the synchronous production of an epidermal generation of cells that differentiate and are subsequently shed entirely or in large fragments (Maderson 1965; Maderson et al. 1998). Between shedding cycles, the epidermal layers of a squamate scale consist of outer keratin layers underlain by two layers of mature epidermal cells (**Figure 4.2A**). All of these layers constitute one epidermal generation of cells, which was formed during the previous shedding cycle. Be-

low this epidermal generation is the stratum germinativum, which produces each new epidermal generation.

Shedding commences with the synchronous proliferation of cells from the stratum germinativum, which form an inner (newer) epidermal generation layer between the outer (older) epidermal generation of cells. Just prior to shedding, the new epidermal generation becomes keratinized and assumes the same histological appearance as the older outer layer. Fluid accumulates in the stratum intermedium, which consists of the α -keratin layer of the outer generation and the cell layers between it and the β -keratin of the inner generation. Finally, the outer layer is sloughed off entirely (snakes) or in large patches (most lizards) (Figure 4.2B,C). Separation of epidermal layers during the shedding cycle is facilitated by localized anaerobic glycolysis, which produces lactic acid, which increases hydration and separation of the outer cell layers. Additionally, the enzyme acid phosphatase aids in breaking down intercellular desmosomes and cementing material, thus freeing the outer cell layers from those underneath (Alibardi 1998).

The process of shedding by crocodylians and turtles differs from that of squamates. Proliferation of new cells starts in the hinge region of the scales of these taxa (Alibardi and

(B)

(C)



Figure 4.2 Reptile skin and shedding. (A) The epidermis of squamates (lizards and snakes) is formed by α - and β -keratins with a mesos layer between them. The outermost layer (cuticle) of β -keratin is called the Oberhäutchen and bears ridges and spines that probably influence the gain and loss of radiant energy. The lipid-rich mesos layer is a barrier to water loss. Two generations of epidermis are shown—the outer and inner generations (OG, IG)—with a layer of cells between them in which fluid accumulates in preparation for shedding. The OG is sloughed when the animal sheds. The IG becomes the new OG, and the stratum germinativum gives rise to a new IG. (B) Snakes normally shed the entire skin in one piece. (C) Lizards shed the skin in patches. (A after Lillywhite 2014; Photographs: B, © Jim Merli/ Visuals Unlimited, Inc; C, © gopause/Shutterstock.)



Minelli 2015). A new generation of β -keratin cells extends from the hinge region and grows beneath the existing scutes of turtles (Alibardi 2005). Most turtles shed the old scutes (see Figure 4.1C), but tortoises retain the old scutes while new and larger scutes accumulate beneath them, creating pyramidal layers of annuli (see Figure 4.1D). Both mechanisms produce traces that are called "growth rings," but counting the number of growth rings does not provide a reliable estimate of age (Wilson et al. 2003).

Sensory systems

Reptiles rely to varying degrees on the senses common to most tetrapods. Reptile chemosensation (smell and taste) is via the nose, taste buds, and vomeronasal organ and is employed during foraging, orientation, and courtship and other social interactions (see Chapters 13, 14, and 15). Sensitivity to Earth's magnetic field and to polarized light is widespread among tetrapods (although neither has been convincingly demonstrated in humans), and reptiles employ both senses for orientation and navigation (see Chapter 12).

Here we detail the familiar senses of touch, hearing, and sight as they pertain to reptiles. In addition, some snakes have an exquisitely sensitive system that perceives infrared radiation.

TOUCH The skin is a major sense organ of some reptiles. The scales of most squamates and the head scales of crocodylians are supplied with small, circular sense organs called lenticular sense organs or simply scale organs (Matveyeva and Ananjeva 1995; Sherbrooke and Nagle 1996). These organs occur in different numbers on individual scales, and on different parts of the body, and may have speciesspecific arrangements. Often they are supplied with simple or complex hairlike structures, or papillae. They appear to have mechanoreceptive properties in the few squamates that have been studied. In the horned lizards (Phryno*soma*), these organs are hypothesized to detect vibrations through the soil from rainfall or surface predators and to locate attacking ants on the body (Sherbrooke and Nagle 1996). Scale organs may help the aquatic snakes Acrochordus detect prev in murky water (Povel and van der Kooij 1997). In addition to scale organs, some snakes have erectile tissue in the snout that is highly vascularized, innervated, and probably mechanoreceptive. The peculiar projections on the snout of the tentacled snake (Erpeton tentaculum) and on certain vipers are examples (Winokur 1977).

HEARING Reptiles have a single sound-transmitting bone in the inner ear—the columella—rather than the three bones that form the ossicular chain of mammals. The columella is homologous with the stapes, which in mammals is the innermost of the three bones. The inner end of the columella rests on the oval window of the inner ear. In lizards that have ears, the outer end of the columella rests on the tympanum. Although snakes lack a tympanum, they are able to detect sound frequencies from 50 to 1,000 Hz (cycles per second). The outer end of the columella attaches by a ligament to the quadrate bone of the lower jaw. Vibrations in the substrate, water, or air are transmitted via the quadrate and columella to the cochlea of the inner ear, where the vibrations are detected by hair cells, as in other tetrapods.

VISION The eyes of many reptiles (including birds) have two distinctive structures: scleral ossicles, and colored drops of lipid in the cone cells. The sclera is a layer of collagen, elastic fibers, and fibroblasts that surrounds all but the portion of the eyeball where the iris and pupil are located. (The sclera of humans is visible as the white of the eye.) Most reptiles have thin plates of bone, the **scleral ossicles**, embedded in the portion of the sclera that surrounds the pupil (**Figure 4.3A,B**). The ciliary muscles, which change the shape of the lens during focusing, originate in part on the scleral ossicles.

The vertebrate retina contains two categories of photoreceptor cells—rods and cones. Rods contain a single photosensitive pigment and so do not distinguish colors, but they are sensitive in dim light. Many species of vertebrates have more than one type of cone in the retina, and each type is sensitive to a specific wavelength of light, thus enabling color vision. Cones function only above a certain light level, however, and the proportion of rods and cones in the retina generally corresponds to the time of day that a species is active—the retinas of nocturnal vertebrates have mostly rods, whereas those of diurnal species have mostly cones.

The cones of nearly all reptiles contain lipid droplets that lie in the path of the light entering the eye. That is, light must pass through the droplets before it reaches the photosensitive pigment in the cone. These droplets have two functions: they act as miniature lenses, channeling light to the photosensitive pigments, and in most reptiles they contain red, orange, or yellow pigments (**Figure 4.3C**). These colored droplets block short wavelengths (i.e., blue light) and allow longer wavelengths to pass through (Hart and Hunt 2007; Stavenga and Wilts 2014).

The eyes of snakes differ in several ways from those of other squamates (Caprette et al. 2004). These differences probably reflect the redevelopment of the eye from a rudimentary state during the fossorial stage in the evolution of snakes, and the eyes of extant fossorial squamates give us an idea of the ancestral form of the snake eye. Some components of the eyes of amphisbaenians and typhlopids have been greatly reduced or lost entirely (Foureaux et al. 2010). For example, all of the structures that focus an image on the retina (the cornea, lens, and ciliary muscles) are rudimentary in these fossorial squamates. Their cornea is a single layer of cells, the lens is just an irregular clump of cells, and ciliary muscles are absent. Photoreceptor cells are present in the retina, however, as are layers of retinal nerve cells. Thus, the eyes of fossorial squamates probably retain sensitivity to light, although they are unable to form an image.

When snakes radiated into epigean (aboveground) habitats, they had to reconstruct a visual system from a ru-



(B)



Figure 4.3 Scleral ossicles and lipid droplets are found in the eyes of many reptiles. (A) Scleral ossicles of the Chinese water dragon (*Physignathus cocincinus*). (B) Scleral ossicles lie in the anterior portion of the sclera, surrounding the lens. (C) A photomicrograph of cone cells from the retina of a turtle reveals four colors of lipid droplets: red, orange, yellow, and clear. (A, © DigiMorph.org; B after Walls 1942; C, photograph courtesy of Joseph C. Corbo.)

dimentary state such as that seen in fossorial squamates (Repérant et al. 2006). That process led to the appearance of characters unique to snakes, as well as to greater elaboration of structures that are found in some lizards (**Table 4.1**).



1. **Spectacle** A transparent scale, the spectacle, covers the eyes of all snakes and is also found in some lizards (e.g., all xantusiids and many geckos). The spectacle and lens contribute about equally to focus-

TABLE 4.1 Comparison of the eyes of lizards and snakes		
Eye structure	Lizards	Snakes
Transparent spectacle	Present in some lineages	Present in all lineages
Cornea	Convex, uniform thickness	Flattened, margin thicker than center
Corneal blood vessels	Absent	Present
Ciliary muscles	Present	Absent
Scleral ossicles	Present in most lineages	Absent
Iris muscles	Ectodermal origin	Mesodermal origin
Oil droplets	Colored oil macrodroplets	Colorless oil microcrodroplets
Lens pigment	Absent	Yellow
Movement of melanin granules in the pigmented epithelium to adjust sensitivity to light	Present	Absent
Muscular movement of photoreceptor cells to adjust sensitivity to light	Present	Absent
Visual relay centers in the brain	Thalamic centers are better developed and tectal centers are reduced in snakes compared with lizards	
Lens shape at rest	Biconvex ellipsoid (i.e., side-to-side length is greater than front-to-back length)	Approximately spherical (i.e., side-to- side and front-to-back lengths are approximately equal)
Lens movement	Absent	Present

After Walls 1931, 1942; Underwood 1970; Sivak 1977; Bossomaier et al. 1989; Wong 1989; Repérant et al. 1992, 2006; Caprette et al. 2004; Caprette 2005; Franz-Odendaal and Vickaryous 2006; Ott 2006; Baker et al. 2007; Bowmaker 2008; Van Doorn and Sivak 2013.

ing an image on the retina (Sivak 1977; Caprette 2005). The spectacle contains blood vessels, which is surprising because blood vessels in the path of light entering the eye interfere with vision. Blood flow is greatly reduced when a snake is responding to a visual stimulus (Van Doorn and Sivak 2013).

- 2. Ciliary muscles and scleral ossicles All epigean lizards have ciliary muscles, and most lineages have scleral ossicles, whereas snakes have neither ciliary muscles nor scleral ossicles.
- 3. **Macro- and microlipid droplets** Lizards have large, colored oil droplets (macrodroplets) in the cone cells. In contrast, snakes have colorless microdroplets.
- 4. **Colored lenses** Many diurnal snakes have ambercolored lenses, whereas the lenses of lizards are colorless. The amber color in the lens may filter out blue light, and thus may be analogous to the colored macrodroplets in the cones of lizards (Walls 1931).
- 5. **Retinal motility** When the intensity of light changes, both snakes and lizards expand or contract the pupillary opening to adjust the amount of light that reaches the retina. Lizards use two additional mechanisms to control the exposure of rods and cones to light: they can change the position of melanin granules in the pigmented layer of the retina, and they can move the rods and cones

to adjust the depth of their photosensitive portions in the pigmented layer. In bright light, lizards move melanin granules outward and the photoreceptor regions deeper into the pigmented layer to reduce the amount of light reaching the photosensitive portion of the receptors. Snakes lack these mechanisms and rely exclusively on contracting or expanding the pupil to adjust the amount of light that reaches the retinal photoreceptors.

6. Visual pathway The restructuring of the visual system that occurred during the evolution of snakes extends to the sites in the brain where visual signals are analyzed. The major processing center is located in the tectum of lizards, but has moved forward to the thalamus in snakes (Repérant et al. 1992, 2006).

The greatest difference in the visual systems of snakes and lizards lies in how they focus the eye. Like mammals (including humans), lizards merely change the shape of the lens to focus on nearby or distant objects, whereas snakes also move the lens forward or backward to focus.

When it is at rest, a lizard's eye is focused for distance vision and the lens has the shape of a biconvex ellipsoid—that is, its side-to-side diameter is greater than its front-to-back diameter (Figure 4.4A). When a lizard focuses on a nearby object, the ciliary muscles contract, squeezing the annular pad, which applies pressure to the sides of the lens and makes it more spherical. The scleral ossicles provide a sturdy origin for the ciliary muscles as they apply this pressure.

The eves of snakes are also focused for distance vision when they are at rest, but snakes have neither scleral ossicles nor ciliary muscles (Figure 4.4B). To focus on a nearby object, a snake moves the lens forward, although the mechanism that produces this movement is unclear (Ott 2006). Moving the lens is analogous to the way a camera focuses, but at least some snakes employ an additional mechanism that is not possible for the rigid lens of a camera: contraction of the iris sphincter muscles pushes against the flexible lens and causes

Figure 4.4 Functional anatomy of the eyes of lizards and snakes.

(A) Lizards focus the eye for close vision by changing the shape of the lens. (B) Snakes focus by moving the lens forward as well as by changing its shape where it bulges through the iris sphincter. (After Caprette et al. 2004.)



it to bulge slightly through the pupillary opening in the iris. The curved surface of this bulge increases refraction (light bending) and aids in focusing the image on the retina. Deformation of the lens has been observed in several species of semiaquatic colubrids, and may occur in other snakes as well (Ott 2006). **PIT ORGANS: INFRARED DETECTION** Specialized facial organs of three distantly related lineages, the boas, pythons, and pit vipers (see Figure 4.44), detect infrared radiation from avian and mammalian prey (Figure 4.5). These pit organs are exquisitely sensitive, capable of detecting temperature differences as small as 0.001°C (Goris 2011). Pit organs



are innervated by branches of the trigeminal nerve, which in all vertebrates carries sensory information from the skin of the head to the brain. In snakes, however, the trigeminal nerve also carries thermal information from the pit organ to the optic tectum—the part of the brain that processes visual information in non-mammalian vertebrates. Thus, spatial information about the thermal environment is superimposed on the visual image, presumably giving the snake a view of its world in a combination of light and heat (Hartline et al. 1978; Molenaar 1992). Pit organs are effective in localizing endothermal prey even in the darkness of a burrow (see Figure 4.5C).

Unlike vision, which relies on light-sensitive opsin molecules located in the rod and cone cells of the retina to transduce light energy into nerve impulses, the receptors of the pit organs are the neurons themselves. Each sensory nerve ends in an expansion known as a terminal nerve mass (TNM) packed with mitochondria (presumably to provide energy to the highly active neurons). Studies of pit vipers have revealed an intricate network of capillaries surrounding the TNMs. The arrangement of the capillaries and direct measurements of blood flow in response to thermal stimuli suggest that capillary flow is tightly controlled and may function to return the receptors to their resting temperature quickly following thermal stimulation (Amemiya et al. 1999; Goris et al. 2000). The surface of the sensory membrane of pit vipers has minute depressions that filter out nonthermal wavelengths, and the irregular lining of the inner chamber prevents reflection of infrared energy back toward the membrane, which would degrade the thermal image.

Visual pigments that absorb infrared wavelengths do not occur in nature, so the mechanism of transduction in the pit organs has been a subject of debate. Two recent papers shed important light on this question. Gracheva et al. (2010) compared the transcriptomes (the collection of genes active in a tissue) from the trigeminal ganglion (a concentration of neuron cells) of a pit viper, boa, and python with the transcriptomes of two colubrid species (which lack pit organs). They also compared the transcriptome from the trigeminal ganglion, which receives information from pit organ nerves, with transcriptomes from a dorsal root ganglion, which carries general sensory information from the skin in all these taxa. A gene that encodes TRPA1, a transient receptor potential (TRP) channel that allows ions to depolarize nerve cell membranes, was highly expressed only in the pit-serving neurons of all three pit-bearing snakes. Yokoyama et al. (2011) compared the amino acid sequences encoded by the TRPA1 genes of a pit viper, boa, and python with those of a colubrid snake and a variety of other vertebrates. Again, the three heat-sensitive species had converged on the same three amino acid substitutions in the encoded proteins, suggesting that these changes render these TRP ion channels sensitive to infrared radiation. This is an exquisite example of organismal integration from the genomic and biochemical level to the morphology and behavior of the whole organism, played out in in three distantly related lineages.

4.2 🔳 Lepidosauria: Rhynchocephalia

Among extant reptiles, tuatara, lizards, and snakes form the clade Lepidosauria, the sister taxon to Archosauria (birds + crocodylians; see Figure 2.7). Lepidosaurs are characterized by a transverse cloacal slit (it is longitudinal in other tetrapods), regular cycles of skin shedding (see Figure 4.2), and many skeletal features (Gauthier et al. 1988). The oldest described lepidosaur fossil is from the Middle Triassic (~240 million years ago [mya]), coincident with many molecular clock dates that suggest that lepidosaurs radiated after the Permian–Triassic extinction when climates were humid and hospitable for reptiles (Jones et al. 2013).

The tuatara

Among lepidosaurs, Rhynchocephalia is the sister taxon to Squamata (see Figures 2.7 and 4.12). Rhynchocephalians achieved their highest diversity during the Mesozoic, when they displayed much of the morphological and ecological diversity seen in extant squamates. They were distributed worldwide and included small insectivores and herbivores, long-legged terrestrial runners, and aquatic species (Evans and Jones 2010). In other words, the "lizard" fauna of the Mesozoic included the same diversity of behavior and body forms seen in modern lizards, except that Mesozoic "lizards" were rhynchocephalians rather than squamates. Today only a single lineage of rhynchocephalians remains, Sphenodontidae, represented by one species, Sphenodon punctatus, with its natural distribution restricted to small islands off New Zealand's North Island (Figure 4.6). The common name tuatara comes from the Maori and means "spines on the back."

Sphenodontidae is characterized by numerous shared derived characters of skeletal morphology. The teeth are relatively large, acrodont (see Figure 4.8), and have a distinctive pattern of regionalization (heterodonty) in the jaws. Caniniform teeth are present at the anterior end of the maxillae and dentaries. Teeth are also present on the palatine bones—a feature rare in lizards. During ontogeny the premaxillary teeth are replaced by bony downgrowths of the premaxilla, forming a pair of chisel-like structures in adults. Tooth replacement capacity is limited, and the teeth of old individuals are often worn down to the jawbone.

Tuatara have shallow paired outpocketings of the posterior wall of the cloaca that are probably homologues of the hemipenes of squamates (see Section 4.3) (Arnold 1984b). Unlike lizards, *Sphenodon* retains the lower temporal bar in its diapsid skull and hence does not have a streptostylic quadrate as in lizards (see Chapter 11); thus, *Sphenodon* skulls are relatively akinetic. Osteoderms are absent. As in many lizards, the tail of *Sphenodon* has autotomic planes (see Figure 4.9) that allow the tail to break off at specific points.

Tuatara are lizardlike in body form and reach about 30 cm SVL. Males have a more prominent crest than females and reach a larger body size. Tuatara are terrestrial and con-

4.3 Lepidosauria: Squamata 115



(A)

Figure 4.6 Rhynchocephalia. (A) The tuatara, *Sphenodon punctatus*, is the only extant rhynchocephalian. (B) Tuatara occur in 32 natural island populations, 9 translocated island populations, and 5 translocated populations in fenced sanctuaries on the North and South Islands. (A, photograph courtesy of Harvey Pough; B after Cree 2014.)

struct their own burrows or use those of ground-nesting seabirds. They bask in the sun at the entrances to their burrows but are most active at night. Tuatara are carnivorous and eat invertebrates, bird eggs and nestlings, lizards, and *Leiopelma* frogs.

Fossil record

The earliest rhynchocephalian fossils are from the Middle Triassic of Europe and North America, approximately 240 mya (Jones et al. 2013). By the Early Jurassic rhynchocephalians were widespread over Pangaea. They became extinct in Asia in the Early Jurassic and in Laurasia by the Middle Cretaceous, a period that coincided with the rise of squamate reptiles. However, the discovery of a large deposit of Late Cretaceous sphenodontid fossils in South America shows that rhynchocephalians coexisted with early squamate lineages longer than previously assumed (Apesteguía and Novas 2003). Fossils of Early Miocene (19-16 mva) sphenodontids in New Zealand indicate that modern-day Sphenodon are not recent immigrants to the island. Instead, Sphenodon is a relict lineage of rhynchocephalians that became isolated on the New Zealand subcontinent when it separated from Antarctica 82-60 mya (Jones et al. 2009). Rhynchocephalian fossils are also known from the Gondwanan landmasses of Madagascar (Flynn et al. 1997), Brazil (Ferigolo 1999), India (Evans et al. 2001), and southern Africa (Gow and Raath 1977; Sues and Reisz 1995).

Classification, distribution, and conservation The isolation of the remaining natural populations of tuatara on islands that extend from 35°S to 41°S has complicated the question of whether the genus Sphenodon should be treated as multiple species or a single species (Daugherty et al. 1990). Here we follow Cree (2014) and recognize 1 species, S. punctatus, with substantial genetic variation among populations (Hay et al. 2010). Sphenodon once inhabited the two main islands of New Zealand but was extirpated after the arrival of humans in the late 13th century and the subsequent introduction of rodents and domestic animals. It now occurs naturally on 32 small offshore islands (see Figure 4.6), but there are ongoing conservation efforts to reintroduce tuatara to the two main islands (Miller et al. 2012). The IUCN lists S. punctatus as Vulnerable.

Systematics references Hay et al. (2010), Jones et al. (2013).

4.3 🔳 Lepidosauria: Squamata

Lizards (including amphisbaenians) and snakes comprise the Squamata. Squamates were previously classified into coequal Linnean suborders called Lacertilia, Amphisbaenia, and Serpentes. However, phylogenetic analyses of morphology and of DNA have shown that both amphisbaenians and snakes are derived from within lizards (see discussion below). Because Lacertilia is not monophyletic, it is no longer formally recognized as a taxon. Nevertheless, we use the term lizards (including amphisbaenians) for convenience, and because of many differences in their biology and natural history, we discuss lizards and snakes



Figure 4.7 Structure of hemipenes of squamates. (A) Parasagittal sections through the base of a snake tail showing a hemipenis inverted (left) and everted (right). (B,C) Everted hemipenes showing external ornamentation. (B) Hemipenis of the sand lizard (*Lacerta agilis*). (C) Hemipenis of the copperhead (*Agkistrodon contortrix*). (After Dowling and Savage 1960.)

separately. This treatment should cause no confusion as long as their phylogenetic relationships are kept in mind.

General anatomy of squamates

Squamates can be diagnosed by more than 70 anatomical characters, primarily of the musculoskeletal system (Estes et al. 1988). A characteristic feature of squamates is a pair of copulatory organs called **hemipenes** (singular *hemipenis*). These are outpocketings of the hindwall of the vent at the base of the tail of males (**Figure 4.7**; see also Figure 9.12) (Arnold 1984b). Penes of all other amniotes are single and, if internal, reside in the cloaca. A groove in the surface of each hemipenis, the sulcus spermaticus, transports sperm flowing from the cloaca during copulation. Hemipenes often have spines, ridges, and other ornamentation. Varanid lizards have mineralized structures (hemibacula) that add rigidity to their hemipenes (Card and Kluge 1995).

Hemipenes are everted during copulation and retracted by their own intrinsic musculature. Only a single hemipenis (either the left or right) is used during copulation. Some female squamates have tiny homologues of hemipenes, dubbed diverticula (singular diverticulum) (Arnold 1984b) or hemiclitori (singular hemiclitoris) (Böhme 1995), housed within their tail base. However, the presence and development of these homologues in female squamates appear highly variable, unlike the clitoris of mammals (Myers and Cadle 2003).

Squamates have two distinct patterns of tooth attachment (Figure 4.8). **Acrodont** teeth are attached to the crests of the jaw bones, whereas **pleurodont** teeth are attached to the inner sides of the jaw bones (**Figure 4.8A,B**). The pleurodont pattern is thought to be the ancestral condition. Derived snakes have a modified type of pleurodonty in which bony material invests the base of each tooth so that a rudimentary socket forms (Figure 4.8C) (Zaher and Rieppel 1999).

Reproduction and sex determination

Reproductive and sex-determining mechanisms are extremely diverse in squamates, and even casual inspection suggests that most patterns have evolved numerous times. Although most squamates are oviparous (egg-laying), approximately 20% of squamate species are viviparous (giving birth to live young), and viviparity has evolved independently more than 100 times (see Section 9.3) (Blackburn 2014). All viviparous species have at least a rudimentary placenta that transports gas, water, and inorganic ions to the embryo. In many viviparous species, the mother



Figure 4.8 Forms of tooth implantation. Diagrammatic views of a single tooth showing its attachment to the jawbone. (A) Acrodont implantation (chamaeleons, agamids, and some amphisbaenians). Teeth are attached to the crest of the jawbone and are rarely replaced. (B) Pleurodont implantation is found in other lizards. The tooth is attached to the inner (lingual) side of the jawbone. Pleurodont teeth are replaced in a staggered sequence. (C) Modified pleurodont implantation is found in advanced snakes. It is similar to the pleurodont condition with the addition of bony material at the base of each tooth giving the appearance of a rudimentary socket. (D) Tooth replacement in the upper jaw of a green iguana (*Iguana iguana*). Staggered waves of replacement move from anterior to posterior so that adjacent teeth are never replaced at the same time. (D after Edmund 1969.)

ovulates eggs with large amounts of yolk and little or no nutrient provisioning occurs across the placenta. A more elaborate placenta has evolved independently in at least five lineages of skinks (Scincidae). In these lineages, mothers ovulate eggs with small yolks, and the embryos instead receive a substantial amount of nutrients across the placenta. An analysis of gene expression in the non-pregnant and pregnant uterus of the viviparous skink *Chalcides ocellatus* demonstrated that viviparous lizards and therian mammals use many of the same genes for the maintainance and specialized functions of the placenta (Brandley et al. 2012).

Parthenogenesis, the ability to produce offspring without mating, occurs in several lizard families (e.g., Agamidae, Gekkonidae, Teiidae, Gymnophthalmidae, Lacertidae, Xantusiidae) and in the snake *Indotyphlops braminus* (Typhlopidae). Except in Xantusiidae, parthenogenesis is thought to result from interspecific hybridization of two sexually reproducing species that results in a species with no males (see Figure 9.5).

Sex-determining mechanisms have been investigated in relatively few lineages, but tremendous diversity prevails. *Sphenodon* and about 17 species of skinks, lacertids, gekkonids, and agamids are known to have temperature-

Vertebrae with fracture planes

(A)

dependent sex determination (TSD) whereby the embryos may vary between 100% male or 100% female, depending on the incubation temperature. Genetic sex determination is also known in these and other families (see Figure 9.3). TSD is unknown among snakes.

Tail autotomy

Many squamates lose the tail as a defensive mechanism. Tail breakage, or **caudal autotomy**, can be intravertebral or intervertebral (reviewed in Bateman and Fleming 2009). Most squamates have intravertebral autotomy, wherein tail breakage is facilitated by the presence of fracture planes in specific vertebrae and by an arrangement of caudal muscle bundles and connective tissue that permits easy separation (**Figure 4.9**). The tail commonly contains several vertebrae with fracture planes; these are concentrated in the region of the tail closest to the body. The animal controls when to break and release the tail, after which the tail may twitch or flop for up to 30 minutes, presumably distracting a predator while the

> Figure 4.9 Intravertebral tail autotomy. (A) Many lizards have fracture planes in vertebrae near the base of the tail. (B) The fracture planes are near the center of each vertebra, and the break occurs within a vertebra. (C) A rod of cartilage grows from the point of fracture as the tail is regenerated. A regenerated tail is not as long as the original tail, so the cartilage has no fracture planes and any second autotomy can only occur closer to the lizard's body than the first autotomy. (D) A Mediterranean house gecko (Hemidactylus turcicus) with its recently shed tail. (E) H. turcicus with regenerated tail. (A-C from Amorim et al. 2015, courtesy of Joana D.C.G. de Amorim; D C Matt Jeppson/Shutterstock; E © nico99/Shutterstock.)

> > Cartilage rod



now stump-tailed lizard prey escapes. A regenerated tail is shorter than the original tail and is supported internally by a solid rod of cartilage rather than by discrete bony vertebrae. The regenerated tail is often quite obvious as it is usually a different color or color pattern than the original tail.

In contrast, a break between vertebrae (intervertebral autotomy, or pseudoautotomy) is not under voluntary control, and the tail will not regenerate. Intervertebral autotomy occurs in a few genera of colubrid snakes (e.g., *Dendrophidion*, *Pliocercus, Scaphiodontophis, Thannophis*), many iguanian lizards, and isolated cases in other squamate families (Arnold 1984a). Although it is a shared derived character of Lepi-

(B)

dosauria, caudal autotomy has been lost many times over the course of squamate evolution (Arnold 1984a), including in Chamaeleonidae, Helodermatidae, Lanthanotidae, Varanidae, Xenosauridae, some Scincidae, and multiple Pleurodonta clades.

Limb reduction

The repeated independent evolution of limb reduction is a striking morphological trend in squamates. Most cases of limb reduction consist only of the loss of a few phalanges in the hand or foot (Greer 1991), but a completely limbless body form has evolved at least 25 separate times (Wiens et al. 2006; Brandley et al. 2008). Many genera of skinks, including *Chalcides* and *Lerista*, display extreme variation in limb development among species (Greer 1990; Greer et al. 1998; Skinner and Lee 2009), including pentadactyl and limbless species as well as species with one to four digits on





the hand or foot (**Figure 4.10**). Nor is limb reduction limited to extant groups; limb reduction appears in Late Cretaceous fossil snakes and in the extinct squamate genus *Adriosaurus* (Palci and Caldwell 2007). Limb reduction is strongly correlated with body elongation, with the limbless species also being the most elongate.

Venom and venom-delivering structures

All animals synthesize proteins that have destructive effects on other proteins or on cellular structures. Most of these proteins either participate in intracellular housekeeping, disassembling damaged proteins and antigens; or they are digestive enzymes that break down food in the digestive system. Reptile venoms consist of complex mixtures of proteins, many of which have highly toxic effects when they are injected into prey. Some venoms are rich in enzymes that break down living tissues, including blood cells, blood vessels, and clotting proteins, so that prey die from massive internal hemorrhage. Other venoms target synaptic or neuromuscular junctions, disrupting the cardiovascular and respiratory systems. Molecular phylogenetic studies of genes that code for destructive proteins have identified a proposed clade of squamates, Toxicofera, that express these genes in oral glands (Vidal and Hedges 2005; Fry et al. 2006, 2009, 2013). By this interpretation, venom evolved in the common ancestor of the Iguania, Anguimorpha, and Serpentes (see Figure 4.12).

However, recent genomic and proteomic studies have spawned a controversy over what constitutes venom and the property of being venomous. No one doubts that helodermatid lizards and viperid and elapid snakes are venomous, and some authors feel that a taxon can be considered venomous if its oral glands express genes homologous to venom genes of those taxa. However, many of these genes are expressed in a variety of body tissues in addition to oral glands-including the skin and cloacal scent glands-suggesting that these are housekeeping genes (Hargreaves et al. 2014a,b). Other researchers insist that genetic homology is insufficient to identify a toxin, and that the proteins must be shown to function in subduing or digesting prey (Kardong 2012; Weinstein and Keyler 2012). The distinction is not a trivial one, as it determines whether we regard all members of the Toxicofera (including many small, seemingly innocuous lizards and snakes) as venomous, and whether we regard venom systems as evolving once or many times within that lineage or only twice or three times: once at the base of Colubroidea, once in the helodermatid lineage, and possibly once in monitor lizards (Varanidae) (Weinstein et al. 2009).

Squamate phylogeny

Camp's 1923 Classification of the Lizards laid the foundation of modern squamate systematics by classifying squamates into taxonomic groups based on assumed evolutionary history. Some parts of his classification scheme survive today, including the clades Gekkota and Iguania. Estes et al. (1988) provided the first cladistic analysis of squamates based on morphology (**Figure 4.11A**). Several clades described in this phylogeny, especially Iguania, Scleroglossa, Autarchoglossa, Anguimorpha, and Scincomorpha, have been used frequently in the literature and have heavily influenced the interpretation of squamate biology. Recent cladistic analyses based on morphological data for both extant and extinct species have largely supported the major clades of the Estes et al. (1988) phylogeny; these include Conrad (2008) (**Figure 4.11B**) and Gauthier et al. (2012) (**Figure 4.11C**).

In the mid-2000s, the first comprehensive analyses of squamate molecular phylogenetic data were published (e.g., Townsend et al. 2004; Vidal and Hedges 2004). Although these studies supported many relationships inferred from morphology, they also supported some radically different relationships (**Figure 4.12**). Most notably, in DNA-based phylogenies:

- 1. Iguania is nested deep within the squamate phylogeny rather than being the sister lineage to all other squamates. Instead, either geckos or dibamids are the sister lineage to the rest of the squamates.
- The clades Scleroglossa and Autarchoglossa are not monophyletic and are no longer recognized. Anguimorpha, Scincomorpha, and Lacertoidea as defined by morphological data are also not monophyletic, but these names have been redefined to reflect the the molecular phylogenetic relationships.
- 3. Lacertidae, with a classic lizard-like body plan, and the limbless Amphisbaenia are sister taxa.
- 4. Shinisauridae and Xenosauridae are not sister taxa.
- 5. Helodermatidae, Lanthanotidae, and Varanidae do not form a clade (Varanoidea or Platynota).

More recent phylogenetic analyses of thousands of species and numerous nuclear genes have provided even more support for a phylogenetic history of squamates differing from that inferred from morphological data (e.g., Vidal and Hedges 2004, 2005, 2009; Wiens et al. 2010b, 2012; Mulcahy et al. 2012; Jones et al. 2013; Pyron et al. 2013a). However, molecular data have not solved all phylogenetic mysteries. For example, the interrelationships of pleurodont iguanians remain largely unresolved, as does the placement of snakes with respect to other squamates. It seems unlikely that there will ever be a widely accepted consensus of morphological and molecular squamate phylogenies.

The molecular phylogeny does not yet have universal support, especially in the paleontological community. This is understandable because many clades in the molecular tree have no known morphological synapomorphies, and it is therefore difficult to include fossil data in this phylogenetic framework (but see Wiens et al. 2010b). Nonetheless, molecular phylogenies are gaining increasing acceptance, especially as they are corroborated by increasingly larger molecular data sets, and this textbook follows the molecular phylogenetic framework shown in Figure 4.12.



(C) Gauthier et al. (2012)





Figure 4.11 Three squamate phylogenies based on analysis of morphological data. (A) Estes et al. (1988) provided the first cladistic analysis of squamates based on morphological data. These major clades were largely supported in subsequent phylogenetic analysis of morphological data by (B) Conrad (2008) and (C) Gauthier et al. (2012).

Fossil record

Attributing fossil taxa to extant squamate clades can be challenging because of the conflicting relationships inferred from molecular and morphological data. Molecular dating analyses and the presence of rhynchocephalian fossils in the Middle Triassic (Jones et al. 2013) indicate that the squamate lineage (although not necessarily identifiable modern clades) may also have been present in the Middle Triassic. However, no undisputed squamate fossils exist for this time period (Evans and Jones 2010; Hutchinson et al. 2012).

Figure 4.12 Phylogenetic analysis of squamates based > on DNA data. Recent molecular phylogenetic analyses support a squamate history that differs from those inferred from morphological results. This is the phylogeny followed in this textbook. Toxicofera has been proposed as a clade name based on molecular phylogenetic studies of genes that code for several destructive proteins (i.e., venoms), but its use remains controversial (see p. 119).



By the Middle Jurassic, the fossil record contains taxa that resemble some modern lizard lineages (e.g., iguanians), suggesting that the radiation of crown group squamates was well underway by this time. Indeed, molecular dating estimates support the age of crown group (extant clades) Squamata as about 176–213 mya, some time in the Late Triassic or Early Jurassic (Jones et al. 2013). Jurassic lizard assemblages include primarily extinct groups, whereas by the Late Cretaceous most fossils belong to extant clades (Evans 1993). The Early Cretaceous marks the first appearance of several squamate groups, including snakes and amphisbaenians (Rage and Richter 1995; Gao and Nessov 1998). All known Jurassic lizard fossils are from Laurasian landmasses, and their early history in Gondwana is obscure. See Estes (1983) and Evans (2003) for overviews of the fossil record of lizards.

4.4 Squamata: Lizards

Lizards (including amphisbaeninans) account for more than 6,100 extant squamate species (Uetz and Hošek 2015). Lizards inhabit all continents except Antarctica, elevations from from sea level to above treeline, and habitats ranging from deserts to tropical rainforests to alpine meadows. The ranges of a few species, including the lacertid lizard *Zootoca vivipara* even extend north of the Arctic Circle.

Systematics and Phylogeny of Lizards

As the phylogenetic relationships of squamates have changed over the years, so has lizard taxonomy. We use the Linnean family level suffix -dae for subclades of geckos, iguanians, and amphisbaenians that were sometimes previously classified as subfamilies, and we recognize Gekkota, Iguania, and Amphisbaenia as names for the larger clades (see Figure 4.12). We adopt Acrodonta for the iguanian clade containing Agamidae and Chamaeleonidae, and Pleurodonta for all other iguanians. We also recognize Anguimorpha, Scincomorpha, and Lacertoidea, but the membership of those clades differs from that in previous morphological analyses. The generic content of different taxonomic groups used here is derived from The Reptile Database (Uetz and Hošek 2015).

Dibamidae • Blind Skinks

These are small (25 cm total length), attenuated burrowers with vestigial eyes covered by scales. They lack external ear openings. Both ends of the body are blunt. Males have small, flaplike hindlimbs, and females are limbless. Dibamids are oviparous, and all of the available records indicate that the clutch size is 1 egg. *Anelytropsis* are found in seasonally dry habitats in Mexico, such as deciduous scrubland and pine-oak forests. *Dibamus* (**Figure 4.13A**) occur in rainforests and secondary forests in Asia. Although the two genera have a remarkably disjunct distribution, both molecular phylogenetic data and a long list of unusual morphological attributes corroborate their relationship.

Although they diverged very early in squamate evolutionary history and thus are potentially the sister lineage to all other squamates, the highly modified body form of dibamids almost certainly does not represent the ancestral body form of extant squamates. Instead, the dibamid body form evolved over the >180-million-year history of this lineage (Brandley et al. 2008).

Classification, **distribution**, **and conservation** 2 genera (*Anelytropsis*, *Dibamus*), 23 species. Their distribution is



disjunct, with *Anelytropsis* in northeastern Mexico (Figure 4.13B) and *Dibanus* in extreme mainland Southeast Asian (Vietnam and Malaysia) east through the southern Philippines and islands of the Sunda Shelf to western New Guinea (Figure 4.13C). The prevailing hypothesis for the unusual distribution of *Dibanus* and *Anelytropsis* is that the ancestor of one or the other genus dispersed to or from North America via Beringia in the Late Paleocene or Eocene. No species are listed by the IUCN as an extinction risk, but given their secretive nature, little information about natural history or population sizes has been collected for these species.

Systematics references Greer (1985), Townsend et al. (2011a).

GEKKOTA

Gekkotans—the geckos—are a diverse clade with more than 1,500 species, accounting for approximately 25% of the total number of lizard species (Uetz and Hošek 2015). They are distributed worldwide and often are major components of the local reptile fauna. Extant species range in SVL from a maximum of 24 cm in the New Caledonian *Rhacodactylus leachianus* to 15–18 mm in the Caribbean *Sphaerodactylus ariasae* and *S. parthenopion*, which rival dwarf chameleons as the smallest amniotes in the world (Hedges and Thomas 2001). The extinct New Zealand *Hoplodactylus delcourti* reached 37 cm SVL (62 cm total length), but the only existing representative of the species is a stuffed museum specimen (Bauer and Russell 1986).

Many species of geckos have toe pads that enable these animals to cling to surfaces. These pads have been gained and lost repeatedly over the course of gekkotan evolution, and there is little evidence that adhesive toe pads affect speciation rates (Gamble et al. 2012). Although the digital modifications of geckos function primarily on vertical surfaces, such as rock faces or in trees, many species of geckos are secondarily terrestrial and show a reduction in the elaboration of digital pads, as well as other specializations for terrestriality.

Most geckos are nocturnal, although some geckos of tropical forests are diurnal—for example, *Gonatodes* and *Sphaerodactylus* (Sphaerodactylidae) of the Neotropics, *Lygodactylus* (Gekkonidae) of Africa and Madagascar, and some species in desert regions, including *Rhoptropus* (Gekkonidae) and *Quedenfeldtia* (Sphaerodactylidae) of Africa. Species of *Phelsuma* (Gekkonidae), commonly called day geckos, are all diurnal. Many species of *Phelsuma* have patterns of green, blue, yellow, and red, bright colors that are unusual among geckos. And although vocal communication is rare among squamates, many geckos (except eublepharines) emit clicks or chirps for intraspecific communication, including territorial calls, intersexual communication, and distress calls (Tang et al. 2001).

Geckos are predominantly oviparous; only the New Zealand diplodactylid genera and two species of New Caledonian *Rhacodactylus* are viviparous. Oviparous species have only 1 or 2 eggs per clutch. The eggshells of carphodactylids, eublepharids, pygopodids, and diplodactylids are leathery or parchmentlike, like those of virtually all squamates. In contrast, the eggshells of gekkonids, phyllodactylids, and sphaerodactylids are rigid and calcified. Calcium in the form of calcium carbonate is stored in expansions of the endolymphatic system of gekkonids and is mobilized for eggshell production and for rapid bone growth.

Parthenogenesis occurs in some gekkonids, including *Heteronotia binoei*, several species of *Hemidactylus*, *Lepido-dactylus lugubris*, and *Nactus pelagicus*. As in other parthenogenetic squamates, most of these are species complexes of diploid and polyploid forms, and the parthenogens result from hybridization. Temperature-dependent sex determination occurs in multiple clades of geckos, including some Diplodactylidae, Eublepharidae, Phyllodactylidae, and Gekkonidae (see Gamble 2010 for review).

Defensive mechanisms are especially well developed among geckos. The tail of most species is highly autotomic. Some geckos, such as the gekkonids *Geckolepis* and *Gehyra* and the sphaerodactylids *Sphaerodactylus* and *Teratoscincus*, shed large patches of skin as an antipredator strategy (Bauer and Russell 1992). When grasped, *Gehyra* leaves the predator with only a patch of skin to consume. Both the epidermis and layers of the dermis are shed, even revealing the underlying muscle under the patch of missing skin. In this case, skin loss is facilitated by a splitting zone within the dermis (Bauer et al. 1989); it takes weeks to months for the lost skin to regenerate.

There is no question that geckos form a clade, but the phylogenetic placement of the group within Squamata has changed over the years. Some taxonomic treatments continue to use Gekkonidae rather than Gekkota and refer to the families we describe in this text as subfamilies. Pygopodidae was recognized as separate from Gekkonidae/ Gekkota in older taxonomies. In phylogenetic analyses of morphological data, geckos and all non-iguanian squamates form a clade called Scleroglossa. However, analyses of molecular data have yielded strong evidence that geckos are instead one of the earliest lineages of exant squamates. The fossil record of geckos includes one of the earliest squamate fossils, the Late Jurassic *Eichstaettisaurus*, a putative stem gekkotan (Gauthier et al. 2012).

Systematics references Underwood (1954), Kluge (1967, 1976, 1987), Gamble et al. (2008a,b, 2011).

Diplodactylidae • Pacific Geckos

Diplodactylids are the only geckos in New Zealand and are the dominant gecko family in Australia and New Caledonia. Unlike Australian carphodactylid geckos, all diplodactylids have broadened adhesive toe pads (except *Lucasium damaeum*, in which toe pads were secondarily lost). Diplodactylid geckos are usually nocturnal, but a few species are diurnal. Various species are arboreal or terrestrial.



Though all diplodactylids have the typical gecko appearance (**Figure 4.14A**), they exhibit many traits unique within Gekkota. For example, this clade contains the only viviparous geckos. The tails of *Hoplodactylus*, *Bavayia*, *Eurydactylodes*, *Rhacodactylus*, and *Pseudothecadactylus* are prehensile and possess adhesive pads with a structure similar to that of adhesive toe pads. Some diplodactylid species can squirt a stucky fluid from their tail to deter predators. Recent molecular studies have uncovered significant cryptic diversity within Diplodactylidae, with numerous new species described.

Classification, distribution, and conservation 25 genera, 128 species. Representative genera include *Bavayia, Diplodactylus, Oedura, Naultinus, Rhacodactylus, Pseudothecadacty-*

(A) Pygopodidae



lus, and *Strophurus.* Diplodactylids occur in Australia, New Caledonia, and New Zealand (**Figure 4.14B**). The IUCN lists 6 species as Critically Endangered or Endangered and 13 species as Near Threatened or Vulnerable.

Systematics references Bauer (1990), Oliver and Sanders (2009), Oliver et al. (2009), Nielsen et al. (2011), Oliver and Bauer (2011).

Pygopodidae • Flap-Footed Lizards

Pygopods are elongate, snakelike lizards without forelimbs and with hindlimbs reduced to scaly flaps at the level of the vent. Their eyes are covered by an immovable spectacle, and external ear openings are sometimes absent. Most species are surface dwelling and may hide in leaf litter, under surface objects, or in low vegetation. These species have a classic grass swimming morphology with a relatively short body (SVL), but a very long tail that is autotomic. The exception is *Aprasia*, which secondarily evolved a burrowing morphology with a long body and short tail (<50% SVL) (Wiens et al. 2006). Some *Delma, Ophidiocephalus*, and *Pletholax* are highly modified sand-swimmers (**Figure 4.15A**).

Delma and some species of Pygopus are nocturnal, other species of Pygopus are diurnal, and Lialis has been reported

Figure 4.15 Pygopodidae and Carphodactylidae. (A) Peace delma, *Delma pax*. (Pygopodidae). (B) Spiny knob-tailed gecko, *Nephrurus asper* (Carphodactylidae). (C) Distribution. (Photographs courtesy of Stephen Zozaya.)

(B) Carphodactylidae





as being both nocturnal and diurnal. Most pygopods consume arthropods (insects and spiders), but *Lialis burtoni* and *L. jicari* are scincid lizard specialists. Predation on skinks by *Lialis* is facilitated by unusual anatomical modifications, including pointed, recurved, hinged teeth and highly mobile kinetic joints in the elongate skull (Patchell and Shine 1986a,b). Pygopods lay clutches of 1–2 eggs.

Classification, distribution, and conservation 8 genera, 44 species. Representative genera include *Aprasia, Delma, Lialis, Pletholax,* and *Pygopus.* They inhabit Australia and New Guinea (**Figure 4.15C**). The IUCN lists 1 species (*Aprasia aurita*) as Critically Endangered and 6 species as Vulnerable.

Systematics references Kluge (1974, 1976), Jennings et al. (2003), Lee et al. (2009), Oliver and Sanders (2009).

Carphodactylidae • Knob-Tailed Geckos

Carphodacytilids are medium-size geckos (70–145 mm SVL) native to Australia. The tail of carphodactylids is short and fat, often with a knobbed tip that may be flattened into a leaf shape (**Figure 4.15B**). They are nocturnal and occupy terrestrial or arboreal habitats. All species lack adhesive toe pads and are oviparous, laying leathery eggs.

(A)



Classification, distribution, and conservation 7 genera, 30 species. Genera include *Carphodactylus, Nephrurus, Orraya, Phyllurus, Saltuarius, Underwoodisaurus,* and *Uvidicolus.* They inhabit Australia (**Figure 4.15C**). The IUCN lists 2 species as Critically Endangered or Endangered.

Systematics references Oliver and Sanders (2009), Oliver and Bauer (2011).

Eublepharidae • Eyelid Geckos

Eublepharids are nocturnal and inhabit terrestrial environments, with the exception of Aeluroscalabotes felinus, which is semiarboreal. They lack the toepads and subdigital setae that give many geckos exceptional climbing ability. Eublepharids are also the only geckos that retain functional eyelids. In other gekkotans the eyes are covered by an immovable spectacle. Most eublepharids occupy arid or subhumid environments, and some (e.g., Hemitheconyx, Holodactylus) are highly modified for life in sandy habitats. Hemitheconyx taylori and Holodactylus africanus are even semifossorial and construct burrow systems in sand. Coleonyx species of Central America inhabit seasonally dry tropical forests, whereas the northern species inhabit deserts. Aeluroscalabotes felinus has opposable digits (Grismer 1997). The family includes the leopard gecko Eublepharis macularius (Figure 4.16A), a common pet and research subject.

Classification, distribution, and conservation 6 genera, 36 species. Genera include *Aeluroscalabotes, Coleonyx, Eublepharis, Goniurosaurus, Hemitheconyx,* and *Holodactylus.* The family has a widespread but disjunct distribution, including East and West Africa, the Middle East, South and

Figure 4.16 Eublepharidae. (A) Leopard gecko, *Eublepharis macularius*. (B) Distribution. (Photograph © Juniors Bildarchiv GmbH/Alamy.)



Southeast Asia, and North and Central America (Figure 4.16B). The IUCN lists 1 species (*Goniurosaurus kuroiwae*) as Endangered.

Systematics references Grismer (1988), Ota et al. (1999), Jonniaux and Kumazawa (2008).

Sphaerodactylidae • Dwarf Geckos

Sphaerodactylids are medium to very small lizards (15 mm SVL for some *Sphaerodactylus*) inhabiting primarily mesic and xeric habitats (**Figure 4.17A**). Most species are ground dwellers, but some are arboreal or fossorial. Most sphaero-dactylids are diurnal, although crepuscular and nocturnal species exist. Their diet is primarily insectivorous, and some species of *Pristurus* consume ants. The presence or absence of toepads is variable across the family. Sphaerodactylids are oviparous and lay a single hard-shelled egg rather than a 2-egg clutch like other geckos. The disjunct distribution of the family probably results from a combination of the formation of the Atlantic Ocean about 120–100 mya with subsequent island and continental dispersal (Gamble et al. 2008a).

Classification, distribution, and conservation 12 genera, 209 species. Representative genera include *Aristelliger, Lepidoblepharis, Gonatodes, Pristurus, Sphaerodactylus*, and *Teratoscincus*. They have a disjunct distribution, primarily in Central and South America, the Caribbean, North Africa, East Africa, the Arabian Peninsula, and western Asia (**Figure 4.17B**). The IUCN lists 6 species as Critically Endangered or Endangered and 12 species as Near Threatened or Vulnerable.

Systematics references Gamble et al. (2008a,b).

Phyllodactylidae • Leaf-Toed Geckos

Phyllodactylids are medium-size (50–110 mm SVL) and occur mostly in semiarid to desert habitats, often in rocky areas. The common name of this family refers to the lateral expansions of the distal tips of the toes of some species (**Figure 4.18A**). These expanded toe tips usually contain adhesive pads.

Most species of phyllodactylids are nocturnal. *Tarentola* is unusual among geckos in being diurnal and basking during the day. The Moorish wall gecko (*T. mauritanica*) is native to the western Mediterranean but has been introduced widely in North America and Asia. *Tarentola* also are notable because they possess three phalanges in the first digit of both the hand and foot rather than the ancestral state of two phalanges (Greer 1992).

Classification, distribution, and conservation 9 genera, 134 species. Representative genera include *Asaccus, Homonota, Phyllodactylus, Tarentola,* and *Thecadactylus.* They have a disjunct distribution: Central and South America, the Caribbean, North Africa (including the Sahara Desert), circum-Mediterranean region, Arabian Peninsula, and the Middle East (**Figure 4.18B**). The IUCN lists 1 species (*Tarentola gigas*) as Endangered and 6 species as Near Threatened or Vulnerable.

Systematics references Gamble et al. (2008a).

Gekkonidae • Spectacled Geckos

With more than 950 species, gekkonids are one of the largest lizard families (second to Scincidae) and are distributed worldwide. Species may be diurnal or nocturnal, terrestrial or arboreal. Most gekkonid genera have adhesive toepads, al-





Figure 4.18 Phyllodactylidae. (A) Musandam leaf-toed gecko, Asaccus caudivolvulus, Arabian Peninsula. (B) Distribution. (Photograph courtesy of Todd W. Pierson.)

though these have been secondarily lost in some genera. The clade contains many species recognizable to the lay public, such as day geckos (Phelsuma), the Tokay gecko (Gekko gecko), and multiple Hemidactylus species that have been accidentally introduced to human dwellings around the globe.



About 10% of gekkonid species lay eggs in communal nests, where the presence of adults may reduce egg mortality. The Australian Heteronotia binoei is notable because parthenogenesis has evolved multiple times. All parthenogenenic individuals are triploid (3n) and the result of repeated hybridizations between populations over the past 300,000 years. Parthenogenetic clones subsequently spread over a wide range of arid western and central Australia, suggesting that this reproductive mode is highly adaptive for this environment (Fujita et al. 2010).



(A)

Classification, distribution, and conservation 54 genera, 996 species. Representative genera include *Cnemaspis, Cyrtodactylus, Gehyra, Gekko, Hemidactylus, Heteronotia* (Figure 4.19A), and *Phelsuma*. They have a cosmopolitan distribution with the exception of northern North America and Eurasia (Figure 4.19B). The IUCN lists 47 species as Critically Endangered or Endangered and 67 species as Near Threatened or Vulnerable.

Systematics references Feng et al. (2007), Gamble et al. (2008a,b), Bauer et al. (2013).

SCINCOMORPHA

Scincomorpha includes three relatively small families (Cordylidae, Gerrhosauridae, and Xantusiidae) and Scincidae, the largest and most morphologically diverse family of lizards (see Figure 4.12). Although Cordylidae, Gerrhosauridae, and Scincidae have long been thought to form a clade supported by numerous morphological synapomorphies (Scincomorpha of Estes et al. 1988; see Figure 4.11A), Xantusiidae was only recently included in Scincomorpha after molecular data strongly supported the sister relation-



ship of this family to a clade composed of Cordylidae + Gerrhosauridae. This suggests that morphological characters supporting a close relationship of Cordylidae, Gerrhosauridae, and Scincidae were lost in the evolutionary history of the Xantusiidae lineage. Scincomorpha is sometimes called Scincoidea (e.g., Pyron et al. 2013a); both clade names include the same families.

Scincidae • Skinks

Scincidae is the most species-rich lizard family, with almost 1,600 species. Body forms are extremely variable, from rather typical lizards with robust limbs and a short body to limbless species with an elongate, snakelike body (**Figure 4.20A–D**). This morphology reflects the diversity of habitats that skinks occupy, although terrestrial and fossorial species of skinks are more common than arboreal and aquatic species.

Many species of skinks are litter- or sand-swimmers. For example, the Australian genus Lerista includes nearly 100 species, most of which burrow in loose substrates (Pough et al. 1997; Bergman et al. 2009). Amphiglossus astrolabi from Madagascar is aquatic and can be caught using fish traps. Cryptoblepharis boutonii, a small skink native to intertidal regions of southern Africa, feeds on copepods (small crustaceans known as sand fleas), and its tolerance for saline environments has facilitated its colonization of islands throughout the Indo-Pacific region. The size range of extant skinks is considerable, from less than 35 mm SVL in the Australian Menetia to over 80 cm in the Solomon Islands skink (Corucia zebrata). Most skinks are diurnal, although some are nocturnal or crepuscular. Their reproductive strategies are diverse, as expected for such a large clade. Viviparity has evolved among skinks more often than in any other lizard family. In most squamates, the placenta transports only simple molecules such as water, oxygen, and ions to the embryo, but the complex placenta of some skinks transfers macromolecules, such as proteins and lipids (Blackburn 2014).

Most skinks are characterized by smooth, shiny cycloid scales that are underlain by osteoderms, giving a very hard exterior to the body. The osteoderms of skinks are unusual in that each is composed of a mosaic of smaller bones rather than a single bone as in most other lizards. Lygosomine skinks and some other genera have a well-developed secondary palate that separates their nasal cavity from their mouth; most squamates lack a secondary palate.

◄ Figure 4.20 Scincidae. (A) Haacke's legless skink, *Typhlosaurus braini* (Acontinae), Namib Desert, Africa. (B) *Ctenotus fallens* (Lygosominae), one of the comb-eared striped skinks of Australia. (C) Centralian blue-tongued skink, *Tiliqua multifasciata* (Lygosominae). (D) Mountain skink, *Plestiodon callicephalus* ("Scincinae"). (E) Distribution. (Photographs: A, © Robert Harding World Imagery/Alamy; B, courtesy of Harvey Pough; C, courtesy of Stephen Zozaya; D, courtesy of R. D. Bartlett.)

Limb reduction has evolved more often in Scincidae than in any other lizard family. Some genera (e.g., *Brachymeles*, *Chalcides*, *Hemiergis*, *Lerista*) contain species with wide variation in limb development. For example, *Lerista* includes species with fully developed limbs and others with digit or limb reduction (see Figure 4.10) (Greer 1987). Some species of *Lerista* have totally lost the forelimbs but retain rudimentary hindlimbs. The genus *Plestiodon* contains about 47 species with typical lizard morphology, but one species that is specialized for burrowing in sand, *Plestiodon* (formerly *Neoseps*) *reynoldsi*, has a countersunk jaw, forelimbs reduced to flaps, and hindlimbs with only two digits.

Because of their hard, rounded bodies, skinks are difficult lizards for many predators to handle, but some snakes and lizards are skink-eating specialists. In addition to *Lialis* (Pygopodidae), snakes in several different lineages (e.g., *Liophidium, Scaphiodontophis, Psammodynastes*) have evolved specializations, including hinged teeth or the development of a gap (diastema) within the tooth rows, to facilitate capturing skinks (see Chapter 11) (Cadle 1999).

Classification, distribution, and conservation 115 genera, 1,582 species, although the number of genera is expected to change as the phylogenetic relationships in several speciesrich genera are clarified. 3 subfamilies: Acontinae (Acontias, Typhlosaurus) in southern Africa and Kenya; Lygosominae (representative genera Carlia, Cryptoblepharus, Ctenotus, Egernia, Emoia, Lerista, Lygosoma, Mabuya, Trachylepis, Oligosoma, Scincella, Sphenomorphus, Tiliqua, Tropidophorus), which is distributed worldwide, including on Indian and Pacific Ocean islands, except northern Eurasia and northern and western North America; and "Scincinae" (representative genera Amphiglossus, Brachymeles, Chalcides, Eumeces, Plestiodon, Scelotes, Scincus), which are also distributed worldwide except for South America, Australia, and New Zealand (Figure 4.20E). The IUCN lists 79 species as Critically Endangered or Endangered and 16 species as Vulnerable.

Greer (1970a) provided a 4-subfamily taxonomy of skinks consisting of Acontinae, Feylininae, Lygosominae, and Scincinae, with Lygosominae containing the vast majority of species. Molecular phylogenetic research since the mid-2000s has supported the monophyly of Acontinae and Lygosominae (but see Whiting et al. 2003; Siler et al. 2011), and the placement of the West African Feylininae (genus *Feylinia*) deep within the skink tree; thus the subfamily Feylininae is no longer recognized and is instead part of "Scincinae." However, "Scincinae" is polyphyletic, and because no widely accepted taxonomic rearrangement for this group has been proposed, we instead use the name in quotation marks to indicate that it is not a monophyletic group.

Systematics references Greer (1970a,b), Whiting et al. (2003), Brandley et al. (2005, 2011, 2012, 2015), Schmitz et al. (2005), Skinner (2007), Skinner et al. (2011, 2013), Carranza et al. (2008), Lamb et al. (2010), Siler et al. (2011), Hedges (2014).

(A)





Xantusiidae • Night Lizards

Xantusiids are medium-small lizards (100 mm SVL) that occur in humid to arid habitats. Xantusiids have a relatively flat body and head, lack movable eyelids, and are secretive, often nocturnal, and relatively sedentary. Several species are habitat specialists (Bezy 1988, 1989b). For example, *Xantusia vigilis* is often associated with the Joshua tree formations of the Mojave Desert (living under the bark of dead trees during the day), and *X. henshawi* occurs only where there are exfoliating granitic outcrops. Species of *Lepidophyma* (Figure 4.21A) occur in habitats ranging from rainforests and dry forests to montane conifer forests. Several species are associated with limestone outcrops or boulders and live in caves and crevices. Xantusiids are long-lived for such small animals—up to 10 years in the case of *X. vigilis*.

Several species of *Lepidophyma* reproduce parthenogenetically, but the parthenogens do not appear to result from interspecific hybridization (Sinclair et al. 2010) as is the case in teiids, lacertids, and gymnophthalmids. Moreover, some parthenogenetic *Lepidophyma* species are bisexual while others are unisexual (all female). Within *Lepidophyma flavimaculatum*, populations from southern Central America are all female, whereas populations from Guatemala and

Figure 4.21 Xantusiidae. (A) Yellow-spotted night lizard, *Lepidophyma flavimaculatum*. (B) Distribution. (Photograph courtesy of Todd W. Pierson.)

Honduras contain both males and females (Bezy 1989b). All mainland xantusiids are viviparous, but *Cricosaura* from Cuba is oviparous.

Classification, distribution, and conservation 3 genera, 34 species. Genera include *Cricosaura* in eastern Cuba; *Lepidophyma* from Mexico to Panama; and *Xantusia* from the southwestern United States to northern Mexico (Figure 4.21B). The IUCN lists 1 species (*Lepidophyma lipetzi*) as Endangered and 4 species as Near Threatened or Vulnerable.

Systematics references Bezy (1989a), Vicario et al. (2003), Noonan et al. (2013).

Gerrhosauridae • Plated Lizards

These African lizards range in size from 15 cm total length in Cordylosaurus to 70 cm total length in Gerrhosaurus validus and Zonosaurus maximus. Their common name refers to their scales, which are underlain by osteoderms and arranged in transverse rows, giving the appearance of medieval plate armor (Figure 4.22A). They do not develop spines to the extent seen in the closely related cordylids. Gerrhosaurids have a prominent lateral fold along the body, a feature also seen in some anguids. Angolosaurus and Tetradactylus have reduced limbs and live in shifting-sand environments or grasslands. The Madagascan species of Tracheloptychus and Zonosaurus are terrestrial and inhabit both forests and sandy areas. Zonosaurus maximus is semiaquatic and takes to water to escape disturbance, hiding under bottom debris for long periods. All gerrhosaurids are oviparous.

Classification, distribution, and conservation 6 genera, 37 species. Genera include *Tracheloptychus* and *Zonosaurus* in Madagascar and *Angolosaurus, Cordylosaurus, Gerrhosaurus,* and *Tetradactylus* in sub-Saharan Africa (**Figure 4.22C**). The IUCN lists 1 species (*Zonosaurus subunicolor*) as Endangered and 8 species as Near Threatened or Vulnerable.

Systematics references Lang (1990, 1991), Bates et al. (2013), Lamb and Bauer (2013), Recknagel et al. (2013).

Cordylidae • Girdled Lizards

Cordylids are characterized by scales arranged in transverse circles around the body, and they often have a strongly keeled or very spiny tail (**Figure 4.22B**). The body is heavily armored with osteoderms, much like gerrhosaurids. Many species of cordylid lizards are rock-dwelling and use body inflation to wedge themselves into rock crevices for defense. *Smaug giganteus*, the largest cordylid (>30 cm total length), is terrestrial and digs long burrows in the soil. It has a bat-


Figure 4.22 Gerrhosauridae and Cordylidae. (A) Madagascar plated lizard, *Zonosaurus subunicolor* (Gerrhosauridae). (B) Giant girdled lizard, *Smaug (Cordylus) giganteus*. (C) Distribution. (Photographs: A, courtesy of Miguel Vences and Frank Glaw; B, courtesy of Robin Andrews.)

tery of large spines projecting from the rear of the head and also many rows along the tail. If pursued into its burrow, it can defend itself by backing toward the intruder, swinging its strong tail from side to side. As a last resort, it anchors itself inside its burrow by hooking its head spines into the roof of the tunnel.

Another cordylid, *Cordylus cataphractus*, has an unusual defense for a lizard. It rolls into a tight ball, holding the tail base in its mouth and exposing only the hard, spiny scales to the exterior; this behavior is occasionally observed in other cordylids. As in many other squamate lineages, limb reduction has occurred in cordylids of the genus *Chamaesaura*, which have a long, snakelike body and extremely reduced limbs.

Many cordylids are solitary and territorial, but a few species have a complex social structure. *Platysaurus* live in dense colonies with retreats normally shared by 1 male and up to 10 females and subadults (Broadley 1978). *Cordylus cataphractus* also exhibits grouping behavior, but groups in this species may comprise multiple males as well as females and subadults (Mouton et al. 1999). All species of cordylids are viviparous except for *Platysaurus* species, which are oviparous.

Classification, distribution, and conservation 10 genera, 64 species. Representative genera include *Chamaesaura, Cordylus, Pseudocordylus, Platysaurus,* and *Smaug.* Stanley et al. (2011) found that *Cordylus sensu lato* was not mono-

phyletic and described 6 new genera (including *Smaug*, named for the dragon in J.R.R Tolkien's book *The Hobbit*). Cordylids inhabit eastern and southern Africa (**Figure 4.22C**). The IUCN lists 2 species as Endangered and 5 species as Vulnerable.

Systematics references Lang (1991), Stanley et al. (2011).

LACERTOIDEA

Lacertoidea as defined here is supported only by molecular data; the clade has no morphological synapomorphies. Phylogenies based on morphological data have long supported a clade composed of Lacertidae, Teiidae, and Gymnophthalmidae, and thus the strongly supported relationship between Lacertidae and Amphisbaenia (see Figure 4.12) was one of the most surprising results of early squamate molecular analyses (e.g., Townsend et al. 2004). The molecular data suggest that morphological characters supporting a close relationship of Lacertidae, Teiidae, and Gymnophthalmidae were lost early in the evolution of the amphisbaenian lineage.

Teiidae • Whiptails, Tegus, and Relatives

Teiids are active, diurnal lizards found in habitats ranging from extremely arid deserts to tropical rainforests. *Aspidoscelis* (formerly included in the genus *Cnemidophorus*) is a major component of the lizard fauna of the desert southwest of the United States. Most teiids are larger than 7 cm SVL, and the total length of *Tupinambis* and *Dracaena* may reach 1 m or more. Species of *Dracaena* and *Crocodylurus* are semiaquatic and freely enter water for refuge and foraging. *Dracaena* may be seen in trees over watercourses or swimming about in flooded forests; its diet consists mainly of





Figure 4.23 Teiidae. (A) Blue whiptail lizard, *Cnemidophorus murinus* (Teiinae). (B) Caiman lizard, *Dracaena guianensis* (Tupinambinae). (C) Distribution. (Photographs: A, © Buiten-Beeld/Alamy; B, © Iakov Filimonov/Shutterstock.)



snails and bivalves that it crushes with its teeth and large jaw muscles. *Teius*, with four digits on its hindlimb, is the only teiid that shows any form of limb reduction. All teiids are oviparous. Some species nest communally. Parthenogenesis is prevalent in *Aspidoscelis*, *Cnemidophorus*, *Kentropyx*, and *Teius*. *Aspidoscelis* in particular has provided model systems for the study of this phenomenon (see Section 9.3).

Classification, distribution, and conservation 10 genera, 146 species. Harvey et al. (2012) distinguish 16 genera based on phenotypic characters, compared with 10 genera that have been identified by molecular studies (e.g., Reeder et al. 2002; Giugliano et al. 2013). We take a conservative approach and recognize the traditional 10 genera. 2 subfamilies: Teiinae (Figure 4.23A; *Ameiva, Aspidoscelis, Cnemidophorus, Dicrodon, Kentropyx, Teius*) and Tupinambinae (Figure 4.23B; *Callopistes, Crocodylurus, Dracaena, Tupinambis*). Teiids inhabit the northern United States through most of South America and the West Indies (Figure 4.23C). The IUCN lists 2 species as Critically Endangered and 12 species as Near Threatened or Vulnerable.

Reeder et al. (2002) showed that Ameiva and Cnemidophorus (sensu lato) were paraphyletic and placed all species of "Cnemidophorus" north of Panama in the genus Aspidoscelis, thereby restricting Cnemidophorus to only the South American Cnemidophorus lemniscatus species group. Therefore, although Aspidoscelis is now widely used for North American teiids, literature prior to the early 2000s uses Cnemidophorus for these species, and many herpetologists continue to refer to Aspidoscelis species by the colloquial name "cnemis."

Systematics references Presch (1974), Reeder et al. (2002), Giugliano et al. (2007, 2013), Harvey et al. (2012).

Gymnophthalmidae • Microteiids

Most gymnophthalmids are active, diurnal lizards found in habitats ranging from deserts to tropical rainforests to highelevation paramo (alpine shrubland) in the Andes. They are often informally called microteiids because they are generally smaller than Teiidae, their sister lineage. However, sizes overlap when the extremes in both families are considered. Many gymnophthalmid species are secretive and inhabit the leaf litter of the forest floor (e.g., *Arthrosaura, Iphisa, Prionodactylus*). Some are semifossorial (e.g., *Bachia*) or occupy specialized habitats such as loose sand (*Calyptommatus*). Some species of *Potamites* and other gymnophthalmids (A) Bachiinae



Figure 4.24 Gymnophthalmidae. (A) Quadrangular scaled spectacled lizard, *Bachia flavescens* (Bachiinae); note the greatly reduced forelimb (arrow). (B) Keel-bellied shade lizard, *Alopoglossus atriventris* (Alopoglossinae) in Ecuadorian Amazonia. (C) Distribution. (Photographs: A, courtesy of Todd W. Pierson; B, © Pete Oxford/Minden Pictures/Corbis.)

(B) Alopoglossinae





are semiaquatic and enter water for refuge and foraging. *Bachia bresslaui* of southern Brazil forages aboveground on ants, beetles, scorpions, and spiders (Colli et al. 1998). Like teiids, all gymnophthalmids are oviparous, and communal nesting has been reported for some species (e.g., *Proctoporus, Macropholidus*). Some species of gymnophthalmids are parthenogenetic (see Chapter 9).

Limb reduction and body elongation have evolved multiple times in microteiids (Pellegrino et al. 2001). The genus *Bachia* shows a range of limb reduction, with species differing in the number of digits on the hand and foot. *Bachia* is the only squamate genus other than *Bipes* (Amphisbaenia) with species that possess forelimbs but no hindlimbs (**Figure 4.24A**). As in *Bipes*, there is anatomical and phylogenetic evidence that digits have re-evolved in *Bachia* (Kohlsdorf and Wagner 2006; Kohlsdorf et al. 2010). *Calyptommatus* is completely limbless.

Classification, distribution, and conservation 46 genera, 244 species. 6 subfamilies (Pellegrino et al. 2001; Castoe et al. 2004; Pyron et al. 2013a): Alopoglossinae (Figure 4.24B) *Alopoglossus, Ptychoglossus*), Bachiinae (*Bachia*), Cercosaurinae (representative genera *Cercosaura, Pholidobolus, Proctoporus, Riama*), Ecpleopinae (representative genera *Ecpleopus, Leposoma, Arthrosaura*), Gymnophthalminae (representative genera *Calyptommatus, Gymnophthalmus, Iphisa, Nothobachia, Tretioscincus*), and Rhacosaurinae (*Rhacosaurus*). They inhabit southern Mexico to Argentina and the southern

Lesser Antilles (**Figure 4.24C**). The IUCN lists 6 species as Endangered and 6 species as Vulnerable.

Systematics references Presch (1980), Pellegrino et al. (2001), Castoe et al. (2004), Doan and Castoe (2005).

Lacertidae • Wall Lizards and Relatives

Lacertids are small to moderate-size lizards (~5–21 cm SVL) with well-developed limbs. Dorsal scales are usually small and granular. Their gross morphology is similar to that of teiids and gymnophthlamids, and molecular data overwhelmingly support a sister relationship between Lacertidae and Amphisbaenia.

Most lacertids are active terrestrial or rock-dwelling species, and all are diurnal. They occupy a wide range of habitats, including desert, rocky, and forested habitats. *Zootoca* (formerly *Lacerta*) *vivipara* is noteworthy because some populations live above the Arctic Circle, farther north than any other reptile. Lacertids are primarily insectivores, although some are partially herbivorous. The vivid colors of some genera, especially *Podarcis*, play an important role in the reproductive behavior of these species (i de Lanuza et al. 2013). Lacertids are oviparous except for *Z. vivipara*, which is reproductively biomodal with both oviparous and viviparous populations (Huelin et al. 1993; Surget-Groba et al. 2006).



(B) Lacertinae



Hybrid parthenogenetic species of *Lacerta* occur in the Caucasus Mountains of southwestern Asia (Surget-Groba et al. 2001). Outside Europe, lacertids have diversified into many different habitats. Several species of *Meroles* in southern Africa are adapted to live among windblown sands and have developed fringes on the feet. They have a pointed head and a countersunk lower jaw that facilitate their sand-diving habits (Arnold 1995). Juveniles of *Heliobolus lugubris* of the Kalahari Desert mimic, in size, behavior, and color pattern, a sympatric species of noxious beetle, thus avoiding predation by birds and mammals (Huey and Pianka 1977). This is a case of size-limited mimicry; the mimetic color and pattern of the juvenile lizards change to a cryptic color and pattern as they grow larger than the beetle models.

Classification, distribution, and conservation 14 genera, 321 species. Different subfamily and tribe classifications have been proposed, but we recognize 2: Gallotinae (*Gallotia, Psammodromus*) and Lacertinae (representative genera

Acanthodactylus, Eremias, Lacerta, Podarcis, Takydromus, Zootoca). The phylogenetic interrelationships of the Lacertinae genera have been difficult to resolve, and this is probably due to a rapid radiation early in lacertine history. They inhabit Africa, Eurasia, and islands of the Sunda Shelf (Figure 4.25C). The IUCN lists 30 species as Critically Endangered or Endangered and 28 species as Near Threatened or Vulnerable.

Systematics references Arnold (1989), Harris et al. (1998), Arnold et al. (2007), Mayer and Pavlicev (2007), Pavlicev and Mayer (2009), Edwards et al. (2013).

AMPHISBAENIA

Amphisbaenians differ in many respects from other squamates. They are elongate and, with the exception of *Bipes* and *Blanus*, completely limbless. And although the left lung is reduced in most elongate reptiles (i.e., snakes, and other limbless lizards), in amphisbaenians it is the right lung that is reduced.

Amphisbaenians occupy many environments, including lowland rainforests, deciduous subtropical forests, and extremely arid deserts. Although they occasionally venture onto the surface, all species burrow and their bodies show numerous adaptations to this lifestyle. Unique among squamates, the brain is entirely surrounded by the frontal bones. Head shape varies considerably in amphisbaenians according to the type of burrowing a particular species uses (see Figure 10.20). Distinct cranial shapes include shovel-shaped, spade-shaped, keeled, and rounded, the last two having evolved convergently in multiple amphisbaenian lineages (Gans 1987; Kearney 2003; Kearney and Stuart 2004).

In most cases the skin can move independently of the underlying trunk. This peculiar modification is associated with the use of internal concertina locomotion in subterranean tunnels: amphisbaenians are able to use virtually any point along the body as a fixed point to anchor against tunnel walls, and the trunk can move forward within the skin during burrowing. This anatomical feature reduces the drag created by friction of the skin against the tunnel walls. Such locomotion is unknown in squamates other than amphisbaenians and uropeltid snakes.

Complete limb reduction is not uncommon among squamates, but amphisbaenians possess some uniquely peculiar characteristics of the appendicular skeleton. Most squamates that lack forelimbs retain some vestiges of the pectoral girdle, often the clavicle. However, most amphisbaenians lack all pectoral girdle elements, except *Amphisbaena*, Trogonophiidae, Blanidae, and Bipedidae. All amphisbaenians possess a vestige of the pelvic girdle (usually the ilium), but *Blanus* and *Bipes* retain all three pelvic bones (ilium, ischium, and pubis) as well as rudimentary femurs that do not breach the body wall (Kearney 2002). Phylogenetic and anatomical evidence suggests that limbs may have re-evolved in *Bipes* (Brandley et al. 2008) (see Bipedidae below).

Amphisbaenian bodies are distinctly annulated. Unlike the primary annuli of caecilians and the ventral scales of most snakes, which have a one-to-one correspondence to the vertebrae, there are two body annuli per vertebra in all amphisbaenians other than *Blanus*. Some species of amphisbaenians have an autotomic tail, but regeneration does not occur if the tail is lost.

Systematics references Gans (1978), Kearney (2003), Kearney and Stuart (2004), Vidal et al. (2008a).

Rhineuridae • Florida Worm Lizard

Rhineura floridana (Figure 4.26A) is the sole representative of Rhineuridae. It uses its shovel-shaped head to burrow through soft sand. Rhineurids have a rich fossil history and were widespread in central and western North America during the Eocene and Oligocene (Hembree 2007). The family is now restricted to central Florida. The phylogenetic relationship of Rhineuridae to other amphisbaenians is also notable because the lineage is much older (Middle to Late Cretaceous) than the crown group of other amphisbaenians that originated in the Early Paleogene.

Classification, distribution, and conservation 1 species, *Rhineura floridana*. It inhabits central Florida (**Figure 4.26E**). It is not listed by the IUCN as an extinction risk.

Systematics references Mulvaney et al. (2005), Hipsley and Müller (2014).

Bipedidae • Mole-Limbed Worm Lizards

Bipes inhabit arid scrublands or deserts in western Mexico. They are the only amphisbaenians with visible limbs, which they use while burrowing 10-20 cm into the soil from the surface but not for locomotion in existing subterranean tunnels. The morphology of the forelimbs is bizarre (Figure 4.26B): the toes are clawed and as well developed as those of most limbed squamates, but anatomical evidence suggests that all five digits have the same identity and are actually homologous to the first digit (thumb) (Zangerl 1945; Kearney 2002). The pectoral girdle of Bipes is unusually close to the head. Whereas the pectoral girdle of most squamates is at or posterior to the level of the sixth cervical vertebra, the pectoral girdle of Bipes is located at the third cervical vertebra. Using phylogenetic ancestral state reconstruction (see Chapter 2), Brandley et al. (2008) found evidence that forelimbs reevolved in Bipes from a limbless ancestor. If this hypothesis is supported by future analysis of embryonic and gene expression data, an explanation for the odd morphology of the hand and girdle placement is a consequence of rebuilding a limb, digits, and pectoral girdle from a limbless ancestor. The short tail has a single autotomic fracture plane. The autotomized portion of the tail probably plugs the tunnel in front of a predator while the amphisbaenian escapes. All species of Bipes are oviparous. The average clutch size is 2-3 eggs, but females reproduce only every other year (Papenfuss 1982).

Classification, distribution, and conservation 1 genus (*Bipes*), 3 species. The three species are diagnosed by the number of digits of the forelimb: five (*B. biporus*), four (*B. tetradactyla*), or three (*B. caniculatus*). *Bipes* inhabit southern Baja California (Mexico) and the mainland Mexican states of Guerrero and Michoacán (Figure 4.26E).

Systematics references Papenfuss (1982), Macey et al. (2004).

Cadeidae • Cuban Worm Lizards

Cadeidae consists of two species in the genus *Cadea* (Figure 4.26C). The biology of Cadeidae is not well known, and its phylogenetic relationships within Amphisbaenia were only recently elucidated. Both species have a total length of less than 28 cm.



Figure 4.26 Rhineuridae, Bipedidae, Cadeidae, Blanidae. (A) Florida worm lizard, *Rhineura floridana* (Rhineuridae). (B) Ajolote, *Bipes biporus* (Bipedidae). (C) Cuban spotted amphisbaena, *Cadea blanoides* (Cadeidae) with two eggs. (D) Mediter-

Classification, distribution, and conservation 1 genus (*Cadea*), 2 species. They inhabit Cuba (**Figure 4.26E**).

Systematics references Zug and Schwartz (1958).

Blanidae • Mediterranean Worm Lizards

The Mediterranean genus *Blanus* (**Figure 4.26D**) was previously placed in the Amphisbaenidae, but it has several unique features (e.g., a one-to-one ratio of annuli to verranean worm lizard, *Blanus cinereus* (Blanidae). (E) Distribution. (Photographs: A, courtesy of R. D. Bartlett; B, © Chris Mattison/Alamy; C, courtesy of S. Blair Hedges; D, courtesy of Harvey Pough.)

tebrae) as well as a relatively well developed pelvic girdle (Renous et al. 1991). The diet of *Blanus* includes insect larvae and ants.

Classification, distribution, and conservation 1 genus (*Blanus*), 7 species. Their distribution is disjunct and includes the Iberian Peninsula, Morocco, Greece, Turkey, and the Middle East (**Figure 4.26E**).

(A) Amphisbaenidae



(B) Trogonophiidae





Figure 4.27 Amphisbaenidae and Trogonophidae. (A) Vanzolini's worm lizard, *Amphisbaena vanzolinii* (Amphisbaenidae), Guyana. (B) Lateral fold lizard, *Trogonophis wiegmanni*. (Trogonophiidae). (C) Distribution. (Photographs: A, © Piotr Naskrecki/Minden Pictures/Corbis; B, © blick-winkel/Alamy.)

Systematics references Vaconcelos et al. (2006), Albert et al. (2007), Sampaio et al. (2014).

Amphisbaenidae • Worm Lizards

Amphisbaenidae is the largest and most geographically widespread amphisbaenian family, and shows the greatest diversity in burrowing specializations, including shovelheaded, keel-headed, and round-headed species. Amphisbaena alba (South America) is one of the largest amphisbaenians, with large females reaching over 80 cm in total length. Amphisbaena alba do not differ in characters that are often sexually dimorphic in other squamates, including body proportion, scalation, and precloacal glands. In the dry forests (cerrado) of central Brazil, the diet of A. alba consists primarily of beetles, ants, spiders, and termites; however, other arthropods and even lizards, snakes, and rodents, are occasionally eaten. In southern Africa a small colubrid snake, Cryptolycus nanus, is extremely modified for burrowing and is often associated with the amphisbaenid Chirindia swynnertoni. Dietary studies suggest that Cryptolycus eats nothing but Chirindia. Some amphisbaenid species are viviparous.

Classification, distribution, and conservation 11 genera, 169 species. Representative genera include *Amphisbaena* (**Figure 4.27A**), *Chirindia, Cynisca, Dalophia, Geocalamus,* and *Monopeltis.* They have a disjunct distribution that includes the West Indies, South America, sub-Saharan Africa, and circum-Mediterranean areas (Figure 4.27C). The IUCN lists 3 species as Critically Endangered or Endangered and 4 species as Near Threatened or Vulnerable, largely due to habitat destruction in Madagascar.

Systematics references Kearney and Stuart (2004), Mott and Vieites (2009), Measey and Tolley (2013).

Trogonophiidae • Spade-Headed Worm Lizards

Trogonophiids are unusual amphisbaenians in that they lack caudal autotomy, have acrodont teeth (teeth are pleurodont in other amphisbaenians), and have a relatively short trunk (**Figure 4.27B**). The blunt heads of trogonophiids are rimmed by sharp scales, and they use oscillating movements of the head to drill through soil (see Figure 10.20C). Unlike other amphisbaenians, trogonophiids use their tail to apply force during burrowing, and the skull rotates on the vertebral column during penetration of the soil. Some *Trogonophis* are viviparous.

Classification, distribution, and conservation 4 genera (*Agamodon, Diplometopon, Pachycalamus, Trogonophis*), 6 species. They have a disjunct distribution including North Africa and the Middle East (**Figure 4.27C**).

Systematics references Gans (1978).

ANGUIMORPHA

Anguimorpha is a clade of six families of morphologically diverse lizards, including the largest lizard on earth, the Komodo monitor (*Varanus komodoensis*, better known by its highly descriptive name of Komodo dragon); the only venomous lizards (*Heloderma*); and numerous limbless forms. The monophyly of Anguimorpha is supported by molecular data and numerous anatomical synapomorphies (see Estes et al. 1988; Conrad 2008).

Helodermatidae Gila Monster and Mexican Beaded Lizard

Helodermatids are large lizards (up to 50 cm SVL) with short, blunt tails that are used for fat storage (Figure 4.28A). Both species of *Heloderma* are venomous, but the venom glands are non-muscularized and are located in the tissue alongside the mandible (lower jaw) rather than the maxilla (upper jaw) as is the case for dangerously venomous snakes (see Chapter 11).

The diets of *Heloderma* consist mostly of vertebrates, including nestling mammals and birds, lizards, insects, and even turtles (*Kinosternon*). Eggs of ground-nesting birds and tortoises are also consumed. *Heloderma* are actively foraging diurnal or noctural predators but spend as much as 95% of their time in underground shelters (Beck 1990), preferring cooler temperatures than do many lizards. Their tails are somewhat prehensile and lack fracture planes. Both species climb readily, ascending to considerable heights in order to reach bird nests. Both species are oviparous, and females lay eggs in July and August. Because neonates first appear in late April, it is likely that deposited eggs overwinter before hatching (Goldberg and Lowe 1997). Males engage in grappling combat for dominance, especially during the May breeding season.

Classification, distribution, and conservation 1 genus, 2 species (*Heloderma suspectum, H. horridum*). They inhabit the southwestern United States to Guatemala (**Figure 4.28C**). The IUCN lists *H. suspectum* as Near Threatened.

Systematics references Bogert and del Campo (1956), Pregill et al. (1986), Douglas et al. (2010).

Xenosauridae • Knob-Scaled Lizards

Xenosauridae has only 1 genus (*Xenosaurus*) comprising 10 species that live primarily in lowland and lower montane humid forests, although *X. rectocollaris* inhabits high-elevation, semiarid habitats, and *X. phalaroanthereon* lives in upland oak or pine-oak forests. *Xenosaurus* are moderate-size rock-dwellers with SVLs of 9–15 cm (Figure 4.28B). The best-known species, *Xenosaurus grandis*, lives in crevices in limestone outcrops. Xenosaurids are diurnal, consume primarily arthropods, and have a somewhat spiny, non-autotomic tail. *Xenosaurus* species are viviparous. The xenosaurid lineage is old, having diverged from the lineage of





(B) Xenosauridae





Figure 4.28 Helodermatidae and Xenosauridae. (A) Gila monster, *Heloderma suspectum*, Arizona. (B) Flathead knob-scaled lizard, *Xenosaurus platyceps*. (C) Distribution. (Photographs: A, © Rick & Nora Bowers/Alamy; B, © Tim Burkhardt.)

anguids and helodermatids some 100 mya. It is quite likely that xenosaurids were much more diverse and widespread in the past.

Classification, distribution, and conservation 1 genus (*Xenosaurus*), 10 species. They occur in southern Mexico and Guatemala (**Figure 4.28C**). Because *Xenosaurus* are restricted to small, fragmented areas, often near areas of rapid human population growth, species are becoming increasingly vulnerable to extinction (Zúñiga-Vega et al. 2007). The IUCN lists 2 species as Endangered and 1 species as Vulnerable.

Systematics references King and Thompson (1968), Bhullar (2011), Recknagel et al. (2013).

Anguidae • Slowworms, Glass Lizards, Alligator Lizards, and Relatives

Anguidae is widespread, primarily in Holarctic tropical and temperate regions. Most species are terrestrial, but *Anniella* are burrowers and *Abronia* are entirely arboreal. Habitats include open grasslands (*Ophiodes, Ophisaurus*), sand dunes (*Anniella*), pine-oak and cloud forests (*Abronia*), lowland rainforest (some *Diploglossus*), and chaparral (*Elgaria*). Most anguids are diurnal and prefer relatively cool and humid

(A) Anguinae



environments. Sizes range from total lengths of less than 7 cm to the European legless lizard (*Pseudopus apodus*), which exceeds 1.3 m. Most anguids are insectivorous, but *P. apodus* includes small rodents and birds in its diet.

The tail of anguids autotomizes readily, a phenomenon responsible for the common name glass lizards for *Ophisaurus*. Limb reduction and loss occur in many anguids and have evolved several times in the family. Species of *Ophisaurus* and *Anniella* are entirely limbless. *Ophiodes* has lost the forelimbs but retains tiny hindlimbs, and many species of *Diploglossus* have relatively short limbs.

Several genera are viviparous (Barisia, Abronia, Mesaspis, Anniella, Celestas, Anguis, Ophiodes). Diploglossus and Elgaria have both oviparous and viviparous species, and Ophisaurus and Gerrhonotus are oviparous. Numerous species attend their eggs during incubation (Greene et al. 2006). Most species of the Central American genus Abronia are threatened with extinction because of the destruction of their cloudforest habitats (Campbell and Frost 1993).

Classification, distribution, and conservation 14 genera, 130 species. 4 subfamilies: Anguinae (**Figure 4.29A**; *Anguis, Dopasia, Ophisaurus, Pseudopus*) in North America and Eurasia; Anniellinae (*Anniella*) in extreme western North

(B) Diploglossinae



(C) Gerrhonotinae

Figure 4.29 Anguidae.

(A) European glass lizard, *Pseudopus apodus* (Anguinae). (B) Rose-sided galliwasp, *Diploglossus monotropis* (Diploglossinae), Panama. (C) Southern alligator lizard, *Elgaria multicarinata* (Gerrhonotinae). (D) Distribution. (Photographs: A, © blickwinkel/ Alamy; B, © Oyvind Martinsen Wildlife Collection/Alamy. C, courtesy of Todd W. Pierson.)



America; Diploglossinae (Figure 4.29B; Celestus, Diploglossus, Ophiodes) in the West Indies; and Gerrhonotinae (Figure 4.29C; Abronia, Barisia, Coloptychon, Elgaria, Gerrhonotus, Mesaspis) in western North America and Central America. Anniella and diploglossines are sometimes recognized as separate families (Anniellidae and Diplogossidae). Either the single-family or three-family taxonomic scheme is valid, provided their phylogenetic relationships are kept in mind. They have a disjunct distribution in North, Central, and South America; the West Indies; western Eurasia and northwest Africa; and Southeast Asia and islands of the Sunda Shelf (Figure 4.29D). The IUCN lists 22 species as Critically Endangered or Endangered and 10 species as Near Threatened or Vulnerable.

Systematics references Good (1987, 1988, 1994), Campbell and Camarillo (1994), Macey et al. (1999).

Shinisauridae • Chinese Crocodile Lizard

Shinisauridae includes a single species, *Shinisaurus crocodiluris*, that inhabits montane forested stream habitats (**Figure 4.30A**). It is semiaquatic, spending much of its time in the water feeding on insects, tadpoles, and fish. The species is diurnal and has been observed basking on branches overhanging streams. Females are viviparous and give birth in February to March. Like Xenosauridae, Shinisauridae is also an old (~100 mya) and species-depauperate lineage that was more widespread in the past, as demonstrated by a well-preserved Eocene shinisaurid fossil from North America (Conrad 2006).

Classification, distribution, and conservation 1 species, *Shinisaurus crocodilurus*. It inhabits south-central China and northeast Vietnam (**Figure 4.30B**). *Shinisaurus* is sometimes placed in Xenosauridae, but molecular phylogenetic analyses unambiguously reject a sister relationship between *Shinisaurus* and Xenosauridae. *S. crocodiluris* is restricted to only 10 known populations in China and Vietnam (Bei et al. 2012). The IUCN lists it as Critically Endangered.

Systematics references Ziegler et al. (2008), Huang et al. (2014).

Varanidae • Monitors and Goannas

Varanids (Figure 4.31A) include a single genus (Varanus) of active, diurnal, fast-moving foragers that feed on a variety of invertebrates and vertebrates in forests, grasslands, and deserts. Ranging in total length from the 23 cm SVL V. brevicauda to the 3 m V. komodoensis (the Komodo dragon), they show the greatest body size range of any lizard family. Although V. komodoensis is the largest extant lizard, V. (formerly Megalania) prisca, an extinct species from Pleistocene Australia, was over 6 m long and weighed approximately 2,200 kg (Head et al. 2009). The great variation in body size, as well as differences in head shape, among varanids probably represents different specializations for living in diverse habitats, including terrestrial, arboreal, rocky, sandy, and aquatic habitats (Collar et al. 2011; Openshaw and Keogh 2014). The semiaquatic V. niloticus has a vertically compressed tail with a dorsal crest for swimming and feeds on crabs and crocodile eggs. The active lifestyle of varanids requires high rates of oxygen consumption, and the lungs of varanids are larger and more structurally complex than those of other lizards. Moreover, varanids can use their throat muscules to help pump air into the lungs (see Chapter 7). There is evidence that some varanids may produce venom in their mandibular glands (Fry et al. 2009; Hargreaves et al. 2014a).

Males of many species of *Varanus* determine dominance by ritualized combat that may include rearing up on the hindlimbs, inflating the throat and/or trunk, hissing, striking with the tail, and grappling. All varanids are oviparous, and females of some species dig into termite mounds where they lay their eggs. The tail does not regenerate when broken.

Classification, distribution, and conservation 1 genus (*Varanus*), 74 species. Although all varanids are placed in a single genus, the varanid systematics literature commonly uses species group designations when discussing subclades of *Varanus*. For example, the *V. niloticus* group contains the African species *V. albigularis, V. exanthematicus,* and *V. niloticus* (see Vidal et al. 2012). Varanids occur in Africa, across southern Asia to China, and through the Indo-Australian



Figure 4.30 Shinisauridae. (A) Chinese crocodile lizard, *Shinisaurus crocodilurus*. (B) Distribution. (Photograph courtesy of Harvey Pough.)



(A) Varanidae



Figure 4.31 Varanidae and Lanthanotidae. (A) Ridge-tailed monitor, *Varanus acanthurus* (Varanidae). (B) Borneo earless monitor, *Lanthanotus borneensis* (Lanthanotidae). (C) Distribution. (Photographs: A, © reptiles4all/ Shutterstock; B, courtesy of Indraneil Das.)

Archipelago to Australia (**Figure 4.31C**). Two-thirds of the species are in Australia. The IUCN lists 1 species (*V. mabitang*) as Endangered and 3 species as Near Threatened or Vulnerable.

Morphological phylogenetic evidence overwhelmingly supports a clade (Varanoidea or Platynota) composed of Varanidae, Lanthanotidae, and Helodermatidae (see Figure 4.11), but this hypothesis is strongly rejected by molecular data (see Figure 4.12). Phylogenetic analyses based on morphology also place extinct taxa such as mosasaurs in the Varanoidea/ Platynota clade (e.g., Conrad 2008; Conrad et al. 2011), although support for this hypothesis is not universal (e.g., Caldwell 2012; Gauthier et al. 2012).

Systematics references Conrad et al. (2011), Collar et al. (2011), Vidal et al. (2012), Welton et al. (2013).

Lanthanotidae • Earless Monitors

Lanthanotidae includes only *Lanthanotus borneensis*, a burrowing and semiaquatic nocturnal lizard with short limbs and a somewhat prehensile tail that is endemic to western Borneo (Figure 4.31B). Individuals are rarely seen in the wild, and information about the species' natural history is scant. *Lanthanotus* is oviparous. There is no trace of an external ear (giving the group its common name), and as in Varanidae, there is no tail regeneration.

Classification, distribution, and conservation 1 species, Lanthanotus borneensis. It inhabits the Malaysian state of Sarawak on Borneo (Figure 4.31C). Lanthanotus is some(B) Lanthanotidae



times placed in Varanidae, its sister lineage. It is not listed by the IUCN as an extinction risk, but few data have been collected for this species.

Systematics references McDowell and Bogert (1954).

IGUANIA

Iguanian lizards inhabit all continents and include some of the most recognizable lizards, such as the green iguana (*Iguana iguana*), African chameleons (*Chamaeleo* and other genera), and the New World anoles (*Anolis*). Iguanians comprise two major clades, Acrodonta and Pleurodonta, which are distinguished by their dentition. Acrodont iguanians include the Old World families Agamidae and Chamaeleonidae, whereas pleurodont iguanians primarily inhabit the New World, although Opluridae occurs only on Madagascar. Species in both clades are similar in overall ecology and are primarily diurnal, sit-and-wait predators. **Systematics references** Etheridge and de Queiroz (1988), Frost and Etheridge (1989), Schulte et al. (2003), Townsend et al. (2011b), Blankers et al. (2013).

Acrodonta

Acrodont iguanians are sometimes called Old World iguanians because of their distribution in Africa, Asia, and Indo-Australian Archipelago. The monophyly of Acrodonta has been supported consistently by both molecular and morphological data. Although Gauthier et al. (2012) find 46 synapomorphies supporting the monophyly of the group, acrodonts are best known for possessing acrodont dentition.

Chamaeleonidae • Chameleons

Chameleons are among the most easily recognizable lizards because of the extensive development of casques, horns, and crests on the head in most species, and a laterally compressed body (Figure 4.32A). They also are well known for their ability to change color. Their feet are zygodactylous, with adjacent digits fused on each hand and foot, forming opposable grasping pads (see Chapter 10).



Figure 4.32 Chamaeleonidae. (A) Arabian chameleon, *Chamaeleo arabicus*. (B) Distribution. (Photograph courtesy of Todd W. Pierson.)

The tail is prehensile in arboreal species. The tongue can be projected from the mouth at high speeds to capture prey more than one body length distant (see Chapter 11) (Bell 1989; Wainwright et al. 1991). Chameleons range in size from less than 16 mm SVL (*Brookesia micra*) to more than 30 cm SVL (*Furcifer oustaleti*). They are exclusively diurnal and primarily insectivorous. However, birds have been recorded in the diets of the largest species, *Chamaeleo melleri* and *Furcifer oustaleti*.

Chameleon eyes can move independently and have many structural modifications that are unique among vertebrates. Unusually, chameleons use accommodation (focusing depth) to measure the distance of objects, whereas virtually all other vertebrates use triangulation.

The dwarf chameleons of Madagascar (*Brookesia*) and Africa (*Bradypodion* and *Rhampholeon*) are exceptions to many of the generalizations usually made about chameleons. They are small and drab (usually brown to gray) with little ability to change color. They have a short, nonprehensile tail and are terrestrial inhabitants of rainforests, although they retain the zygodactylous feet characteristic of the family.

Most chameleons are oviparous, but all species of *Brad-ypodion* and some species of *Triceros* are viviparous. The European *Chamaeleo chamaeleon* has a serially polygynous mating system, in which a male mates with, and guards, a series of females during a breeding season, but only one at a time. Males stop guarding a particular female after mating, when she takes on rejection behaviors and characteristic colors indicating gravidity (Cuadrado 2001). These behaviors have been little studied in other chameleons.

Classification, distribution, and conservation 11 genera, approximately 200 species. Representative genera include *Bradypodion, Kinyongia, Rhampholeon,* and *Triceros* (Africa), and *Brookesia, Calumma,* and *Furcifer* (Madagascar). Species of the genus *Chamaeleo* inhabit Africa, the Middle East, India, Sri Lanka, and parts of southern Europe (**Figure 4.32B**). The IUCN lists 27 species as Critically Endangered or Endangered and 36 species as Near Threatened or Vulnerable, largely due to habitat destruction in Madagascar.

Systematics references Klaver and Böhme (1986), Rieppel (1987), Townsend et al. (2009), Glaw et al. (2012), Tolley et al. (2013).

Agamidae • Dragons and Relatives

Agamids are moderate-size to large (>1 m total length in *Hydrosaurus*). They are diurnal and primarily terrestrial, although some genera are semiaquatic. Limbs are well developed, and instances of limb reduction are rare and do not involve more than a single digital phalanx (Greer 1991). Scales are often modified to form extensive crests, frills, or spines. These structures are sexually dimorphic in many agamids and are used in intraspecific interactions.

Southeast Asian agamids of the genus *Draco* are the only extant lizards capable of true gliding flight, which they ac-





(C) Hydrosaurinae

(E)



Figure 4.33 Agamidae. (A) Peninsular horned tree lizard, *Acanthosaura armata* (Agaminae). (B) Western bearded dragon, *Pogona minor* (Amphibol-urinae). (C) Sailfin lizard, *Hydrosaurus* sp. (Hydrosaurinae). (D) Yemeni spiny-tailed lizard, *Uromastyx benti* (Uromastycinae). (E) Distribution. (Photographs: A, courtesy of L. Lee Grismer; B, courtesy of Harvey Pough; C, courtesy of Scott Corning/www.SailfinDragon.com; D, courtesy of Todd W. Pierson.)

(B) Amphibolurinae



(D) Uromastycinae





With the exception of a single viviparous genus (*Phrynocephalus*), agamids are oviparous. Many species of *Agama* live in dense colonies with well-developed social hierarchies and territories. Several agamids, including *Agama*, *Physignathus*, and *Laudakia*, have evolved intervertebral pseudautotomy, an unusual contrast to the intravertebral autotomy characteristic of other lizards.

Classification, distribution, and conservation Approximately 53 genera, 444 species. 6 subfamilies: Agaminae (Figure 4.33A; representative genera Acanthocercus, Agama, Laudakia, Phrynocephalus, Pseudotrapelus, Trapelus), Amphibolurinae (Figure 4.33B; representative genera Chlamydosaurus, Ctenophorus, Moloch,

complish by extending elongate and highly mobile ribs that support a thin flight membrane made of skin (see Figure 10.26). The Australian *Moloch* is similar in overall appearance to North American *Phrynosoma* (Phrynosomatidae) in having a tanklike, heavily spined body and short tail (see Figure 6.2), and like most species of *Phrynosoma*, it feeds primarily on ants. *Physignathus, Pogona*), Draconinae (representative genera *Bronchocela, Calotes, Draco, Japalura*), Leiolepinae (*Leiolepis*), Hydrosaurinae (**Figure 4.33C**; *Hydrosaurus*), and Uromastycinae (**Figure 4.33D**; *Uromastyx*). They inhabit Africa, southern and central Asia, the Indo-Australian Archipelago, Australia, New Guinea, and the Solomon Islands (**Figure 4.33E**). The IUCN lists 6 species as Critically Endangered or Endangered and 16 species as Near Threatened or Vulnerable.

Systematics references Macey et al. (2000), Hugall et al. (2008), Okajima and Kurasawa (2010), Townsend et al. (2011b).

Pleurodonta

Although few morphological characters support the monophyly of Pleurodonta (Frost and Etheridge 1989; Frost et al. 2001; Gauthier et al. 2012), it is well supported by molecular data (Schulte et al. 2003; Townsend et al. 2011b; Blankers et al. 2013). The taxonomy of Pleurodonta has been historically contentious, but the taxonomic scheme we use in this textbook has become widely adopted. It is common in older and some current literature to name the group Iguanidae instead of Pleurodonta and to see its constituent clades identified as subfamilies (e.g., Phrynosominae, Polychrotinae) rather than families (e.g., Phrynosomatidae, Polychrotidae). The phylogenetic relationships among most pleurodont lineages are still uncertain. Molecular evidence suggests that pleurodonts underwent a rapid radiation early in their history (Townsend et al. 2011b) and explains the few diagnostic morphological or molecular characters that support these relationships.

Tropiduridae • Lava Lizards

Tropidurids inhabit a broad range of habitats, including lowland rainforests and dry forests (*Stenocercus, Tropidurus*, *Uracentron*), savannas (some *Tropidurus*), and deserts (some *Tropidurus*). All species are diurnal. Body form and natural history are variable. Many tropidurids are relatively small (~5 cm SVL), but some species of *Tropidurus* and *Stenocercus* are much larger (up to 9 cm SVL). Some species of *Stenocercus* and *Tropidurus* are rock-dwelling. Others, such as species of the genus *Plica* (**Figure 4.34A**), are arboreal. *Uranoscodon superciliosus* is arboreal and lives closely associated with streams in Amazonian rainforests; this species has toe fringes that permit it to run across water. All tropidurid species are oviparous.

Some tropidurids apparently have resource-based polygyny, a social system seen in many small iguanians. For example, a single reproductively active male of the arboreal Amazonian *Uracentron flaviceps* usually occupies a tree with up to 15 females and juveniles. Retreat and nesting sites are tree holes that are defended by males (Vitt and Zani 1996).

Most tropidurids are primarily insectivorous. Diets of several species (e.g., *Uracentron flaviceps, Plica umbra, Strobilurus torquatus, Tropidurus torquatus*) consist primarily of ants, including noxious stinging species (Vitt and Zani 1996). This may be a widespread dietary preference in this group, but the lizards' defensive mechanisms against the ants are unknown.

Classification, distribution, and conservation 8 genera, 125 species. Genera include Eurolophosaurus, Micro-



Figure 4.34 Tropiduridae. Collared tree lizard, *Plica plica*. (B) Distribution. (Photograph © Patrick K. Campbell/Shutterstock.)

lophus, Plica, Stenocercus, Strobilurus, Tropidurus, Uracentron, and *Uranoscodon.* They inhabit central and northern South America and the Galápagos Islands (**Figure 4.34B**). Tropiduridae previously included genera now placed in Liolaemidae. The IUCN lists 1 species (*Stenocercus haenschi*) as Critically Endangered and 7 species as Near Threatened or Vulnerable.

Systematics references Harvey and Gutberlet (1998, 2000), Frost et al. (2001), Torres-Carvajal et al. (2006).

Phrynosomatidae • Spiny and Sand Lizards

Phrynosomatids are morphologically and ecologically diverse and constitute a significant portion of the lizard fauna of the desert southwest of the United States and northeast Mexico. Species of *Phrynosoma* are small, often spiny lizards with a flat, stout body and short tail (see Figure 6.2B). *Sceloporus*, the most species-rich phrynosomatid genus (96 species), includes terrestrial, arboreal, and rock-dwelling forms, in habitats that extend from tropical rainforests to high mountain scrub. Species of *Uma* are sand-diving lizards adapted to areas of loose sand (Figure 4.35A). Many aspects of their morphology are modified for such habitats, including the development of fringes on the toes, a countersunk lower jaw, and modifications of the eyelids and nostrils (Arnold 1995). *Callisaurus* can sprint bipedally at great speed. When threatened, *Callisaurus* raise and rhythmically wag their black-and-white striped tail. This display is thought to communicate to the predator that it has been identified and further pursuit is futile (Hasson et al. 1989).

Because of their accessibility to North American investigators, short life spans, and often high population densities, some phrynosomatids have become model systems for research in the evolutionary and behavioral ecology of natural vertebrate populations. *Sceloporus* and *Uta* have figured prominently in the development of life-history evolution theory and in the integration of physiological and population ecology (e.g., Tinkle and Dunham 1986; Sinervo et al. 1992; Niewiarowski et al. 2004). Similarly, complex chromosomal polymorphisms and hybridization among species of the *Sceloporus grammicus* complex have provided fruitful systems for understanding hybrid zones and chromosome evolution (e.g., Marshall and Sites 2001; Leaché and Cole 2007). **Classification, distribution, and conservation** 9 genera, 148 species. Genera include *Callisaurus, Cophosaurus, Holbrookia, Petrosaurus, Phrynosoma, Sceloporus, Uma, Urosaurus,* and *Uta.* Phrynosomatids occur from southern Canada to Panama (**Figure 4.35C**). The IUCN lists 7 species as Critically Endangered or Endangered and 16 species as Near Threatened or Vulnerable.

Systematics references Reeder and Wiens (1996), Wiens (1998), Leaché and McGuire (2006), Leaché (2009), Wiens et al. 2010c).

Polychrotidae • Bush Anoles

Polychrotids consist of a single genus (*Polychrus*) with seven species of moderately large (~15 cm SVL), long-legged, highly cryptic arboreal lizards of wet and dry forests in Central and South America (**Figure 4.35B**). Polychrotids move slowly and have a long, prehensile, non-autotomic tail. *Polychrus acutirostris* is sexually dimorphic, with males approximately 75% the SVL of females. Polychrotids are phenotypically and ecologically similar to *Anolis* (Dactyloidae) but differ in characteristics of their threat display and fecundity. The clutch size of *P. acutirostris* is 7–31 rather than 1 as in *Anolis* (Vitt and Lacher 1981).

Classification, **distribution**, **and conservation** 1 genus (*Polychrus*), 7 species. They occur from Nicaragua to central South America (**Figure 4.35C**). Polychrotidae once contained *Anolis* and some genera now placed in Leiosauridae,



(A) Phrynosomatidae



(B) Polychrotidae



Figure 4.35 Phrynosomatidae and Polychrotidae. (A) Coachella Valley fringe-toed lizard, *Uma inornata* (Phyrnosomatidae). (B) South American bush anole, *Polychrus femoralis* (Polychrotidae). (C) Distribution. (Photographs: A, courtesy of Harvey Pough; B, courtesy of John E. Cadle.)

but molecular phylogenetic analyses have shown that these genera do not form a clade. No species are listed by the IUCN as an extinction risk, but basic data are lacking for most species.

Systematics references Koch et al. (2011).

Leiocephalidae • Curly-Tailed Lizards

The family contains one genus (*Leiocephalus*) of moderatesize (up to 9 cm SVL), terrestrial lizards. They are primarily insectivorous but may also consume plants and other lizards. Males of some leiocephalid species are larger than females (Schoener et al. 1982). Their common name refers to their behavior of coiling their tail dorsally when threatened (**Figure 4.36A**).

Classification, distribution, and conservation 1 genus (*Leiocephalus*), 29 species. They inhabit the western Caribbean, including Cuba, Hispañola, the Bahamas, and nearby islands and small islets (**Figure 4.36C**). *Leiocephalus* was previously placed in Tropiduridae. Two species have recently become extinct, and the IUCN lists 2 other species as Near Threatened or Vulnerable.

Systematics references Etheridge (1966), Schwartz (1967), Pregill (1992).

Hoplocercidae • Clubtails and Wood Lizards

Hoplocercids are moderate-size lizards, up to about 16 cm SVL. *Enyalioides* and *Morunasaurus* inhabit rainforests,

whereas *Hoplocercus* is found primarily in cerrado in Brazil and Bolivia. These are primarily terrestrial lizards with a spiny tail (extremely so in *Hoplocercus*). *Hoplocercus spinosus*, *Morunasaurus annularis*, and several species of *Enyalioides* use burrows in the ground that they apparently construct themselves; *Morunasaurus groi* has been taken from rock crevices. *Hoplocercus spinosus* inflates its body to prevent extraction from its burrow, a defensive measure that is also used by *Sauromalus* (Iguanidae), *Uromastyx* (Agamidae), and some cordylids and gerrhosaurids. All species of hoplocercids are oviparous.

Classification, distribution, and conservation 3 genera, 16 species. Genera include *Enyalioides* (Figure 4.36B) in Panama, northwestern South America, and Amazonia; *Hoplocercus* in the cerrado of Brazil and Bolivia; and *Morunasaurus*, which includes 2 species with disjunct distribution, in eastern Peru and Ecuador and in Panama (Figure 4.36C). No species are listed by the IUCN as an extinction risk, but complete data are available for only 1 species.

Systematics references Wiens and Etheridge (2003), Torres-Carvajal and de Queiroz (2009).

Iguanidae • Iguanas

Iguanid lizards are moderate size (14 cm SVL in *Dipsosaurus*) to large (more than 70 cm SVL in *Cyclura*) and may be terrestrial (*Dipsosaurus*, *Cyclura*), rock-dwelling (*Sauromalus*, *Ctenosaura*; **Figure 4.37A**), or arboreal (*Iguana*, *Brachylophus*). Iguanids are primarily herbivorous as adults



Figure 4.36 Leiocephalidae and Hoplocercidae. (A) Northern curly-tailed lizard, *Leiocephalus carinatus* (Leiocephalidae). (B) Bin Zayed's wood lizard, *Enyalioides binzayedi* (Hoplocercidae). (C) Distribution. (Photographs: A, © blickwinkel/Alamy; B, courtesy of Pablo J. Venegas.)



Figure 4.37 Iguanidae. (A) Northeastern spiny-tailed iguana, *Ctenosaura acanthura*. (B) Distribution. (Photograph by René Clark, © Dancing Snake Nature Photography.)

and consume leaves, fruits, and flowers; juvenile *Iguana* are also exclusively herbivorous, and this is probably true of other juvenile iguanids. The colon has partitions that serve several functions associated with digestion of plants, including slowing the passage of food through the gut, increasing the surface area available for absorption, and providing a microhabitat for an extensive microbe fauna involved in the breakdown of cellulose (see Chapter 15) (Iverson 1980; Mackie et al. 2004). All species are oviparous.

Classification, distribution, and conservation 8 genera, approximately 39 species. Genera include *Amblyrhynchus* and *Conolophus* (Galápagos Islands), *Cyclura* (West Indies), *Brachylophus* (Fiji), and *Iguana, Ctenosaura, Dipsosaurus*, and *Sauromalus* (southwestern United States through tropical South America) (**Figure 4.37B**). The IUCN lists 19 species as Critically Endangered or Endangered (50% of iguanid species) and 11 species as Near Threatened or Vulnerable.

Systematics references Etheridge and de Queiroz (1988), Hollingsworth (1998).

Dactyloidae • Anoles

The family contains only one genus—*Anolis*—but that genus is extraordinarily diverse, with more than 390 described species and an array of ecomorphs (see Section 5.5). *Anolis* is perhaps the most widely studied genus of lizards, with literally thousands of studies of behavior, ecology, thermal biology, and evolution (Losos 2011). West Indian species of *Anolis* have become a model system to study adaptive radiation and the influence of ecological conditions on evolution and speciation. *Anolis carolinensis* (**Figure 4.38A**) has been widely used for studies of sexual behavior and evolutionary



development and is the first non-avian reptile to have its complete genome sequenced (Alföldi et al. 2011).

Anolis range in size from 3 to 19 cm SVL. Most are arboreal, although some live in grass or bushes. The elevational range of the genus extends from sea level to the high Andes and the high tablelands known as tepuis in the Guayanan region of South America. Anolis are primarily insectivorous, but some species consume plant matter, especially fruits and flowers.

Anoles are characterized by the presence of subdigital lamellae bearing setae similar to those of geckos (Ruibal and Ernst 1965). The setae of anoles are simple, unbranched, and smaller than those of geckos, and unlike geckos, *Anolis* cannot cling to glass.

Anolis have brightly colored dewlaps, usually more prominent in males than in females, that are used in intraspecific communication (see Figure 13.26). Some Anolis, especially large-bodied species, have well-developed casques on the head (e.g., A. equestris). All Anolis are oviparous but are unusual in that they lay a single egg every 1–2 weeks during their breeding season rather than a single clutch of multiple eggs.

The taxonomy of *Anolis* has been contentious because the genus is so diverse. It is now widely agreed that the formerly recognized genera *Chamaelinorops*, *Chamaeleolis*, and *Phenacosaurus* are nested within *Anolis*, but there have been numerous efforts to split the entire genus *Anolis* into multiple genera with the goal of better representing the phylogenetic diversity of the group (see Nicholson et al. 2012, 2014). Although no multigeneric taxonomy has become widely accepted, the name *Dactyloa* for primarily South American anoles has seen some use in the literature.



Figure 4.38 Dactyloidae. (A) Green anole, *Anolis carolinensis*. (B) Distribution. (Photograph © Kenneth Jones/Alamy.)

However, we have adopted the traditional single-genus taxonomy, primarily because the name has a long history of scientific and lay usage. Although splitting it would improve the phylogenetic specificity of dactyloid lizard taxonomy, that advance could come at the cost of impeding interdisciplinary research in the group (see Poe 2013).

Classification, distribution, and conservation 1 genus (*Anolis*), 391 species. *Anolis* inhabit the southeastern United States through Central America and most of South America and the Caribbean (**Figure 4.38B**). The IUCN lists 16 species as Critically Endangered or Endangered and 12 species as Near Threatened or Vulnerable.

Systematics references Etheridge (1959), Jackman et al. (1999), Poe (2004), Alföldi et al. (2011), Castañeda and de Queiroz (2011, 2013).

Crotaphytidae • Collared and Leopard Lizards

Crotaphytids are moderately large (~10–15 cm SVL), diurnal, often colorful lizards of mesic and arid areas of North America. Species of *Gambelia* (leopard lizards) and *Crotaphytus reticulatus* occur in flatland deserts, using rocky outcrops occasionally, whereas other species of *Crotaphytus* are exclusively rock-dwelling (**Figure 4.39A**).

In addition to eating insects, most crotaphytids consume some vertebrates. *Crotaphytus* in particular are voracious predators of vertebrates, especially other lizards, but also eat rodents and snakes. Predation is aided by large jaw adductor muscles that deliver a powerful bite (especially in *Crotaphytus*). Social dominance in *Crotaphytus collaris* is determined by male–male combat, and bite force is the dominant factor in fighting success (Lappin and Husak 2005).

Unlike other iguanians except dactyloids, crotaphytids use squealing vocalizations when stressed. Autotomic fracture planes are present in the tail of *Gambelia*, whereas they are absent in *Crotaphytus*. *Crotaphytus* use an unusual form



of saltatorial bipedalism when moving among boulders. All species are oviparous.

Classification, distribution, and conservation 2 genera (*Crotaphytus, Gambelia*), 12 species. They occur from the south-central United States to northern Mexico (**Figure 4.39D**). The IUCN lists 2 species (*C. antiquus* and *G. sila*) as Endangered and 1 species (*C. reticulatus*) as Vulnerable.

Systematics references McGuire (1996), McGuire et al. (2007).

Corytophanidae • Basilisk and Casquehead Lizards

These lizards are recognizable by their well-developed head crests and casques. The crests are sexually dimorphic in *Basiliscus* (only males have well-developed crests; **Figure 4.39B**), whereas both sexes have crests in *Corytophanes* and *Laemanctus. Corytophanes* (see Figure 15.14) uses the crest in a defensive display in which the lateral aspect of the body is oriented toward a predator, thus making the lizard appear larger than it is.

Corytophanids are highly arboreal, but juvenile *Basiliscus* are well known for their ability to run bipedally across the surface of water (see Figure 10.5), and their toes are equipped with enlarged, squarish scales associated with this behavior. They occasionally seek refuge underwater, lodging themselves among boulders on the bottom for short periods. Corytophanids are primarily insectivorous, and all species are oviparous.

Classification, distribution, and conservation 3 genera (*Basiliscus, Corytophanes, Laemanctus*), 9 species. They inhabit central Mexico to northwestern South America (A) Crotaphytidae

(D)

(B) Corytophanidae



(C) Liolaemidae



Figure 4.39 Crotaphytidae, Corytophanidae, Liolaemidae. (A) Collared lizard, *Crotaphytus collaris.* (B) Basking male plumed basilisk, *Basiliscus plumifrons.* (C) Thin tree or jewel lizard, *Liolaemus tenuis.* (D) Distribution. (Photographs: A, courtesy of Harvey Pough; B, © George Grall/National Geographic Creative/Corbis; C, © Paul John Fearn/Alamy.)



(Figure 4.39D). No species are listed by the IUCN as an extinction risk.

Systematics references Lang (1989), Viera et al. (2005).

Liolaemidae

Tree Iguanas, Snow Swifts, and Relatives

Liolaemids are small to medium-size lizards (6–10 cm SVL). The genus *Liolaemus* is notably diverse, with at least 280 described species that vary considerably in morphology, ecology, and behavior. The habitats occupied by *Liolaemus* range from the extremes of the Atacama Desert (the driest place on Earth) to elevations of 5,000 m in the Andes.

Nearly all *Phymaturus* species are herbivorous, approximately half of *Liolaemus* species are omnivorous, and at least six species of liolaemids are exclusively herbivorous. The transition to a predominantly herbivorous diet (defined here as a diet comprising at least 70% plant matter) in *Liolaemus* evolved independently an estimated 18 or more times and is correlated with inhabiting cool climate localities and having a small body size (Espinoza et al. 2004). This is paradoxical because herbivory in reptiles is usually associated with large body size and warm climates (see Chapter 15). Liolaemids are also notable for the repeated evolution of viviparity; about half of *Liolaemus* are viviparous, as are all *Phymaturus*.

Classification, distribution, and conservation 3 genera (*Ctenoblepharys, Liolaemus, Phymaturus*), currently 286 spe(B)

20°

Madagascar

Opluridae



Figure 4.40 Opluridae. (A) Madagascar swift, *Oplurus quadrimaculatus.* (B) Distribution. (Photograph courtesy of Miguel Vences and Frank Glaw.)

cies, although it is expected that many more species will be described. Liolaemidae was previously part of Tropiduridae. Liolaemids occur in South America from central Peru to Tierra del Fuego (**Figure 4.39D**). The IUCN lists 1 species (*Liolaemus arambarensis*) as Endangered and 6 species as Near Threatened or Vulnerable.

Systematics references Etheridge (1995), Etheridge and Espinoza (2000), Schulte et al. (2000, 2013), Pincheira-Donoso et al. (2008, 2013), Breitman et al. (2011), Fontanella et al. (2012).

Opluridae • Madagascan Iguanas

Oplurids are terrestrial (*Chalarodon*) to rock-dwelling or arboreal (*Oplurus*; **Figure 4.40A**) lizards that occur primarily in subhumid to arid areas of Madagascar (Cadle 2003). *Chalarodon madagascariensis* is a small lizard (20 cm total



length) that lives only in areas with open sand. It has locomotory adaptations for running on loose sand and uses terrestrial burrows.

All oplurids are oviparous. Clutch size in *Chalarodon* is 2; the young mature the first year, and most individuals die before the second year. Species of *Oplurus* are larger than *Chlarodon*, up to 39 cm total length. Several species have a spiny tail. Rock-dwelling species of *Oplurus* deposit eggs underneath rocks or in rock crevices. Oplurids may be brightly colored during the breeding season, and males actively defend territories with body postures and displays.

Classification, distribution, and conservation 2 genera (*Oplurus, Chalarodon*), 7 species. They inhabit Madagascar (**Figure 4.40B**). No species are listed by the IUCN as an extinction risk, but this situation probably reflects lack of data rather than evidence of stable populations.

Systematics references Titus and Frost (1996), Münchenberg et al. (2008), Okajima and Kumazawa (2009), Chan et al. (2012).

Leiosauridae South American Tree and Ground Lizards

Leiosaurids are terrestrial, arboreal, or rock-dwelling lizards ranging in size from 8 to 13 cm SVL, that are poorly studied compared with other iguanians. *Anisolepis grilli* and species of *Urostrophus* have a relatively long tail and are arboreal inhabitants of southern South America. Other

> species of *Anisolepis* occur in seasonally flooded grasslands. Species of *Enyalius* are known from Atlantic and Amazonian forests of eastern Brazil. *Enyalius leachii* has a color pattern matching that of dead leaves and becomes immobile when disturbed. *Pristidactylus* species (**Figure 4.41A**) are known from both *Nothofagus* (southern beech) forests and open formations of southern South America. All species are oviparous.

> Figure 4.41 Leiosauridae. (A) Achala big-headed lizard, *Pristidactylus achalensis*, endemic in mountain grasslands of central Argentina. (B) Distribution. (Photograph courtesy of Guillermo Garcia Mendive and Mario G. Alvarez.)

TABLE 4.2 Aspects of snake body form

associated with specific habitats^a

Classification, distribution, and conservation 6 genera, 32 species. Genera include *Anisolepis, Diplolaemus, Enyalius, Leiosaurus, Pristidactylus,* and *Urostrophus.* Leiosaurs were previously included in Polychrotidae. They inhabit southern Amazonian Brazil south to southern Argentina (**Figure 4.41B**). The IUCN lists 1 species (*Anisolepis undulatus*) as Vulnerable.

Systematics references Etheridge and Williams (1985, 1991), Abdala et al. (2009).

4.5 ■ Squamata: Serpentes, the Snakes

Although just one of many examples of the evolution of loss of functional limbs among the Squamata (Wiens et al. 2006; Brandley et al. 2008), snakes are so behaviorly, ecologically, morphologically, and physiologically distinct from other limbless lizards that they have always had a special recognition in the field of herpetology. Snakes lack scleral ossicles, the bony dermal plates that are present in the eyes of many lizards (see Figure 4.3). Many other derived features of snakes involve losses of skull or hyoid elements (lacrimal, jugal, epipterygoid, and squamosal bones in the skull, and several elements of the hyoid) and are associated with increased skull kinesis. In snakes, the anterior mandible consists of the dentary bone, and the posterior mandible of a compound bone formed by the fusion of the articular, prearticular, and surangular bones. The coronoid is also present in the mandible of early diverging lineages of snakes, but is lost in the common ancestor of Caenophidia (see Figure 4.44).

Body proportions and some details of morphology reflect the microenvironment used by a snake (Cadle and Greene 1993). Suites of correlated morphological features have evolved repeatedly in different snake lineages in response to these environmental demands. Thus, it is often easy to infer the macrohabitat (arboreal, fossorial, aquatic, etc.) of an unfamiliar snake even with a relatively superficial examination. Some examples of these macrohabitats and their associated characters are given in **Table 4.2**.

Unique morphological features of snakes

Snakes exhibit other unique morphological features. The supraoccipital bone is excluded from the margin of the foramen magnum by the exoccipitals. Alone among squamates, snakes have 120 or more precloacal vertebrae (the number ranges up to >400). Some limbless lizards have more than 200 total vertebrae, but most of these are in their long tail. In snakes the ophthalmic branch of the trigeminal nerve is enclosed within the braincase by downgrowths of the parietal bone and enters the orbit through the optic foramen. In other squamates the nerve is not enclosed and enters the orbit posteriorly. Snakes lack muscles in the ciliary body of the eye, which accounts for their peculiar mode of focusing (see Figure 4.4). Tail breakage is rare in snakes, and when

Habitat Associated form Arboreal Compressed body Relatively long tail (often prehensile) Relatively large eyes Enlarged vertical scale row Center of gravity shifted posteriorly Small body size (length) Fossorial Reduced head width Downward-projecting (inferior) mouth Scale reductions on head and body; scales very smooth Small eyes Cranial reinforcement Narrow and/or pointed snout Dorsal and terminal displacement of Aquatic eyes and nostrils Valvular nostrils Laterally compressed body and/or tail Cryptozoic^b Small body size (length and mass) Pointed or wedge-shaped snout

These are generalizations; some species are exceptions.

^b Cryptozoic species live within leaf litter or under cover objects

it occurs it is intervertebral, rather than intravertebral as in most lizards.

Many of the morphological features that we use to distinguish snakes from lizards, such as characters responsible for the generally increased gape and mobility of snake jaws, are associated with the feeding system (see Chapter 11). Specific examples include the elongation of the quadrates and supratemporals, further loosening of the mandibular symphysis, a general reduction in articulations between bones of the palatomaxillary arch and the skull, and a similar reduction or elimination of articulations between bones of the palate. That this complex of characters is shared among many snake families has been used as evidence that snakes with this condition form a clade called Macrostomata (from the Greek macro, "big," + stoma, "mouth")-a relationship consistently supported by phylogenetic analyses of morphological data (Figure 4.42). This hypothesis assumes that the "macrostomate" condition evolved a single time in snake evolutionary history. However, molecular phylogenetic analyses universally reject the monophyly of Macrostomata with respect to other clades-including Aniliidae, Anomochilidae, Cylindrophiidae, and Uropeltidae-that do not have the macrostomate condition, thereby suggesting





Figure 4.42 A phylogenetic analysis of Serpentes based on morphological data.

that the macrostomate character complex evolved multiple times in snake evolutionary history or was secondarily lost numerous times.

The skulls of most snakes are as kinetic or more kinetic than the skulls of most lizards, but this kinesis occurs in a rather different way. Whereas most lizards have lost only the lower temporal arch (exceptions are gekkotans and varanids, among others), snakes have lost both temporal arches and the quadrate attaches to the skull via the supratemporal bone (Figure 4.43). Unlike most lizards, the brain of snakes is enclosed in a rigid box formed by downgrowths of the frontals and parietal, which have an extensive articulation with the sphenoid below the brain. Thus, the mesoand metakinetic joints of the skull roof, which are present in lizards, are lost in snakes. A new and complex prokinetic joint is formed between the frontals and the nasal region (nasals and/or septomaxillae). The snout kinesis of some snakes is also aided by mobility of the prefrontal relative to the skull roof and of the maxilla relative to the prefrontal as seen, for an extreme example, in the fang erection mechanism in Viperidae (see Section 11.3).

Reproduction

Snakes are oviparous or viviparous, and in some cases a reproductive mode characterizes large clades, despite otherwise variable life histories. In other cases, however, closely related species differ in reproductive mode. For example, all Boidae (except *Eryx jayakari, Eryx muelleri*, and *Calabaria*

Figure 4.43 The skulls of lizards crush prey, whereas the skulls of snakes engulf prey. Comparison of the skull of a lizard (Ameiva) with that of a snake (Lampropeltis) reveals differences related to modes of feeding. (A) Lizards have relatively rigid skulls and jaws that can crush hard-shelled prey like beetles or shear fibrous plant material. The connection between the quadrate and the pterygoid stabilizes the articulation of the jaw with the skull, and the tooth-bearing dentary is rigidly attached to the posterior bones of the jaw. A bony suture rigidly joins the two mandibles, and firm sutures between the bones of the skull make the upper jaw rigid. (B) Snakes have lost the connection between the pterygoid and quadrate and developed a flexible articulation between the quadrate and supratemporal, permitting extreme kinesis at the rear of the jaw. The tooth-bearing dentary bone is loosely articulated with the posterior jaw bones, and the two mandibles are attached by soft tissue and can move independently. The bones of the snout are also loosely articulated, allowing the maxilla and the tooth-bearing pterygoid of the left and right sides of the head to be moved independently. The brains of snakes are enclosed by the frontal and parietal bones, whereas the brains of most lizards are protected only by the soft tissues of the roof of the mouth.

reinhardtii) are viviparous. In contrast, natricine colubrids from the Old World are oviparous, whereas those from the New World are viviparous. Genetic sex determination occurs in all species in which the mechanism has been determined. Sex chromosome heteromorphism is the rule in Colubroidea (where females are the heterogametic sex) but is unknown in other snakes (Gorman 1973).

Females of many species of snakes are larger than males and have a proportionately shorter tail. Males of some species have keels on the supra-anal scales or tubercles on the chin scales, and these tubercles are smaller or absent in females. Vestigial pelvic elements are retained in Scolecophidia, Aniliidae, Boidae, Loxocemidae, Pythonidae, and Tropidophiidae. These are usually larger in males than in females and are often used during courtship to stimulate the females. Sexual differences in coloration are not common in snakes but are known in some species, such as the boomslang (*Dispholidus typus*; Colubridae) and many vipers (Shine 1993).

Dentition

Typical snake teeth are long, slender, and slightly curved. They are attached to the jaws in a modified pleurodont manner, in which each individual tooth is set within a shallow depression (see Figure 4.8C). In alethinophidians, the clade that contains all snakes other than blindsnakes, teeth are universally present on the maxillae, palatines, and pterygoids in the upper jaw and on the dentary in the lower jaw. The premaxilla bears teeth in some basal alethinophidians. Scolecophidians (blindsnakes) have extremely reduced dentition, and the pattern of reduction is characteristic of each family (see family accounts). Ancestrally within alethinophidians, all teeth are roughly of the same form (homodont), but various forms of heterodonty have evolved. For example, the teeth on different parts of the tooth-bearing bones differ in size in colubroid snakes and in arboreal boas and pythons-only in colubroids are individual teeth modified as grooved or hollow fangs. The number of teeth on the tooth-bearing bones varies considerably; only two or three maxillary teeth are present in colubrids such as Dasypeltis (African egg-eating snakes) and Tomodon (a South American slug eater), whereas snakes closely related to these genera have more than 30 teeth in the maxilla.

Various classification schemes have been proposed for patterns of maxillary dentition in colubroids, but none entirely reflects the variation within this large clade. The simplest scheme recognizes four general categories. **Aglyph** dentition refers to maxillary dentition with little variation in size or shape (homodont dentition). **Opisthoglyph** dentition is often referred to as "rear-fanged" because the englarged, grooved fangs are located on the posterior portion of the maxilla (see Figure 11.26). Aglyph and opisthoglyph dentition are characteristic of colubrids and most lamprophiids. In **proteroglyph** dentition, each maxilla bears a single hollow fang on its anterior end (and usually additional teeth behind the fang), and the fang is not erected by extensive rotation of the maxilla around the prefrontal bone. This condition is seen in elapids and the lamprophiid *Homoroselaps*. Finally, snakes with **solenoglyph** dentition have an extremely reduced maxilla that never bears teeth other than a hollow fang, and the fang is erected by rotation of the maxilla on the prefrontal bone (see Figure 11.27). This dentition is characteristic of vipers and the lamprophiid *Atractaspis*. The enlarged posterior maxillary teeth of colubrids are often, but not always, separated from more anterior teeth by a gap.

The front fangs of vipers, elapids, and lamprophilds have a venom canal, which is a hollow tube distinct from the pulp cavity of the tooth. The details of structure of the fangs and their placement on the maxillary bones suggest that the front fangs of vipers and elapids are homologous with the posterior maxillary fangs of colubrids. However, tubular venom-conducting front fangs do not develop embryonically by closure of an open groove as seen in rear-fanged snakes, but by elongation of a fundamentally tubular structure in embryos and adult replacement teeth (Jackson 2002).

Glands that produce venom are associated with the fangs of colubroid snakes (see Figure 11.25). Venom may contain several hundred components (see Fry et al. 2009, 2012), which accounts for some of the difficulty in treating snakebite and also in understanding the evolution of venom. The toxins in snake venoms are proteins that range from small peptides to complex enzymes and nonenzymatic proteins with high molecular weights. They are classified by their physiological actions and chemical structures.

Fossil record

The fossil record of snakes is poor compared with that of other squamate groups. Snake skulls are delicate, and fossilized skulls are extremely rare; most snake fossils consist of isolated vertebrae. The systematics of extant snakes relies very little on vertebral characters, so correlating the results of systematic research on extant and fossil groups has been problematic. The oldest snake fossil was recently described from geological deposits 167-143 mya (Caldwell et al. 2015), but the Cenomanian-Turonian boundary (~95 mya) fossil record is particularly interesting to paleontologists because it contains five genera of snakes with hindlimbs. Phylogenetic analyses of fossil and extant snakes suggest that Dinilysia and Najash are basal snakes (Zaher and Scanferla 2012; Palci et al. 2013). Furthermore, like limbed reptiles, Najash retains a sacrum that articulates with the hindlimbs, while the hindlimbs of the other four genera are not directly attached to the vertebral column. These two fossils are therefore important transition fossils between limbless snakes and their limbed ancestors.

The other three fossil genera with hindlimbs are the marine snakes *Eupodophis*, *Haasiophis*, and *Pachyrachis*. The phylogenetic relationships of these forms to other snakes are controversial because researchers studying the same material have come to different conclusions. Some phylogenetic analyses place these three taxa at the base of

the snake tree like *Dinilysia* and *Najash* (e.g., Palci et al. 2013). However, other analyses place these three taxa as derived snakes within Alethinophidia, usually within or sister to "Macrostomata" (e.g., Zaher and Scanferla 2012). This placement suggests that the hindlimbs of *Eupodophis*, *Haasiophis*, and *Pachyrachis* either re-evolved from limbless snakelike ancestors or were retained over a long period of snake evolutionary history. The alternative interpretations of these limbed marine snakes have implications for interpreting the terrestrial or aquatic origins of snakes, the evolution of the snake feeding system, and limblessness (Lee et al. 1999; Greene and Cundall 2000), as well as character evolution in squamates (Rieppel and Zaher 2000a,b).

Snakes became widespread in the Late Cretaceous, with representative fossils in India (Rage and Prasad 1992), South America (Albino 1996), China (Gao and Hou 1996), and Africa (Rage and Wouters 1979). Putative fossil Aniliidae have been found in North America, South America, and India. Colubroid fossils have been recovered from Middle Cretaceous deposits in Sudan, a considerable stratigraphic range extension for that clade (Werner and Rage 1994); the next colubroids do not appear until the Tertiary.

Tertiary fossil snakes include some families (Russellophiidae, Nigerophiidae, Paleophiidae, and Anomalophiidae) that became extinct by the end of the Eocene (~38 mya); their relationships to other snakes are not clear. The earliest colubrid appears in the Eocene of Thailand (Rage et al. 1992). Other early colubrids appear in the early and middle Oligocene of France, Oman, and the United States (Holman 1984). Viperids and elapids first appear in early Miocene deposits of Europe and North America and are common in deposits after that time. Snakes, especially caenophidians, are reasonably well represented in later Tertiary (Miocene-Recent) deposits of both Europe and North America (Szyndlar 1991a,b; Szyndlar and Böhme 1993; Holman 1995). Overviews of the snake fossil record are presented by Szyndlar (1991a,b), Albino (1996), Holman (2000), and Vidal et al. (2009).

Systematics and Phylogeny of Snakes

Several major clades of Serpentes are supported by morphological and molecular analyses of snake phylogeny. For example, the monophyly of Alethinophidia is supported by numerous characters of the skull, nervous system, and axial muscles. Likewise, monophyly of Caenophidia is supported by several osteological characters (see taxonomic accounts below). But there are also numerous differences in phylogenetic relationships estimated by morphology and DNA data.

As we discussed previously, morphological evidence supports the clade Macrostomata that includes snakes with a complex of characters that permit a wide mouth gape (see Figure 4.42). However, this relationship is wholly unsupported by molecular data. Morphological data also support the sister relationship of boas and pythons, snakes that bear a striking phenotypic resemblance, in a clade named Boidae. However, molecular data strongly reject the monophyly of this clade. Instead, Pythonidae forms a clade with Xenopeltidae and Loxocemidae (Figure 4.44). A recently redefined Boidae (see Boidae family account) includes the genus *Calabaria*, formerly recognized in its own family, Calabariidae (Pyron et al. 2014a). Thus, Boidae refers to different clades depending on whether an author is following a morphological or molecular phylogeny, or is using an older or newer taxonomy.

One of the most significant advancements in snake systematics in the past decade has been resolving the phylogenetic relationships of colubrid and lamprophiid snakes (compare the morphological phylogeny in Figure 4.42 to the molecular phylogeny in Figure 4.44). It was long recognized that no known shared derived morphological characters support a monophyletic Colubridae, and the group essentially contained species that could not be placed confidentally in other snake clades. Comprehensive molecular phylogenetic analyses of "colubrids" have resulted in the recognization the new families Homalopsidae, Pareatidae, and Lamprophiidae. Lamprophiidae also contains the unusual aparallactines (centipede-eating snakes) and Atractaspis (stiletto snakes), the latter a genus whose phylogenetic relationships have been extensively debated and was previously classified as its own family, Atractaspididae (see Figure 4.42).

Even with large molecular data sets, the interrelationships of some major clades remain uncertain, especially for basal Alethinophida, Colubridae, and Lamprophiidae. Snake systematics and evolution will therefore continue to be a fruitful area of research for some time.

Classification, distribution, and conservation Approximately 25 families and more than 3,400 species of snakes are recognized, and about half of these are in Colubridae. Snakes are cosmopolitan, even occurring above the Arctic Circle in Europe (*Vipera berus*) and above timberline in the Himalayas (*Thermophis baileyi*). The IUCN lists 118 species in 14 families as Critically Endangered or Endangered and 151 species in 14 families as Near Threatened or Vulnerable. The secretive lifestyles of many snakes prohibit easy collection of basic distribution and natural history data that are crucial for evaluating the stability of populations. Therefore, the number of endangered species is certainly higher than is currently recognized. Causes for population declines vary, but habitat destruction, willful killing by humans, and collection for the pet trade are major contributors.

Systematics references Underwood (1967), Cadle (1988), Vidal et al. (2007, 2009), Wiens et al. (2008, 2012), Vidal and Hedges (2009), Pyron et al. (2011, 2013a,b, 2014b), Gauthier et al. (2012), Zaher and Scanferla (2012), Palci et al. (2013).



SCOLECOPHIDIA: BLINDSNAKES

Extant scolecophidians are surprisingly conservative in morphology and ecology, even though the lineage arose in the Jurassic, approximately 150 mya. They are typically small snakes, ranging in total length from 10 cm (*Leptotyphlops carlae*) to a maximum of 95 cm (*Afrotyphlops schlegelii*). They have a short, blunt tail often tipped with a spine, and smooth scales, and they lack enlarged ventral scales. The head is blunt, except in some typhlopids such as *Acutotyphlops*, and the eyes are vestigial. Scolecophidians retain ves-

Figure 4.44 Phylogenetic analysis of Serpentes based on DNA data. This phylogeny is the one followed in this textbook. The placement of Anomalepididae is uncertain.

tiges of their pelvic girdle, and their skull is highly modified for burrowing. All scolecophidians are oviparous.

Although in general snakes consume one or only a few large prey items in a feeding bout, most scolecophidians are exceptions. Their diets consist mainly of ant or termite pupae, larvae, eggs, and (less frequently) adults. These snakes frequently appear to gorge themselves inside ant or termite nests, for entire guts from esophagus to cloaca are packed with food-more than 1,500 items have been found in the gut of some individuals. Rena (formerly Leptotyphlops) dulcis, and presumably other leptotyphlopids, feed by mandibular raking, continually rotating the two halves of the mandible like a pair of swinging doors and pulling ant pupae and larvae into their mouths (Kley and Brainard 1999). Typhlopids also evolved a raking mechanism, but instead of moving the mandibles, they move two halves of their highly modified maxilla (upper jaw). The New Guinean Acutotyphlops subocularis (Typhlopidae) differs from other typhlopids-its only food is earthworms.

The historic taxonomy of Scolecophidia recognized three families: Anomalepididae, Leptotyphlopidae, and Typhlopidae. A recent comprehensive molecular phylogenetic analysis of Scolecophidia identified two additional and distinct lineages, Gerrhopilidae and Xenotyphlopidae, that diverged from other typhlopids about 100 mya (Vidal et al. 2010a).

Because of the distinct morphology of scolecophidians, the monophyly of the

group has rarely been challenged on the basis of anatomical data. However, despite its blindsnake phenotype, no recent molecular phylogenetic analyses support the inclusion of Anomalepididae in Scolecophidia. Rather, molecular data support Anomalepididae as either the sister lineage to all other snakes (Scolecophidia + Alethinophidia) (Pyron et al. 2013a,b), or the sister lineage to Alethinophidia (Wiens et al. 2008, 2012). Resolving these relationships will have important consequences for the interpretation of snake diversity. If Anomalepididae represents either the sister lineage to all snakes or just alethinophidian snakes, this would suggest that the common ancestor of all extant snakes had a ter-



Figure 4.45 Anomalepididae. (A) White-nosed blindsnake, *Liotyphlops albirostris.* (B) Distribution. (Photograph courtesy of Christopher J. Williams.)

restrial scolecophidian phenotype. Therefore, the spectacular morphological diversity of alethinophidian snakes may have evolved from this ancestral blindsnake morphology.

Classification, distribution, and conservation 27 genera, 404 species. Scolecophidians are distributed worldwide. Few species are listed by the IUCN as an extinction risk, but this situation reflects lack of data for these secretive snakes rather than the absence of threats.

Systematics references McDowell (1974), Vidal et al. (2010a), Hedges et al. (2014), Pyron and Wallach (2014).

Anomalepididae • Primitive or Dawn Blindsnakes

Anomalepidids (**Figure 4.45A**) are similar to typhlopids in having toothed, movable maxillae. They differ in that anomalepidids lack pelvic vestiges and have one to three teeth on the dentary, an M-shaped hyoid skeleton, and prefrontal bones that extend posteriorly over the orbits the last two characters unique among squamates. Little is known about their natural history, but they have typical scolecophidian habits, such as fossoriality and a diet of ant and termite larvae and pupae.

Classification, distribution, and conservation 4 genera (*Anomalepis, Helminthophis, Liotyphlops, Typhlophis*), 18 species. Anomalepidids have a disjunct distribution in southern Central America and northern South America (**Figure 4.45B**). No species are listed by the IUCN as an extinction risk.

Systematics references Dixon and Kofron (1983), Kofron (1988).

Leptotyphlopidae Slender Blindsnakes, or Thread Snakes

The cranium and upper jaws (maxillae, palatines, and pterygoids) of leptotyphlopids are immobile, and teeth are pres-



ent only on the dentary bones. The lower jaw consists of an enormous, horizontally placed quadrate, a tiny compound bone, and relatively larger dentary, angular, splenial, and coronoid bones.

Leptotyphlopids do not attain the large sizes that some typhlopids reach; the largest species are *Tricheilostoma macrolepis* (South America) and *Namibiana occidentalis* (Africa), which reach total lengths of about 30 cm. Most species are much smaller, some no more than about 10 cm and are sometimes confused with earthworms upon first glance. All species of leptotyphlopids are oviparous, and in known cases the elongate eggs are attached in a string. Females of the Texas blindsnake (*Rena dulcis*; **Figure 4.46A**) tend their eggs. Diets are broad in some species; in North America, *R. dulcis* and *R. humilis* feed on a broad array of soft-bodied arthropods (ants, termites, other insects).

Two remarkable features of the natural history of *R. dulcis* have been reported. First, this snake follows ant trails using chemoreception, even crawling within a column of foraging ants, and lives in ant nests where it feeds on ant larvae and pupae. Cloacal secretions that the snake smears on its body apparently protect it from attack by the ants (Watkins et al. 1969). In addition, although blindsnakes are generally burrowers, they have have been found in dense, apparently stable populations in the nests of screech owls high in trees. These snakes were apparently brought alive to the nests as food for the young birds, but escaped and subsisted on the abundant insect fauna living in the nests (Gehlbach and Baldridge 1987).

Classification, distribution, and conservation 12 genera, 117 species. 2 subfamilies: Epictinae (genera include *Epictia, Guinea, Mitophis, Rena, Rhinoleptus, Siagonodon, Tetracheilostoma, Tricheilostoma*) and Leptotyphlopinae (genera include

8



Epacrophis, Leptotyphlops, Myriopholis, Namibiana). The genus *Rena,* which includes two common North American species, *R. dulcis* and *R. humilis,* was previously placed in the genus *Leptotyphlops* (Adalsteinsson et al. 2009). Leptotyphlopids occur in Africa, the Middle East, and from northern South America to the southwestern United States (**Figure 4.46B**). No species are listed by the IUCN as an extinction risk.

Systematics references Hahn (1978), Hahn and Wallach (1998), Adalsteinsson et al. (2009).

Gerrhopilidae • Worm Snakes

Gerrhopilids have glandlike structures distributed across their head and chin scales, although this trait is not unique among scolecophidians. The function of these glands is unknown. Little is known of the natural history of worm snakes, but aspects of their ecology and diet are presumably similar to those of other scolecophidians.

Classification, distribution, and conservation 2 genera (*Cathetorhinus, Gerrhopilus*; **Figure 4.47A**), 18 species. They occur in India, Indonesia, Mauritius, New Guinea, the Philippines, and Southeast Asia (**Figure 4.47C**). Gerrhopilids were previously part of Typhlopidae (*Typhlops ater* species group), but molecular evidence shows that this lineage is sister to Typhlopidae + Xenotyphlopidae, with which it shares a common ancestor. Authors differ in whether *Cathetorhinus* is a gerrhopilid (e.g., Pyron and Wallach 2014) or typhlopid (e.g., Wallach and Pauwels 2008; Hedges et al. 2014).

Systematics references McDowell (1974), Vidal et al. (2010a), Hedges et al. (2014), Pyron and Wallach (2014).

Xenotyphlopidae • Madagascan Blindsnakes

Almost nothing is known about the natural history of xenotyphlopids. Indeed, more than 100 years elapsed between the description of the genus in 1905 and the discovery of additional specimens in the wild. *Xenotyphlops* inhabits xeric habitats, is oviparous and probably shares classic scolecophidian ecological characters, such as a subterranean lifestyle and a diet composed mostly of ants and/or termites.

Classification, distribution, and conservation 1 species, *Xenotyphlops grandidieri* (Figure 4.47B). It inhabits Madagascar (Figure 4.47C). Previously Xenotyphlopidae was part of Typhlopidae, but molecular evidence shows that this lineage is sister to all other typhlopids, with which it shares a common ancestor of some 100 mya (Vidal et al. 2010a). The IUCN lists *X. grandidieri* as Critically Endangered.

Systematics references Wallach and Ineich (1996), Wallach and Andreone (2007), Vidal et al. (2010a), Wegener et al. (2013).

Typhlopidae • Blindsnakes

Typhlopids are the most species-rich and widely distributed family of scolecophidians. They inhabit a wide variety of habitats, including deserts. *Ramphotyphlops* is unusual among squamates in having a solid, protrusible hemipenis rather than an eversible, hollow structure (Robb 1966). Few species of scolecophidans are more than about 30 cm in total length. However, the largest species, *Afrotyphlops schlegelii* of southern Africa, attains a length of nearly 1 m. All typhlopids lay eggs, but egg retention is common, and freshly laid eggs may contain advanced embryos.

Indotyphlops (formerly Ramphotyphlops) braminus (Figure 4.48A) is a triploid parthenogenetic unisexual species





Figure 4.47 Gerrhopilidae and Xenotyphlopidae. (A) Jan's worm snake, *Gerrhopilus mirus* (Gerrhopilidae), Sri Lanka. (B) Madagascar blind-snake, *Xenotyphlops grandidieri* (Xenotyphlopidae), Madagascar. (C) Distribution. (Photographs: A, courtesy of Ruchira Somaweera; B, courtesy of Miguel Vences and Frank Glaw.)



Figure 4.48 Typhlopidae. (A) Flowerpot snake, *Indotyphlops braminus*. (B) Distribution. (Photograph courtesy of Todd W. Pierson.)



Figure 4.49 Aniliidae. (A) Red pipe snake, Anilius scytale. (B) Distribution. (Photograph © Patrick K. Campbell/ Shutterstock.)

(A)



(Wynn et al. 1987). Thus, it is probably a product of interspecific hybridization, as are most other squamate parthenogens. Parthenogenesis has permitted *I. braminus* to reproduce in any suitable habitat worldwide, giving it the dubious distinction of being possibly the most widespread invasive snake species on earth (see Section 9.2).

Classification, distribution, and conservation 16 genera, 260 species. Representative genera include *Afrotyphlops, Indotyphlops, Letheobia, Megatyphlops, Ramphotyphlops,* and *Typhlops.* Distribution is worldwide (**Figure 4.48B**). The IUCN lists 8 species as Critically Endangered or Endangered and 4 species as Near Threatened or Vulnerable.

Systematics references McDowell (1974), Kornilios et al. (2013), Marin et al. (2013a,b), Hedges et al. (2014).

ALETHINOPHIDIA

All snakes other than scolecophidians form the clade Alethinophidia, whose monophyly is supported by both morphological and molecular phylogenetic analyses (see Figures 4.42 and 4.44). Alethinophia contains the vast majority of snake species that together represent a spectacular diversity of body plans, behavior, and ecological niches.

Aniliidae • Neotropical Pipe Snakes

The single species in the family, *Anilius scytale*, is usually bright red with black bands or irregular markings (**Figure 4.49A**). It reaches about 1 m in total length and is viviparous. Its eyes are very small and lie beneath a large head shield. *A. scytale* is a burrower and is sometimes associated with soft soil along rainforest streams, but it is also surfaceactive and may be diurnal or nocturnal. It feeds on elongate vertebrates, primarily amphisbaenians (81% of diet), snakes (13%), and caecilians (6%) (Maschio et al. 2010).

Classification, distribution, and conservation 1 species, *Anilius scytale*. It occurs in the Amazon basin and Guyanan region of South America (**Figure 4.49B**). It is not listed by the IUCN as an extinction risk.

Systematics references McDowell (1975).

Tropidophiidae • Dwarf Boas

Tropidophiids have a well-developed tracheal lung, and the left lung is substantially reduced or absent. Both of these are derived characters. Species of West Indian *Tropidophis* are small (34 cm to slightly more than 1 m total length), nocturnal, terrestrial or arboreal snakes (Schwartz and Henderson 1991). They occur from xeric scrub habitats to rainforests. The diet of most species consists of frogs and lizards, and the largest species, *Tropidophis melanurus* (**Figure 4.50A**), also eats birds and rodents.

A peculiar defensive behavior is seen in several West Indian *Tropidophis* species: they spontaneously hemorrhage from the mouth and eyes when disturbed (e.g., Hecht et al. 1955; Iverson 1986; Torres et al. 2013), but the function of this behavior, and its effect on potential predators, have not been studied. Tropidophiids also use a more common snake defensive behavior, rolling into a tight ball with the head hidden. Very little is known of the natural history of the mainland species of tropidophiids. *Trachyboa boulengeri* is viviparous and is known to eat fish.

Classification, distribution, and conservation 2 genera (*Tropidophis, Trachyboa*), 34 species. *Tropidophis* inhabit the West Indies (Greater Antilles and the Bahamas) and Ecuador, Peru, and Brazil. *Trachyboa* inhabit Panama and northwestern South America (**Figure 4.50B**). The IUCN lists 1 species (*Tropidophis hendersoni*) as Critically Endangered.

Systematics references Schwartz and Marsh (1960), Mc-Dowell (1975), Hedges (2002), Curcio et al. (2012), Graham et al. (2014).



(A)



Figure 4.50 Tropidophiidae. (A) Cuban wood snake (orange morph), *Tropidophis melanurus*. (B) Distribution. (Photograph © Chris Mattison/Alamy.)





(B) Anomochilidae





Figure 4.51 Xenophidiidae and Anomochilidae. (A) Malayan spine-jawed snake, *Xenophidion schaeferi*. (B) Dwarf pipe snake, *Anomochilus* sp. (C) Distribution. Both families occur in northeastern Borneo (green area). (Photographs: A, courtesy of Wolfgang Grossmann; B, courtesy of Indraneil Das.)

Xenophidiidae • Spine-Jawed Snakes

The two species of *Xenophidion* are known from only a handful of specimens. They appear to be nocturnal, secretive snakes of tropical forests. Both species are less than 35 cm in total length (**Figure 4.51A**). The enlarged caniniform dentary teeth and a dentary diastema suggest a diet of skinks or other hard-bodied lizards (Cadle 1999), and indeed a skink was found in the stomach of one specimen. Most molecular phylogenies place Xenophidiidae as the sister lineage to Bolyeriidae (e.g., Pyron et al. 2013b; Lawson et al. 2004; Reynolds et al. 2014).

Classification, distribution, and conservation 1 genus, 2 species. *Xenophidion acanthognathus* inhabits Borneo, and *X. schaeferi* inhabits the west-central Malaysian peninsula (Figure 4.51C). Neither species is listed by the IUCN as an extinction risk.

Systematics references Günther and Manthey (1995), Wallach and Günther (1998), Lawson et al. (2004).

Anomochilidae • Dwarf Pipe Snakes

Anomochilidae (**Figure 4.51B**) contains three species that have rarely been collected in the

wild. All specimens collected in the wild. All specimens collected are less than 40 cm in total length, and the natural history of the family is virtually unknown. Anomochilids are probably oviparous; one female contained 4 shelled eggs.

Classification, distribution, and conservation 1 genus (*Anomochilus*), 3 species. They inhabit peninsular Malaysia, Sumatra, and Borneo (**Figure 4.51C**). No species are listed by the IUCN as an extinction risk.

Systematics references Cundall and Rossman (1993), Cundall and Wallach (1993), Cundall et al. (1993), Das et al. (2008), Reynolds et al. (2014).

Figure 4.52 Uropeltidae and Cylindrophiidae. (A) Mumbai earthworm snake, Uropeltis macrolepis. (B) Redtailed pipe snake, Cylindrophis ruffus, Sarawak, Malaysia. (C) Distribution. (Photographs: A, courtesy of Vishal Prassad; B, © Ch'ien Lee/Minden Pictures/Corbis.)

Uropeltidae • Shield-Tailed Snakes

The largest uropeltids reach about 80 cm in total length. All uropeltids are viviparous and feed primarily on earthworms. The head of uropeltids is conical and slender and often much narrower than the relatively thick trunk (although the head of *Melanophidium* is somewhat blunted). The head is often provided with a distinct keel (Figure **4.52A**). The tail of uropeltids is blunt and in many species capped with a single large scale with a rough surface. The tail cap collects a plug of dirt and protects the snake from behind when burrowing in a tunnel. Uropeltids have many specializations for burrowing, including anterior body musculature richly supplied with myoglobin, catalytic enzymes, and mitochondria (Gans et al. 1978). These biochemical specializations permit sustained activity of the anterior trunk muscles during burrowing. The vertebral column, body wall muscles, and viscera of uropeltids can move relative to the outer skin, allowing the snakes to press a portion of the body against the tunnel wall as a friction point while the head and anterior body move forward relatively frictionfree (see Chapter 10).

(B) Cylindrophiidae



Classification, distribution, and conservation 8 genera, 54 species. Representative genera include *Melanophidium, Plecturus, Rhinophis,* and *Uropeltis.* Uropeltids inhabit western India and Sri Lanka (**Figure 4.52C**). The IUCN lists 2 species as Endangered and 5 species as Near Threatened or Vulnerable.

Systematics references Cadle et al. (1990), Bossuyt et al. (2004), Reynolds et al. (2014).

Cylindrophiidae • Asian Pipe Snakes

Cylindrophis ruffus (**Figure 4.52B**), the largest cylindrophiid species, reaches a total length of 90 cm. Cylindrophiids are viviparous, and like many relatively basal alethinophidian lineages, they eat longate prey such as eels, caecilians, and snakes. *C. rufus* lives in aquatic edge microhabitats and is relatively sedentary, moving only short distances compared with sympatric homalopsids (Murphy et al. 1999).

Classification, distribution, and conservation 1 genus (*Cylindrophis*), 12 species. Their distribution is disjunct, with 1 species (*C. maculatus*) in Sri Lanka and 9 species in southern Asia and the Indo-Australian Archipelago (**Figure 4.52C**). No species are listed by the IUCN as an extinction risk.

Systematics references Amarasinghe et al. (2015).

Bolyeriidae • Split-Jaw Snakes

Bolyeriidae includes two highly unusual snakes that are unique among tetrapods in having maxillary (upper jaw) bones that are divided by a joint into anterior and posterior sections. The mandibles are also jointed, as in other snakes, and bolyeriids can therefore bend both their upper and lower jaws around prey. Behavioral and anatomical observations suggest that the divided maxillae aid in gripping skinks and geckos (Cundall and Irish 1989). The arrangement is functionally similar to the arched maxillae, with enlarged teeth and diastema, seen in some other skink-eating snakes such as the Lycodon (Colubridae) and Psammophis (Lamprophiidae). Like Caenophidia (see account, below), bolyeriids have hypapophyses (ventral projections of the vertebral centrum) on the posterior trunk vertebrae (absent in all other snakes). Casarea (Figure 4.53A) is viviparous, but the reproductive mode of Bolyeria is unknown.

Classification, distribution, and conservation 2 species (*Bolyeria multocarinata, Casarea dussumieri*). *Bolyeria* has been a victim of anthropogenic extinction, especially from the introduction of exotic species. Once inhabiting Mauritius and surrounding islands, it has not been seen alive since 1975 (Bullock 1986) and is believed to be extinct. *Casarea* now lives only on Round Island a 1.7 km² island 20 km north of Mauritius in the Indian Ocean (**Figure 4.53B**). In the late 1970s the estimated population size of wild *Casarea*



Figure 4.53 Bolyeriidae. (A) Round Island ground boa, *Casarea dussumieri*. (B) Distribution. (Photograph courtesy of Nik Cole.)

was approximately 75 individuals (Cundall and Irish 1989). The IUCN lists *C. dussumieri* as Endangered.

Systematics references Anthony and Guibé (1952).

Boidae • Boas

Boidae includes snakes commonly known as boas. This family includes the green anaconda (*Eunectes murinus*), the heaviest extant snake, weighing as much as 91 kg (well-fed captives can reach twice this mass). The Late Paleocene boid *Titanoboa cerrejonensis* was the largest snake known, estimated to have had a total length of 13 m and a mass of more than 1,100 kg (Head et al. 2009). Not all boids are giants, however; adults of *Exiliboa* are less than 50 cm in total length, and several other species (e.g., *Charina*) are only slightly larger.

Many boids have specialized labial infrared-sensitive sensors. Males of many species retain vestiges of a pelvis and femurs in the form of spurlike structures used to grasp the female while mating. Boids occur in rainforests, dry tropical forests, montane cloud forests (*Exiliboa*), sandy and

Figure 4.54 Boidae.

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(A) Boinae
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(B) Calabariinae



(D) Charininae

tree boa, Corallus hortulanus (Boinae). (B) African burrowing boa, Calabaria reinhardtii (Calabariinae). (C) Viper boa, Candoia aspera (Candoiinae). (D) Rubber boa, Charina bottae (Charininae). (E) Tartar sand boa, Eryx tataricus (Erycinae). (F) Madagascar tree boa, Sanzinia madagascariensis (Sanziniinae). (G) Distribution. (Photographs: A, courtesy of Todd W. Pierson; B, courtesy of Daniel M. Portik; C, © Michael Kern/Visuals Unlimited, Inc.; D, © Randimal/ Shutterstock; E, © reptiles4all/Shutterstock; F, © Nicolas Cégalerba/ Biosphoto/Corbis.)

(A) Garden





(E) Erycinae

(G)

30°N

Equator

30°S





rocky deserts (Erycinae), and temperate coniferous forests (*Charina*). Terrestrial, arboreal, aquatic, and semifossorial species have evolved body forms as adaptations to these diverse habitats. As the size range and diversity of habitats occupied by boids suggest, diets in the group are extremely varied. Larger species consume vertebrate prey (mammals, birds, and non-avian reptiles), and *Exiliboa placata* (southern Mexico) eats salamanders and frogs (Campbell and Camarillo 1992).

Eunectes (the anacondas) are large boids that inhabit rivers, ponds, and flooded savannas. Anacondas bask during the day on floating or overhanging vegetation or on the shore. Diets of *Eunectes* include a wide variety of vertebrates, including fish, amphibians, turtles, caimans, birds, and large mammals (pacas, capybaras, deer). *Eunectes* are ambush predators and await prey while submerged in water. Although adults are large enough to easily eat a human, no fatalities have been recorded in scientific literature (Rivas 1998).

Calabaria reinhardtii inhabits forests and rainforests in West-Central Africa and was until recently considered a separate family from Boidae. It is fossorial, with a blunt head and tail and enlarged head scales. Little is known about its natural history. A radio-tracking study found that *Calabaria* spends most of its life underground, often in termite nests (Angelici et al. 2000), yet there is no evidence that it eats the termites. The stomach contents from two *Calabaria* contained nestling mice, but no more is known about its diet (Gartlan and Struhsaker 1971).

Viviparity is the ancestral condition for boids and most boids are viviparous (Lynch and Wagner 2010); only *Calabaria reinhardtii*, *Eryx jayakari*, and *E. muelleri* are oviparous. The latter two species are deeply nested within the boid phylogeny, suggesting that oviparity re-evolved from a viviparous ancestor (Lynch and Wagner 2010), although this hypothesis is disputed (Griffith et al. 2015). There is also evidence that *Boa constrictor* can reproduce parthenogenetically (Booth et al. 2011).

Boid phylogenetics and taxonomy have changed considerably over the past 15 years. Pythons, once considered a subclade of Boidae, are now recognized as a distinct family (Pythonidae) more closely related to other snake families than Boidae. Recent molecular phylogenetic analyses have also recognized that the genus *Calabaria*, often recognized as a separate family, Calabariidae, is part of the overall boid clade (Pyron et al. 2013a,b, 2014a; Reynolds et al. 2014a) split Boidae into six families: Boidae, Calabariidae, Charinidae, Erycidae, and Sanziniidae. Although we also recognize each of these clades (**Figure 4.54A–F**), we treat them as subfamilies to preserve historical continuation of the family name Boidae with these groups of snakes.

Classification, distribution, and conservation 15 genera, 59 species. 6 subfamilies: Boinae (*Boa, Chilabothrus, Corallus, Epicrates, Eunectes*) in Mexico through Central and South America and the West Indies; Calabariinae (*Calabaria reinhardtii*) in West-Central Africa; Charininae (*Charina, Exiliboa, Lichanura, Ungaliophis*), also called Ungaliophiinae, in western North America south to Colombia; Candoiinae (*Candoia*) in the southwest Pacific islands; Erycinae (*Eryx*) in central and northern Africa and southern Europe ranging east to Mongolia and southern Asia; and Sanziniinae (*Acrantophis, Sanzinia*) in Madagascar (**Figure 4.54G**). The IUCN lists 2 species as Endangered and 2 species as Vulnerable.

Systematics references Underwood (1976), Kluge (1991, 1993), Noonan and Chippendale (2006), Lynch and Wagner (2010), Pyron et al. (2014a), Reynolds et al. (2014).



Figure 4.55 Xenopeltidae. (A) Sunbeam snake, *Xenopeltis unicolor.* (B) Distribution. (Photograph © reptiles4all/Shutterstock.)



Xenopeltidae • Sunbeam Snakes

The two species of *Xenopeltis* are burrowing, nocturnal snakes reaching slightly over 1 m in total length and inhabiting both forest and open habitat (especially rice paddies). The dorsal scales are black or very dark brown and are highly iridescent (**Figure 4.55A**), which is the source of their common name. The head scales consist of large plates similar to those of colubrids. Pelvic vestiges are absent. *Xenopeltis* are oviparous and feed on skinks, frogs, and rodents. Young individuals have hinged teeth, a specialization for feeding on skinks.

Classification, distribution, and conservation 1 genus, 2 species (*Xenopeltis hainanensis, X. unicolor*). They inhabit India and southern China to Borneo and Sulawesi (Figure 4.55B). Neither species is listed by the IUCN as an extinction risk.

Systematics references Orlov (2011).

Loxocemidae • Mexican Burrowing Python

Loxocemus bicolor (Figure 4.56A) inhabits tropical dry forests of Mexico and Central America. It has a somewhat pointed snout and is at least partially fossorial. It reaches about 1.3 m in total length, is oviparous, and is known to prey on rodents, lizards, and reptile eggs, including those of a sea turtle, *Lepidochelys kempi* (Greene 1997).

Classification, distribution, and conservation 1 species, *Loxocemus bicolor*. It inhabits southernmost Mexico to Costa Rica (**Figure 4.56B**). It is not listed by the IUCN as an extinction risk.

Systematics references Haas (1955), Nelson and Meyer (1967).

Pythonidae • Pythons

Pythons resemble boids in general appearance (**Figure 4.57A**). Many species are very large; the reticulated python (*Malayopython reticulatus*) is the longest of all extant snakes,

reaching a total length of 9 m. The Burmese python (*Py-thon molurus*) and African rock python (*P. sebae*), at about 8 m, are almost as long. Like boids, many pythons possess infrared-sensitive sensors between the labial scales, but unlike in boids, these sensors are located in distinct pits (see Figure 4.5). Both boid and pythonid males also have pelvic spurs. It is therefore unsurprising that morphology-based taxonomies of snakes placed pythons and boas together in Boidae, but this relationship is strongly rejected by all phylogenetic analyses of DNA. Therefore, infrared sensitivity and retention of pelvic remnants either evolved independently in pythons and boas, or evolved in the common ancestor of Pythonidae and Boidae but subsequently were lost in the other lineages derived from that common ancestor, for example in Calabariinae (Boidae), Uropeltidae, Xenopeltidae, and others.

Pythons are typically terrestrial, but some species are semiaquatic or arboreal. The diets of pythons include medium to large vertebrates, including prey as large as deer (and occasionally humans; Headland and Greene 2011) for the larger species. Python physiology is remarkable in that, during periods between feeding, major metabolic functions are severely downregulated. Activity of digestive organs ceases, and the mass of the heart and digestive organs decreases considerably. However, after consuming a meal, pythons experience a 40-fold increase in metabolism and rapid re-growth of tissues in the digestive tract (see Chapter 11) (Secor 2008; Castoe et al. 2011; Wall et al. 2011).

All pythonids are oviparous. Many construct nests of leaves or lay their eggs in burrows. Females of some species coil around the clutches and generate heat for incubation by muscular contractions (see Figure 6.27). As many as 100 eggs are laid by females of the largest species.

Classification, distribution, and conservation 9 genera, 40 species. Representative genera include *Antaresia, Aspidites, Liasis, Malayopython, Morelia,* and *Python.* The family occurs in sub-Saharan Africa and southern Asia from Pakistan eastward throughout the Indo-Australian Archipelago to Australia (**Figure 4.57B**). The IUCN lists 1 species (*Aspidites ramsayi*) as Endangered and 2 species as Vulnerable.



Figure 4.56 Loxocemidae. (A) Mexican burrowing python, *Loxocemus bicolor*. (B) Distribution. (Photograph courtesy of Twan Leenders.)



Figure 4.57 Pythonidae. (A) Australian black-headed python, *Aspidites melanocephalus*. (B) Distribution. (Photograph © Danita Delimont/Alamy.)

Systematics references Underwood and Stimson (1990), Kluge (1993a), Noonan and Chippendale (2006), Rawlings et al. (2008), Reynolds et al. (2014), Barker et al. (2015).

CAENOPHIDIA

Caenophidia includes the highly specialized aquatic snake family Acrochordidae and the massively diverse Colubroidea. The monophyly of Caenophidia is strongly supported by molecular phylogenetic data and osteological characters, including details of the skull structure, loss of the coronoid bone in the mandible, and hypapophyses (ventral projections of the vertebral centrum) on the posterior trunk vertebrae.

Acrochordidae • File Snakes

All species of *Acrochordus* are aquatic and are characterized by their unique loose and baggy skin with small tubercles and triangularly keeled scales that give the skin the texture of a coarse file or sandpaper. The skin texture allows water



to rapidly move over the body surface through interscalar channels, which may be an adaptation for remaining hydrated during rare periods when the snakes are migrating over land to other water sources (Lillywhite and Sanmartino 1993). The ventral scutes are only feebly enlarged, and the tail is slightly compressed laterally. The ventral skin of *Acrochordus granulatus* hangs to form a low ridge that acts as a median "fin" in swimming.

Acrochordus are nearly incapable of movement on land and spend a majority of their time submerged underwater, respiring at the surface only every 1.5–5 h (Lillywhite 1991). The metabolic rates of acrochordids are lower than most snakes, and they appear to reproduce and feed less frequently than most other snakes (Shine 1986). They are nocturnal predators of fish and crustaceans. Acrochordus species differ in body size and in their relative use of marine and freshwater habitats. Of the three species, A. granulatus (<1 m total length) spends the most time in offshore marine habitats and has even been collected up to 10 km from shore (Voris and Glodek 1980). This species also possesses



Figure 4.58 Acrochordidae. (A) Elephant trunk or Java wart snake, *Acrochordus javanicus*. (B) Distribution. (Photography courtesy of Harvey Pough.)


a sublingual salt gland, presumably used for osmoregulation (Dunson and Dunson 1973). *A. arafurae* (~1.7 m total length) and *A. javanicus* (2 m total length; **Figure 4.58A**) primarily inhabit freshwater, although they may enter estuaries, and *A. arafurae* may enter the open ocean. Population densities of *A. arafurae* reach 100 snakes per hectare in some areas of northern Australia (Shine 1986). All species are viviparous, producing up to 30 young in a litter. Individual females of *A. arafurae* are at least occasionally parthenogenetic (Dubach et al. 1997). See Lillywhite (1991) for a review of acrochordid biology.

Classification, distribution, and conservation 1 genus (*Acrochordus*), 3 species. The range extends from India to northern Australia and the Solomon Islands (**Figure 4.58B**). No species are listed by the IUCN as an extinction risk.

Systematics references McDowell (1979), Sanders et al. (2010).

Colubroidea

Colubroidea contains all of the most diverse snake families—including Colubridae, Elapidae, Lamprophiidae, and Viperidae (**Figure 4.59**)—and accounts for more than 80% of snake species. The monophyly of Colubroidea is supported by molecular data and by morphological characters, including characteristic body segmentation (segmental arrangement of intercostal arteries, separation of spinalis and semispinalis muscles in the trunk), peculiarly shaped costal cartilages (Hardaway and Williams 1976; Persky et al. 1976), and several skull characters (Rieppel 1988).

Xenodermatidae • Odd-Scaled Snakes

Xenodermatids are secretive, probably nocturnal snakes that typically range in size from 50 to 80 cm total length. The common name of these snakes refers to the dorsal scales of some genera, which differ in shape and size. The name of the family is derived from the Greek *xeno*, "strange"

> or "different" and *dermis*, "skin." Most, if not all, species are burrowers and inhabit mostly for-

> est or disturbed habitats. Other

than these, few natural history

Classification, distribution, and conservation 6 genera, 17

species. Genera include Achali-

nus (Figure 4.60A), Fimbrios, Parafimbrios, Stoliczkia, Xeno-

dermus, and Xylophis. Xenoder-

matids have a disjunct distribution, inhabiting southern India,

Southeast Asia to Japan, Borneo,

and islands of the Sunda Shelf (**Figure 4.60B**). *Achalinus* was

previously placed in Colubridae.

The IUCN lists 1 species (Achali-

Systematics references Gow-

er and Winkler (2007), Teynié et

nus werneri) as Vulnerable.

data are available.



Figure 4.59 Phylogenetic relationships of Colubroidea based on DNA data.

al. (2015).

(A)



(B)



Figure 4.60 Xenodermatidae. (A) Rufous burrowing snake, *Achalinus rufescens*, China. (B) Distribution. (Photograph © Sam Yue/Alamy.)

Pareatidae • Asian Snail-Eating Snakes

Pareatids feed on slugs and snails and are the Asian ecological equivalents of New World snakes of the genera *Dipsas*, *Sibon*, and their relatives (Colubridae). All species are nocturnal and oviparous. *Aplopeltura* (Figure 4.61A) is arboreal, whereas species of *Pareas* are terrestrial or arboreal.

Classification, distribution, and conservation 3 genera (*Aplopeltura, Asthenodipsas, Pareas*), 17 species. Pareatids occur in Southeast Asia, Borneo, and Sulawesi (**Figure 4.61B**). No species are listed by the IUCN as an extinction risk.

Systematics references Ota et al. (1997), Guo et al. (2011), Loredo et al. (2013).

Viperidae • Vipers

Vipers are terrestrial, arboreal, or semiaquatic and are found in habitats ranging from rainforests to deserts and high mountains. Many terrestrial vipers are heavy-bodied, whereas arboreal species are slimmer. The long fangs of vipers are the sole teeth attached to hinged maxillary bones, so the fangs fold against the roof of the mouth when not in use and are erected when the snake strikes its prey.

Most vipers are terrestrial, but a diverse assemblage of Neotropical vipers are arboreal (e.g., *Bothriechis*, *Bothriopsis*), as are *Atheris* in Africa and several Asian vipers (e.g., *Tropidolaemus*, some *Trimeresurus*). Most small species of viperids and juveniles of large species eat lizards or amphibians, whereas adults of larger species often consume mammals. Viperids occur from low to high elevations, and the range of the European *Vipera berus* extends above the Arctic Circle.

The Crotalinae (pit vipers; **Figure 4.62A**) includes species in eastern Asia and the Western Hemisphere; the clade is characterized by a heat-sensitive pit on the face (see Figure 4.5C). The tip of the tail of rattlesnakes (*Crotalus, Sistrurus*)



Figure 4.61 Pareatidae. (A) Bluntheaded slug snake, *Aplopeltura boa.* (B) Distribution. (Photograph courtesy of L. Lee Grismer.





(B) Viperinae



Figure 4.62 Viperidae. (A) Eyelash viper, *Bothriechis* schlegelii (Crotalinae). (B) Green bush viper, *Atheris squamiger*

(Viperinae). (C) Distribution. (Photographs: A courtesy of Harvey Pough; B, © AGE Fotostock/Alamy.)

is modified into a rattle composed of interlocking segments of keratin, the material that makes up the external layer of scales (Figure 4.63). Vibration of the tail causes portions of the segments to rub against one another, producing a sound that serves as an antipredator defense. The largest New World crotalines, sometimes over 3.5 m in total length, are four species of bushmasters (*Lachesis*), which inhabit lowland rainforests of southern Central America and northern South America. Nearly all pit vipers are viviparous, but *Calloselasma, Ovophis, Lachesis*, and some species of *Tri*- *meresurus* are oviparous. Parental care of neonates or egg clutches is frequent among crotalines (Greene et al. 2002).

The Viperinae (true vipers; **Figure 4.62B**) lack pit organs, but many aspects of their natural history are similar to those of crotalines. The population biology, reproduction, and behavior of some European species have been studied in detail (e.g., Höggren et al. 1993; Andrén 1986; Forsman 1997), but we have only anecdotal information for most tropical species. The largest species of viperines include several heavy-bodied African species of *Bitis* (to 1.5 m total



Figure 4.63 A rattlesnake's rattle. Close-up of the rattle of an eastern diamondback rattlesnake (*Crotalus adamanteus*, Crotalinae). (Photograph © Pete Oxford/Nature Picture Library/Corbis.)

length) and the slimmer *Daboia russelii* of southern Asia (up to 1.7 m total length). The Gaboon viper (*Bitis gabonica*) is a highly camouflaged ambush predator and has the longest fangs of any snake (up to 50 mm). This species defecates only a few times a year, retaining up to 20% of its body mass as feces in the gut. The snake may use the heavy fecal mass as ballast to anchor its body to the ground while it strikes prey (Lillywhite et al. 2002). The lateral midbody scales of saw-scaled vipers (*Echis*) are strongly keeled and produce a buzzing sound when the snake rubs coils of its body in a defensive display.

Causus (Viperinae) includes seven species of comparatively small (<1 m total length) vipers in sub-Saharan Africa. Species of *Causus* have large, symmetrical head plates, unlike most other vipers, which have vertical pupils and fragmented plates or small scales on the head. They are nocturnal and diurnal oviparous snakes that feed primarily on anurans (Ineich et al. 2006). *Azemiops* (Azemiopinae) reaches about 70 cm in total length and feeds on mammals (Greene 1992).

Classification, distribution, and conservation 36 genera, 328 species. 3 subfamilies: Azemiopinae (2 species of *Azemiops*) inhabit rainforests of southern China, Tibet, and northern Burma; Crotalinae (representative genera *Agkistrodon, Bothrops, Crotalus, Gloydius, Lachesis, Sistrurus, Trimeresurus*) inhabit North, Central, and South America, eastern Asia from India to Japan, the Philippines, and islands of the Sunda Shelf; Viperinae (representative genera *Bitis, Causus, Cerastes, Daboia, Echis, Vipera*) inhabit Africa (absent from Madagascar), Eurasia, and islands of the Sunda Shelf (Figure 4.62C). The IUCN lists 25 species as Critically Endangered or Endangered and 31 species as Near Threatened or Vulnerable.

Systematics references Castoe et al. (2005, 2009), Castoe and Parkinson (2006), Wüster et al. (2008), Fenwick et al. (2009), Malhotra et al. (2010), Pyron et al. (2011).

Homalopsidae • Asian Water Snakes

Most homalopsids are estuarine, marine, or freshwater snakes. Like many other aquatic snakes, their eyes are dorsally oriented and the nostrils can be closed by narial muscles in combination with the swelling of cavernous tissue in the nasal chamber (Dos Santos-Costa and Hofstadler-Deiques 2002). Homalopsids are viviparous and possess a tracheal lung.

The evolution of homalopsids can be generalized into two major clades representing the earliest phylogenetic divergence of homalopsid snakes (Murphy et al. 2011; Mur-







Figure 4.64 Homalopsidae. (A) Macleays mud snake, *Pseudoferania polylepis.* (B) Distribution. (Photograph courtesy of Stephen Zozaya.)

phy and Voris 2014). The larger clade includes venomous species with grooved fangs on the posterior maxilla. These rear-fanged species consume a variety of aquatic vertebrates (fish, frogs) and invertebrates, including hard-bodied crustaceans such as crabs. *Fordonia* and *Gerarda* dismember crabs before consumption and are the only snakes known to dismember their prey before eating (Jayne et al. 2002). The other clade includes three fangless genera (*Brachyorrhos, Calamophis, Karnsophis*) that are fossorial and consume primarily worms.

Some species reach very high densities in disturbed habitats (e.g., *Cerberus rynchops* occurs at densities of 3 individuals/m² in some habitats; Jayne et al. 1988). Several species (e.g., *Homalopsis buccata, Pseudoferania polylepis*) use a root-tangle microhabitat along the edges of ditches and bays (**Figure 4.64A**).

Classification, distribution, and conservation 28 genera, 53 species. Representative genera include *Bitia, Brachyorrhos, Cerberus, Erpeton, Homalopsis,* and *Pseudoferania.* See Murphy and Voris (2014) for an extensive review and checklist of homalopsid species. They inhabit South and Southeast Asia east through the Indo-Australian Archipelago (**Figure 4.64B**). The IUCN lists 2 species as Endangered and 1 species as Vulnerable.

Systematics references Voris et al. (2002), Alfaro et al. (2008), Karns et al. (2010), Murphy (2011), Murphy et al. (2011), Murphy and Voris (2014).

Colubridae

Colubridae is the largest and most diverse family of snakes (Figure 4.65). Their reproductive modes, life histories, and habitats encompass most of those seen in Alethinophidia as a whole. Historically, Colubridae was not defined by shared derived characters and contained species that did not have obvious phylogenetic relationships to other colubroids. Consequently, the taxonomy of colubrids has been in flux for decades. Recent phylogenetic analyses have greatly clarified colubrid systematics, and there is broad agreement on the monophyly of many colubroid subclades. However, debate continues about the taxonomic names for these clades (see Vidal et al. 2007; Zaher 2009; Pyron et al. 2011). We follow the taxonomy of Pyron et al. (2011, 2013a, 2014b), defining a large Colubridae (1,800+ species) with seven subfamilies (described below).

Several species of colubrids are dangerously venomous to humans. These include the African colubrines *Dispholidus typus* (boomslang) and *Thelotornis* (twig snake), and several species of the Asian natricine *Rhabdophis*. Two famous herpetologists, Karl P. Schmidt and Robert Mertens, died from bites of *Dispholidus* and *Thelotornis*, respectively (Pope 1958).

Classification, distribution, and conservation Approximately 255 genera, 1,800 species. See subfamily accounts

below. There are at least 10 genera for which there is insufficient phylogenetic evidence to place them in the existing colubrid taxonomic scheme, which includes *Blythia*, *Cyclocorus, Elapoidis, Gongylosoma, Helophis, Myersophis, Oreocalamus, Poecilopolis, Rhabdops,* and *Tetralepis* (Pyron et al. 2013a). The family has a worldwide distribution (see Figure 4.65H).

Systematics references Nagy et al. (2003), Lawson et al. (2005), Burbrink and Lawson (2007), Vidal et al. (2007), Wiens et al. (2008), Zaher et al. (2009), Pyron et al. (2011, 2013a,b, 2014b).

Calamariinae

Calamariines are dwarf burrowing or leaf litter-inhabiting colubrids with burrowing ecomorph traits, such as a small head, short tail, and smooth scales (**Figure 4.65A**). All species are oviparous, but little is known about their natural history.

Classification, distribution, and conservation 7 genera, 87 species. Genera include *Calamaria, Calamorhabdium, Collorhabdium, Etheridgeum, Macrocalamus, Pseudorabdion,* and *Rabdion.* They inhabit southern and southeastern Asia, Japan, Malaysia, Indonesia, and the Philippines. The IUCN lists 4 species as Critically Endangered or Endangered and 2 species as Vulnerable.

Systematics references Leviton and Brown (1959), Inger and Marx (1965), Inger and Leviton (1966).

Colubrinae

The largest clade of colubrids, Colubrinae accounts for some 40% of the species in the family and constitute much of the North American snake fauna, including the king snakes, corn snakes, and rat snakes (**Figure 4.65B**). Most colubrines are terrestrial, but some are arboreal and others are semi-aquatic; there are no marine colubrines and no specialized burrowers. The size range includes some of the smallest and largest colubrids: some species of *Tantilla* are less than 20 cm in total length, whereas *Boiga*, *Chironius*, and *Drymarchon* include species that reach 3 m or more.

Dietary habits of colubrines are extremely variable. Some species have very broad diets (e.g., *Coluber flagellum*, which eats mammals, birds, lizards, snakes, bird eggs, and carrion), whereas others have very narrow dietary spectra across species within genera (e.g., frogs for *Chironius*, softbodied insects for *Opheodrys*, centipedes for *Tantilla* [see Figure 11.34], and bird eggs for *Dasypeltis* [see Figure 11.36]) (Savitzky 1983; Marques and Puorto 1998). Most species are oviparous, but *Conopsis*, *Coronella austriaca*, and *Oocatochus rufodorsatus* are viviparous.

Classification, distribution, and conservation 101 genera, 726 species. They are cosmopolitan except absent from most of Australia. Representative North American genera include Chionactis, Coluber, Drymarchon, Lampropeltis, Opheodrys, Pantherophis, Phyllorhynchus, Pituophis, Salvadora, Tantilla, and Trimorphodon. Representative Neotropical genera include Chironius, Dendrophidion, Drymobius, Leptophis, Mastigodryas, and Oxybelis. Representative genera from Africa, Eurasia, the Indo-Australian Archipelago, and Pacific islands include Ahaetulla, Boiga, Chrysopelea, Coronella, Dasypeltis, Dendrelaphis, Dispholidus, Elaphe, Hapsidophrys, Philothamnus, Telescopus, Thelotomis, and Thrasops. The IUCN lists 20 species as Critically Endangered or Endangered and 27 species as Near Threatened or Vulnerable.

Systematics references Lawson et al. (2005), Burbrink and Lawson (2007), Pyron and Burbrink (2009), Pyron et al. (2011, 2013a,b), Jadin et al. (2013).

Dipsadinae

Dipsadines are a large and diverse clade of colubrids in terms of morphology and ecology. They comprise the largest clade of snakes in Central and South America and occur in the West Indies and Galápagos Islands but are less diverse in North America, where colubrines and natricines dominate the colubrid fauna. Dipsadines are small (<0.5 m total length) to large (1.3 m total length) terrestrial snakes of rainforest, dry forest, and open habitats, including high-elevation grasslands above treeline. Several species are fossorial (e.g., Apostolepis, Atractus, Geophis), aquatic (Hydrodynastes, Hydrops, Tretanorhinus), or arboreal (Dipsas, Imantodes, Siphlophis). The diets of dipsadines are also diverse. Many species feed almost exclusively on invertebrates, such as earthworms (Atractus, Adelphicos, Geophis, Ninia) or gastropods (Dipsas, Sibon, Sibynomorphus). Other species feed on frogs, salamanders, or lizards; arthropods and fish are consumed rarely, and mammals or birds almost never (Cadle and Greene 1993). Species of Erythroplamprus, Oxyrhopus, Pliocercus, and some Atractus are mimics of venomous coral snakes (see Figure 15.28). Most dipsadines are oviparous, but some genera are viviparous, including Calamodontophis, Helicops, Hydrops, Tachymenis, Thamnodynastes, and Tomodon.

Classification, distribution, and conservation 96 genera, 752 species. There are 5 exclusively North American genera of dipsadines: *Carphophis, Contia, Farancia, Diadophis* (**Figure 4.65C**), and *Heterodon*. Representative Neotropical genera include *Alsophis, Atractus, Clelia, Cubophis, Erythrolamprus, Dipsas, Geophis, Philodryas, Pliocercus,* and *Xenodon*. The taxonomy of Dipsadinae varies among authors. It is sometimes considered a family (Dipsadidae) exclusive of Colubridae. Older taxonomies recognize a separate Heterodontinae, but recent molecular phylogenetic work has demonstrated that this clade is nested within Dipsadinae. It is also common to see many dipsadine taxa placed in another clade, Xenodontinae. The IUCN lists 25 species as Critically Endangered or Endangered and 16 species as Near Threatened or Vulnerable. Although Dipsadinae has been considered an exclusively New World group, recent phylogenetic evidence suggests that the genus *Thermophis*, an inhabitant of hot springs in the Tibetan plateau at elevations of 4,000 m or higher, is a dipsadine (e.g., He et al. 2009; Huang et al. 2009; Grazziotin et al. 2012). This distribution is remarkable, as no other Old World dipsadine genus is known.

Systematics references Cadle (1984a,b,c), Zaher et al. (2009), Vidal et al. (2010b), Pyron and Burbrink (2012), Grazziotin et al. (2012).

Grayiinae

Grayiinae, the African water snakes, includes one genus (*Grayia*) that inhabits mangrove swamps (**Figure 4.65D**). The diet of *G. smythii* includes frogs and fish, especially *Xenopus* (Pipidae) and *Ptychadena* (Ptychadenidae). *Grayia* are oviparous and lay 3–4 eggs in small burrows (Akani and Luiselli 2001).

Classification, **distribution**, **and conservation** 1 genus (*Grayia*), 4 species. They inhabit sub-Saharan Africa. No species are listed by the IUCN as an extinction risk.

Systematics references None.

Pseudoxenodontinae

Pseudoxenodontinae is an obscure Asian snake lineage for which there is little natural history information. *Plagliopholis* are nocturnal and feed on worms. *Pseudoxenodon* raise the forebody and flatten the neck in their defensive display (**Figure 4.65E**). Pseudoxenodontines are oviparous.

Classification, distribution, and conservation 2 genera (*Plagiopholis, Pseudoxenodon*), 11 species. They inhabit southern China, Southeast Asia, and Indonesia. No species are listed by the IUCN as an extinction risk.

Systematics references He et al. (2009), Huang et al. (2009).

Figure 4.65 Colubridae. (A) Variable reed snake, Calamaria lumbricoidea (Calamariinae). (B) Yellow rat snake, Pantherophis [Elaphe] obsoleta (Colubrinae). (C) Western ringneck snake, Diadophis punctatus (Dipsadinae). (D) Smith's African water snake, Grayia smithii (Grayiinae). (E) Large-eyed false cobra, Pseudoxenodon macrops (Pseudoxenodontinae). (F) European grass snake, Natrix natrix (Natricinae). (G) Black-headed snake, Sibynophis subpunctatus (Sibynophiinae). (H) Distribution. (Photographs: A, courtesy of L. Lee Grismer; B, © Matt Jeppson/Shutterstock; C, © SuperStock/Alamy; D, Courtesy of Kate Jackson; E, © ephotocorp/Alamy; F, © Marek R. Swadzba/ Shutterstock; G, courtesy of Vishal Prassad.) (A) Calamariinae



(B) Colubrinae



(D) Grayiinae

(E) Pseudoxenodontinae





(F) Natricinae



Natricinae

Natricines are small (200 mm total length) to large (1.5 m total length) colubrids that may be terrestrial, aquatic, or semifossorial. Although often thought of as aquatic (and sometimes referred to as water snakes), natricines include many semifossorial and terrestrial species. Indeed, the common name of *Natrix natrix is* the European grass snake (**Figure 4.65F**). Aquatic natricines are almost exclusively freshwater, although some coastal populations enter brackish or salt water. Diets are extremely varied and include earthworms and slugs (*Storeria, Virginia*), fish and amphibians (*Nerodia*), crayfish (*Regina*), and toads (*Rhabdophis*). Natricines represent a sizable portion of the North American semiaquatic snake fauna, and consequently some North American natricines (e.g., *Nerodia, Thamnophis*) are among the best studied of any snakes.

Nerodia species are known for their aggressive defensive behaviors and often bite and defecate when handled by humans. The Asian species *Rhabdophis tigrinus* has specialized glands on its neck that contain bufadienolide defensive toxins. These toxins are produced by toads, and *R. tigrinus* sequesters these toxins from its toad prey (see Chapter 15) (Hutchinson et al. 2012; Mori et al. 2012).

All New World natricines are viviparous, whereas most Eurasian species are oviparous, and natricines with both reproductive modes occur in Africa. A tropical Australian natricine, *Tropidonophis mairii*, is the only confirmed case in snakes of multiple clutching by single females in a breeding season; females of this species also become sexually mature within a year of hatching, a maturation rate that far exceeds that of most temperate snakes (Brown and Shine 2002).

Classification, distribution, and conservation 36 genera, 225 species. Some authorities recognize Natricinae as a family, Natricidae. Representative Eurasian and North African genera include *Amphiesma, Natrix, Opisthotropis, Rhabdophis,* and *Sinonatrix*. Representative North American genera include *Nerodia, Regina, Storeria, Seminatrix, Thamnophis, Tropidoclonion,* and *Virginia.* African genera include *Afronatrix, Hydraethiops, Limnophis,* and *Natriciteres,* and *Lycognathophis seychellensis* inhabits the Seychelles. *Tropidonophis* inhabit northern Australia. The IUCN lists 7 species as Critically Endangered or Endangered and 15 species as Near Threatened or Vulnerable.

Systematics references Malnate (1960), Rossman (1996), Alfaro et al. (2001), De Queiroz et al. (2002), Gibbons and Dorcas (2004), Huang et al. (2009), Dubey et al. (2012), Guo et al. (2012, 2014).

Sibynophiinae

Sibynophiines are notable for their hinged teeth, which are specializations for capturing hard-bodied skinks, the main component of their diet (Savitzky 1981). The teeth fold as they glide over prey, but lock in an erect position if the prey attempts to back out of the mouth. *Scaphiodontophis* has an unusually long tail. Because this genus has intervertebral tail breakage (pseudoautotomy) and no regeneration, Savage and Slowinski (1996) hypothesize that the length of the tail is a defensive adaptation that allows multiple tail breaks. *Scaphiodontophis* mimics the coloration of venomous coral snakes (Elapidae), although in some individuals the banded coral snake pattern is limited to the front of the body. Sibynophiines are oviparous.

Classification, distribution, and conservation 2 genera (*Scaphiodontophis, Sibynophis*), 11 species. Their distribution is disjunct; *Scaphiodontophis* occur from southern Mexico though Colombia, and *Sibynophis* (**Figure 4.65G**) inhabit southern and southeastern Asia. No species are listed by the IUCN as an extinction risk.

Systematics references Leviton (1963), Zaher et al. (2012), Chen et al. (2013).

Elapidae • Cobras, Coral Snakes, Mambas, Kraits, Sea Snakes, and Relatives

Elapidae includes cobras (e.g., *Naja*, *Ophiophagus*), mambas (*Dendroaspis*), New World coral snakes (*Micrurus*, *Micruroides*), kraits (*Bungarus*), a large radiation of Australo-Papuan endemics (e.g., *Notechis*, *Acanthophis*, *Demansia*, *Pseudechis*), and two marine radiations (sea snakes). They are characterized by proteroglyph dentition, and their relatively immobile maxillae may bear solid teeth posterior to the fang. Elapidae is the sister taxon to the large African colubroid radiation Lamprophiidae (see Figure 4.59). All elapids are venomous, although some are too small to pose a threat to humans. However, mambas (*Dendroaspis*), some sea snakes, and several Australian elapids (*Notechis*, *Oxyuranus*, and *Pseudechis*) rank among the world's most potentently venomous and thus most dangerous snakes.

Elapids may be terrestrial (e.g., Naja, Ophiophagus, Bungarus, some Micrurus), arboreal (Dendroaspis, Pseudohaje), aquatic (Boulengerina, some Micrurus), semifossorial (some Micrurus, Elapsoidea, Aspidelaps, Simoselaps), or marine (e.g., Laticauda, Hydrophis). Elapids have radiated into habitats that extend from extremely arid deserts to tropical rainforests. Likewise, the diets of elapids are extremely variable and reflect habitat and lifestyle. Aquatic elapids of the genus Boulengerina eat primarily fish; the king cobra (Ophiophagus hannah) feeds primarily on other snakes; New World coral snakes (Micrurus) eat mostly elongate vertebrates such as other snakes and amphisbaenians. The aquatic coral snake (Micrurus surinamensis) eats eels. Many elapids have diets that include frogs or toads, lizards, reptile eggs, rodents, and birds. Most sea snakes feed on fish that live in reef crevices; a few (e.g., Aipysurus laevis) are generalized predators on fish and their eggs, crustaceans, and cuttlefish, whereas others (Aipysurus eydouxi, Emydocephalus annulatus) feed almost exclusively on fish eggs.

The size of elapids ranges from less than 50 cm total length in many species (e.g., *Elapsoidea*, some *Micrurus*, and

many Australian terrestrial species) to very large species such as the black mamba (*Dendroaspis polylepis*) and African tree cobras (*Pseudohaje*), which approach or exceed 3 m. The king cobra can exceed 5 m, and in its threat display a snake of that size lifts its head high enough to confront a human eye to eye. It is the longest (although not the most massive) venomous snake in the world.

Ophiophagus hannah and the African forest cobra (*Naja melanoleuca*) are among the few colubroid snakes that construct a nest for egg laying and provide parental care to the eggs. Females guard their nests, which are constructed of leaves and decaying vegetation. Most terrestrial elapids are oviparous, but viviparity occurs in some African species (e.g., *Hemachatus*) and in many Australian elapids (e.g., most species of *Pseudechis* are oviparous, but *Pseudechis porphyriacus* is viviparous). *Laticauda* is oviparous, but all other marine elapids are viviparous and give birth at sea.

Species of Aspidelaps, Naja, and Ophiophagus are known for their hood-spreading defensive displays (Figure 4.66A). Many elapids and other colubrids also have neck-flattening behavior, although that of cobras reveals a larger hood supported by elongate ribs in the neck region. Several species of Naja (e.g., N. nigricollis, N. mossambica, and N. sputatrix) and the southern African Hemachatus are known as spitting cobras, although "spraying cobras" would be more accurate. In these species the openings through which venom is ejected from the fangs point forward rather than downward as in other cobras (Bogert 1943; Wüster and Thorpe 1992b). Contraction of muscles acting on the venom gland creates a spray of venom droplets that can travel as far as 2 m. Spraying venom is a defensive measure; the spray is directed toward the face of an attacker and causes intense pain and temporary blindness if it enters the eyes. Hemachatus also has an alternative defensive strategy-it feigns death if spraying fails to deter an attacker.

Many species of American coral snakes, including about 65 species of the primarily Neotropical genus *Micrurus* (Figure 4.66B) as well as the desert genus *Micruroides*, are mimicked by nonvenomous to mildly venomous colubrids in genera such as *Pliocercus*, *Lampropeltis*, and *Erythrolamprus* (see Figure 15.28) (Greene and McDiarmid 1981). In Asia, similar mimicry complexes involve kraits (*Bungarus*) and colubrids in the genus *Lycodon*.

Two major groups of elapids independently invaded coastal and estuarine waters and coral reefs and evolved similar marine-adapted phenotypes: the sea kraits in the genus *Laticauda* (Figure 4.66D), and the sea snakes comprising about 62 species in the subfamily Hydrophiinae (which also contains terrestrial snakes; see Figure 4.66E–G and the taxonomic account below). *Laticauda* retains the wide ventral scales characteristic of terrestrial elapids, and these have a one-to-one correspondence with the vertebrae. In *Laticauda*, the dorsoventrally flattened tail is poorly developed and is not supported internally by elongated vertebral processes. Species of *Laticauda* occupy inshore marine ar-

eas, spend considerable time on land, and come ashore to lay eggs in caves above the tide line in coral reefs.

Most hydrophiine sea snake genera are more fully adapted to marine life, although some species are found in both fresh and salt water in estuarine situations. The yellowbellied sea snake (Hydrophis [Pelamis] platurus) is pelagic and spends its entire life in the open ocean (see Figure 6.12). The ventral scales of sea snakes are much reduced (almost nonexistent in most species) and the body is often laterally compressed, so much so that some species are long and ribbonlike. Hydrophiine marine species have lost the one-toone association of ventral scales with vertebrae (Voris 1975), and elongate neural spines and haemapophyses of the caudal vertebrae support their paddlelike tails. The nostrils of marine hydrophiines are dorsally located and can be closed with valves. The mouth can be sealed by depression of the tip of the snout, which is facilitated by a loose articulation of the premaxilla to the rest of the skull.

One hydrophiine species, *Hydrophis semperi*, and one sea krait, *Laticauda crockeri*, are restricted to landlocked freshwater lakes in the Philippines and the Solomon Islands, respectively. Ancestors of these populations presumably entered the lakes when there was a previous connection to the sea. *Hydrophis sibauensis* is known only from a river in Borneo more than 1,000 km from the ocean, and may also be an entirely freshwater species (Rasmussen et al. 2001).

Classification, distribution, and conservation 55 genera, 353 species. Historically Elapidae contained three subfamilies: Elapinae (terrestrial elapids), Laticaudinae (sea kraits), and Hydrophiinae (sea snakes). Molecular, and often morphological, phylogenetic evidence supports the monophyly of Hydrophiinae (if defined to include Australo-Papuan terrestrial elapids and true sea snakes), Laticaudinae, and separate "elapine" clades of cobras, coral snakes, mambas, kraits, and other lineages. However, there is insufficient phylogenetic information to determine if these "elapine" groups form a single clade (Elapinae), or if one or more are more closely related to hydrophiines. We therefore recognize Hydrophiinae (including Laticauda and Australo-Papuan terrestrial species) and include the remaining elapids in a non-monophyletic "Elapinae" that awaits revision based on future phylogenetic analyses. "Elapinae": representative genera include Bungarus, Dendroaspis, Micrurus, Naja, and Ophiophagus (Figure 4.66A–C). Hydrophiinae: marine genera include Aipysurus, Emydocephalus, Hydrophis, and Laticauda (Figure 4.66D); semiaquatic genera include Ephalophis, Hydrelaps, and Parahydrophis; and representative terrestrial genera include Acanthophis, Austrelaps, Notechis, Oxyuranus, Pseudechis, and Simoselaps (Figure 4.66E-G).

Elapids occur in southern North America, throughout Central and South America, Africa (absent from Madagascar), southern and eastern Asia, islands of the Indo-Australian Archipelago, and the Indian and Pacific Oceans (**Figure 4.66H**). The IUCN lists 7 species as Critically En-



Figure 4.66 Elapidae. (A–C) Example of species of "Elapinae," a non-monophyletic group that awaits further phylogenetic analysis and revision (see text). (A) Indian or spectacled cobra Naja naja. (B) Eastern coral snake, Micrurus fulvius, North America. (C) The arboreal East African green mamba, Dendroaspis angusticeps. (D) The Chinese sea snake, Laticauda semifasciata, is found in the South China Sea and here represents the marine species of Hydrophiinae. (E-G) Three examples from the many terrestrial hydrophiine species found in Australia. (E) Death adder, Acanthophis antarcticus. (F) Southern Desert banded snake, Simoselaps bertholdii. (G) Tiger snake, Notechis scutatus. (H) Distribution. (Photographs: A, courtesy of Vishal Prassad; B, © Jay Ondreicka/Shutterstock; C, © Danita Delimont/Alamy; D, © Reinhard Dirscherl/Alamy; E. courtesy of John Wombey/CSIRO; F, courtesy of Harvey Pough; G, © Martin Willis/Minden Pictures/Corbis.)

dangered or Endangered and 23 species as Near Threatened or Vulnerable.

Systematics references McCarthy (1985), Wüster et al. (1995, 2007), Scanlon and Lee (2004), Lukoschek and Keogh (2006), Castoe et al. (2007), Sanders and Lee (2008), Sanders et al. (2008, 2013a,b), Pyron et al. (2011), Lukoschek et al. (2012).

Lamprophiidae • House Snakes, Sand Snakes, Stiletto Snakes, and Others

Lamprophiids are a group of morphologically and ecologically diverse snakes and include many taxa whose phylogenetic affinities have only recently been clarified by molecular studies. They are the sister taxon to the highly venomous Elapidae. The taxonomy of the Lamprophiidae remains confusing. Lamprophiid clades have been recognized as different combinations of subfamilies or families in the scientific literature. We recognize seven subfamilies that are reasonably well supported by molecular data (see also Pyron et al. 2013a, 2014b). The sister relationship of atractaspidines and aparallactines is generally accepted, but the phylogenetic interrelationships among the remaining subfamilies are unclear.

Classification, distribution, and conservation 61 genera, 307 species. See subfamily accounts below. The clade is primarily African (including a major radiation in Madagascar), but it also occurs in southern Eurasia and the Philippines (*Oxyrhabdium*) (see Figure 4.67H). The phylogenetic relationships are unresolved for at least 5 genera: *Buhoma*, *Psammodynastes*, *Micrelaps*, *Montaspis*, and *Oxyrhabdium*.

Systematics references Nagy et al. (2003), Vidal et al. (2008b), Glaw et al. (2009), Kelly et al. (2011).

Aparallactinae

Aparallactines are venomous (but rear-fanged) and many resemble atractaspidines except that they are smaller, most-

ly 1 m or less in total length. They inhabit both forested and nonforested habitats throughout their range and are nocturnally active. Most species are secretive, and many are burrowers. Diets consist primarily of elongate vertebrates such as snakes, skinks, caecilians, and amphisbaenians, the last comprising a vast majority of the diet of *Xenocalanus*. However, species of *Aparallactus* eat centipedes almost exclusively (**Figure 4.67A**). Most species are oviparous, but *Aparallactus jacksonii* is viviparous.

Classification, distribution, and conservation 9 genera, 47 species. Representative genera include *Amblyodipsas, Aparallactus, Chilorhinophis, Polemon,* and *Xenocalamus.* They inhabit sub-Saharan Africa and the Middle East. The IUCN lists 1 species (*Aparallactus lineatus*) as Near Threatened.

Systematics references McDowell (1986), Underwood and Kochva (1993), Cadle (1994), Pyron et al. (2011).

Atractaspidinae

Atractaspidinae contains two genera, *Atractaspis* and *Homoroselaps*. *Atractaspis* are small to moderate-size African snakes (~1 m total length) with a slender body (**Figure 4.67B**). In external appearance they are similar to many terrestrial or fossorial colubrids. They are subterranean and consume reptiles and mammals. Atractaspidines are primarily nocturnal, and all are oviparous. Their distinctive features are internal, particularly characters of the dentition, jaw apparatus, venom gland, and venom.

The venom glands of several species of *Atractaspis* are extremely elongate and extend behind the head into the dorsal neck region. The maxilla is greatly reduced and bears a pair of enormous hollow fangs, only one of which is functional at any one time The maxilla of *Atractaspis* has a complex articulation with the prefrontal bone, and the fangs are erected laterally and directed posteriorly. *Atractaspis* envenomate prey by striking with lateral and posterior stabbing motions of the head, giving rise to a common name of stiletto snakes. The ability to erect the fangs without opening the mouth probably facilitates foraging in subterranean tunnels. One class of toxins, sarafotoxins, is unique to *Atractaspis*. Sarafotoxins are cardiotoxic peptides that produce constriction of the coronary blood vessels (Terrat et al. 2013).

Homoroselaps is a small (50 cm total length), semifossorial snake that searches at night for legless skinks (*Scelotes*) in clumps of grass and captures blindsnakes (Typhlopidae) and thread snakes (Leptotyphlopidae) underground. Although an atractaspidine, *Homoroselaps* shares little phenotypic resemblance to *Atractaspis* and was previously considered an elapid or an aparallactine.

Classification, distribution, and conservation 2 genera (*Atractaspis, Homoroselaps*), 23 species. The hypothesized phylogenetic relationships of Atractaspidinae have shifted frequently. *Atractaspis* was originally considered an aber-

(A) Aparallactinae



(C) Lamprophiinae



(E) Psammophiinae



(G) Pseudoxyrhophiinae



(B) Atractaspinae



(D) Prosymninae



(F) Pseudaspidinae





rant viperid, but recent phylogenetic evidence now strongly supports its inclusion in Lamprophiidae. Atractaspidinae is often recognized as a family that includes Aparallactinae (see above). They inhabit Africa and the Middle East. No species are listed by the IUCN as an extinction risk.

Systematics references Laurent (1950), Underwood and Kochva (1993), Nagy et al. (2005), Moyer and Jackson (2011).

Lamprophiinae

Lamprophiines are primarily nocturnal snakes that have earned the common name house snakes from their frequent occurrence around human dwellings, even though most species naturally inhabit terrestrial forest or grassland habitats. The diet of lamprophiines consists mostly of small mammals and lizards, but some *Mehelya* species are ophiophagous (snake-eating). *Lycodonomorphus* are aquatic, with the exception of *L. inornatus*, which inhabits mesic forests and consume frogs and fish (Kelly et al. 2011). *Boaedon fuliginosus* (Figure 4.67C) is notable for its sexual dimorphism—adult females can weigh more than three times as much as males. This species is also a prolific breeder; captive individuals have produced clutches of 5–15 eggs every 40–50 days (Boback et al. 2012).

Classification, distribution, and conservation 12 genera, 70 species. Representative genera include *Boaedon, Gonionotophis, Lamprophis, Lycodonomorphus, Lycophidion,* and *Mehelya.* Lamprophiines inhabit sub-Saharan Africa. The IUCN lists 1 species (*Lamprophis geometricus*) as Endangered and 1 species (*Lycophidion nanus*) as Vulnerable.

Systematics references Broadley (1996), Kelly et al. (2011).

Prosymninae

The rostrum of prosymnines is angled downward, hence the common name shovel-nosed or shovel-snout snakes (**Figure 4.67D**). They use their snout to excavate reptile nests and reach the eggs, which make up the vast majority of their diet (Broadley 1979). Prosymnines are oviparous.

Classification, distribution, and conservation 1 genus (*Prosymna*), 16 species. They inhabit southern Africa. The IUCN lists 1 species (*P. ornatissima*) as Critically Endangered.

◄ Figure 4.67 Lamprophiidae. (A) Black centipede eater, Aparallactus guentheri (Aparallactinae). (B) Mole viper, Atractaspis aterrima (Atractaspinae). (C) Brown house snake, Boaedon fuliginosus (Lamprophiinae). (D) East African shovel-snout snake, Prosymna stuhlmanni (Prosymninae). (E) Big-eyed snake, Mimophis mahfalensis (Psammophiinae). (F) African mole snake, Pseudaspis cana (Pseudaspidinae). (G) Cat-eyed snake, Madagascarophis meridionalis (Pseudoxyrhophiinae). (H) Distribution. (Photographs: A−D, courtesy of Stephen Zozaya; E, courtesy of Miguel Vences and Frank Glaw; F, © EcoPrint/Shutterstock; G, © FLPA/Alamy.) Systematics references Broadley (1965, 1980).

Psammophiinae

Most psammophiine species are active diurnal snakes with a slim body, small head, large eyes, and smooth scales (Figure 4.67E). They are opportunistic predators, feeding mostly on lizards, frogs, and small mammals. Rhamphiophis rostratus feeds on naked mole rats (Bathyergidae), among other prey (Agundey 1997). The hemipenes of male psammophines are so reduced they resemble vestigial tubes. Many psammophiine species inhabit dry environments (hence the common name of sand snakes), and nasal glands secrete lipids that the snakes rub on their body, probably limiting desiccation (de Pury and Böhme 2013). Most psammophiines are oviparous, and most species studied lay clutches of 10 eggs or fewer, but Psammophylax variabilis is viviparous. Clutch-guarding by Psammophylax rhombeatus has been reported. See Shine et al. (2006) and Cottone and Bauer (2010) for ecological reviews.

Classification, distribution, and conservation 8 genera, 51 species. Representative genera include *Malpolon, Mimophis, Psammophis, Psammophylax,* and *Rhamphiophis*. Psammophiines inhabit Africa, Madagascar, the Middle East, and southern Europe to central Asia. No species are listed by the IUCN as an extinction risk.

Systematics references Broadley (1966, 1977a,b, 2002), Kelly et al. (2008), Vidal et al. (2008b).

Pseudaspidinae

This subfamily is composed of two African species. *Pseudaspis cana*, the mole snake (**Figure 4.67F**), inhabits animal burrows and much of the species' diet consists of African golden moles (Chrysochloridae). *Pythonodipsas carinata*, the false viper, superficially resembles viperid snakes, and its posteriormost teeth are elongated and grooved. However, neither genus in this subfamily is venomous. *Pseudaspis* is viviparous, and *Pythonodipsas* is oviparous.

Classification, distribution, and conservation 2 species (*Pseudaspis cana, Pythonodipsas carinata*). They inhabit southern Africa. Neither species is listed by the IUCN as an extinction risk.

Systematics references Schätti and McCarthy (1987), Vidal et al. (2008b).

Pseudoxyrhophiinae

Aside from *Mimophis* (Psammophiinae), all colubroid snakes on Madagascar belong to the lamprophiid subfamily Pseudoxyrhophiinae, and all but three genera in this subfamily (*Amplorhinus, Duberria*, and *Ditypophis*) occur on Madagascar or the nearby Comoro Islands. The Malagasy pseudoxyrhophiines are an example of an evolutionary radiation leading to a diversity of phenotypes and behaviors. Some pseudoxyrhophiines have dental specializations for feeding on skinks and gerrhosaurids (*Liophidium*, *Pseudoxyrhopus*), whereas other genera consume primarily frogs (e.g., *Compsophis, Liopholidophis*), lizards (*Langaha*), or a variety of vertebrates (*Leioheterodon, Madagascarophis*). The African genus *Duberria* preys on molluscs, especially slugs. The group includes diurnal terrestrial (*Dromicodryas, Liopholidophis, Leioheterodon*) and arboreal species (*Ithycyphus, Langaha*), as well as nocturnal terrestrial (*Pseudoxyrhopus, Madagascarophis*; **Figure 4.67G**) and arboreal species (*Compsophis, Lycodryas, Stenophis*). Some pseudoxyrhophines are semifossorial (*Heteroliodon, Pseudoxyrhopus*) or cave-dwelling (*Alluaudina*) (Cadle 1999).

The arboreal *Langaha* have a leaf-shaped extension at the tip of their rostrum, giving them the common name leafnosed snakes. The exact function of this structure is unknown. One hypothesis is that it resembles the long seedpods of local Malagasy trees and thus serves as camouflage; indeed, *Langaha* spend 90% of the day motionless, waiting for prey to wander by (Tingle 2012). However, the shape of the extension is sexually dimporphic and may therefore also have functions related to reproduction.

Reproductive mode is not well studied in pseudoxyrhophiines; available data indicate that most species are oviparous, although *Amplorhinus, Duberria, Liopholidophis sexlineatus, Lycodryas citrinus,* and *Lycodryas pseudogranuliceps* are viviparous (Cadle et al. 2009). Many Madagascan pseudoxyrhophiine species are threatened with extinction due to habitat loss.

Classification, distribution, and conservation 22 genera, 89 species. They inhabit Madagascar and the surrounding islands, sub-Saharan Africa, Socotra, and the southern Arabian Peninsula. Representative genera include *Duberria, Langaha, Liophidium, Lycodryas,* and *Pseudoxyrhopus.* The IUCN lists 10 species as Critically Endangered or Endangered and 21 species as Near Threatened or Vulnerable, due primarily to habitat destruction on Madagascar.

Systematics references Cadle (1996, 1999), Nagy et al. (2003), Glaw et al. (2007, 2009), Vidal et al. (2008b), Franzen et al. (2009), Vieites et al. (2010), Hawlitschek et al. (2012).



Air enters the lungs from here. This hole is behind the flap of skin that separates the mouth from the airway

4.6 Crocodylia

Crocodylians have a heavily armored, elongate body with a long snout and powerful tail and limbs. The dorsal armor is formed by heavy plates of bone (osteoderms) that lie within the dermis underneath heavy epidermal scales (see Figure 4.1D). Osteoderms are also present on the venter in many species. The teeth of crocodylians (and mammals) are **thecodont**, meaning they are set into sockets to which they are attached by ligaments. The limbs of crocodylians are relatively short, and all feet are webbed.

Crocodylian evolution has been marked by two general trends that occurred in parallel in many different lineages. The first was the evolution of increased flexibility and strength of the spine, marked by a transition from amphicoelous vertebrae early in their evolution to procoelous vertebrae later (see Figure 3.19). The second trend was the evolution of a complete secondary palate separating the buccal cavity from the respiratory passages, allowing breathing to continue when the mouth is open underwater (Figure 4.68).

All crocodylian species are aquatic to varying degrees. The eye has a transparent nictitating membrane that is drawn across the eye underwater. The nostrils are dorsally located at the tip of the snout and are closed by valves during diving. Internally, the nasal passages (choanae, or internal nares) open in the throat behind the secondary palate and can be closed off from the throat by fleshy folds on the back of the tongue and palate. These modifications allow crocodylians to breathe in air while holding prey in the mouth.

The skin on the dorsal and ventral surfaces of crocodylians is studded with sensory organs and glands. All extant crocodylians have sensory organs called <u>dome pressure</u> receptors on the dorsal and ventral surfaces of the head (Soares 2002). These organs detect surface waves when the animal is at the air–water interface, permitting behavioral responses to potential predators or prey and to mechanical disturbances such as raindrops. They are present in crocodylian skulls as small foramina (holes), and are also observed in aquatic (but not terrestrial) crocodylians back to the Early Jurassic.

Crocodylians are excellent swimmers but can move surprisingly fast on land. *Crocodylus johnstoni* is known to gallop and can reach a speed of 17 km/h. When walking, crocodylians generally hold the belly high off the ground and place the limbs underneath the body. However, they also use a belly crawl when plunging into water. In water,

> **Figure 4.68 Sagittal section through the head of a crocodilian.** The diagram shows the extensive secondary palate and the positions of the external and internal nares. This arrangement allows the animal to breathe with only the tip of its snout above the water. The lower jaw is not shown.

crocodylians fold the limbs against the body and use lateral undulation of the body and tail to swim.

All crocodylians are oviparous and lay eggs either in mound nests constructed from vegetation and soil (alligatorids, *Tomistoma*, and most crocodylids) or directly in soil on beaches or other exposed areas (*Gavialis* and several species of *Crocodylus*). Temperature-dependent sex determination occurs in all species examined; high incubation temperatures produce males. Parents guard the nest. Some species break open the nest to release the hatchlings, carry the young to water in their mouth (see Figure 9.9), and remain with them for weeks or months. Such extensive parental care is characteristic of all archosaurs, including birds and other dinosaurs.

The social behavior of crocodylians is more complex than that of other reptiles (see Chapters 13 and 14). Their hearing acuity is good, and vocalizations are used in a variety of social contexts, including territorial bellowing during the breeding season, aggressive warnings to intruders, and signals given by neonates in the nest to elicit nest-opening behavior by attending adults. Circumstantial evidence suggests that young within the eggs use vocalizations to communicate with one another, perhaps to synchronize hatching.

Vocalizations are used after hatching to maintain group cohesion and to alert adults to potential threats. Crocodylians have a surprisingly diverse repertoire of sounds, including low-frequency roars, grunts, coughs, and purrs. Most crocodylian sounds are produced by the vocal cords, but sounds barely perceptible to humans are produced by rapid contraction of the body-wall musculature underwater, causing drops of water to leap from the surface (see Figure 13.25). Body postures and head-slapping at the water surface are often used as dominance advertisements. The senses of smell and eyesight are also well developed in crocodylians, and social signals often involve combinations of visual, olfactory, and acoustic cues. Smell is also used to locate food from a distance.

Crocodylians are efficient predators and eat a variety of prey, including fish, turtles, birds, mammals, and shellfish. Small crocodylians eat insects, frogs, and other small prey. Food is often located using their well-developed sense of smell, and they use gular pumping to bring olfactory stimuli into the nasal chamber to enhance these cues. Crocodylians may be active day and night, although predation is generally nocturnal. Most crocodylians either forage in water or attack at water's edge and drag their prey into water. Smaller prey can be directly swallowed or crushed in the jaws, but crocodylians usually drown large prey before eating them. Crocodylians do not chew. Rather, they are gulpers that tear their prey into pieces suitable for swallowing (see Chapter 11).

Crocodylians throughout the world have been exploited for their meat and their skins, which are made into leather. The leather trade in the Americas began with *Alligator mississippiensis* in the 1700s and moved to other species when commercial hunting became unprofitable as populations were reduced to near extinction. Several species, including *Caiman niger* and *Crocodylus mindorensis*, have had their ranges vastly reduced as a result of hunting pressures. More recently some species, including *A. mississippiensis*, have recovered as a result of conservation efforts (see Chapter 17). Wild populations of crocodylians are protected by international agreements, although illegal poaching is still a major problem in many areas. Farming of several species of crocodylians for the leather trade has become commercially successful in many countries.

Fossil record

Crocodylians have an extensive fossil record that spans the last 215 million years (Middle Triassic to Recent), if extinct stem lineages are included (clade Crocodylomorpha). As with turtles, crocodylians' large size, aquatic habits, and extensive ossification enhance fossilization. Fossils of the modern families Alligatoridae and Crocodylidae appear from the Late Cretaceous, whereas the oldest gavialid fossil is from the Eocene. Most crocodylians, extant and extinct, have lived in freshwater environments. However, diverse lineages radiated into more or less fully marine or terrestrial environments during their history (Markwick 1998). For example, metriorhynchid crocodylians (Jurassic to Early Cretaceous) were efficient marine predators that had lost their dorsal armor. Their limbs were transformed into paddles, and their tail bore a fishlike fin at the tip. Kaprosuchus saharicus was a terrestrial crocodylian that lived in the Late Cretaceous in what is now the Sahara Desert (Sereno and Larsson 2009). It is estimated to have reached a length of 6 m, and may have preyed on dinosaurs. The largest crocodile known, Crocodylus thorbjarnarson, was approximately 7.5 m long and lived in the Turkana Basin of present-day Kenya some 3 mya, coexisting with earliest ancestors of humans (Brochu and Storrs 2012). See Brochu (2003) for a review of crocodylian fossil history.

Systematics and Phylogeny of Crocodylians

There are three major lineages of extant crocodylians: Alligatoridae (alligators and caimans), Gavialidae (true and false gharials or gavials), and Crocodylidae (crocodiles). Molecular phylogenetic analyses have been remarkably consistent, and most support the tree in **Figure 4.69** (e.g., Willis et al. 2007; Gatesy and Amato 2008; Willis 2009; Man et al. 2011; Oaks 2011; Shirley et al. 2014). However, morphological and molecular phylogenies disagree on the relationships of *Gavialis* (gharials) and *Tomistoma* (false gharials). All recent molecular phylogenetic analyses support the sister relationship of *Gavialis* and *Tomistoma*, whereas phylogenetic analyses of morphological characters place *Tomistoma* within the Crocodylidae (e.g., Norell 1989; Brochu 2003; Salisbury et al. 2006). As with the phylogeny of Squamata, consensus of the two types of data seems unlikely.

Figure 4.69 Phylogenetic relationships of Crocodylia based on DNA data.

Classification, distribution, and conservation 9 genera, 25 species. They are distributed throughout tropical and subtropical regions, except for *Alligator*, which is found in warm temperate regions of the United States and China. Most species occur primarily in freshwater habitats, but several readily enter brackish or marine habitats. *Crocodylus porosus* of the Indo-Pacific region and *C. acutus* of Central and South America and the Caribbean have been found in the open ocean. The IUCN lists 7 species as Critically Endangered or Endangered and 3 species as Vulnerable.

Alligatoridae • Alligators and Caimans

In alligatorids, the teeth of the lower jaw fit into pits in the upper jaw and cannot be seen when the mouth is closed. Alligatorids include some of the largest (*Caiman niger*; >6 m total length) and the smallest (*Paleosuchus*; ~1.5 m total length) extant crocodylians. With the exception of *Paleosuchus*, alligatorids inhabit large rivers, lakes, swamps, and lagoons. The two species of *Paleosuchus* inhabit small streams and pools of forested areas of the Amazon basin. *Alligator mississippiensis* enters coastal marine waters. The term "alligator" is a corruption of the Spanish *el lagarto* ("the lizard"), which early Spanish explorers applied to these creatures.



Caiman is the name commonly used throughout Latin America for any of these animals (**Figure 4.70A**); it is probably derived from the Carib name *acayuman*.

Alligator mississippiensis (temperate areas of the United States) and A. sinensis (lower Yangtze River of eastern



China) are the only crocodylians inhabiting areas where surface waters freeze regularly during the winter. It was long thought that alligators sought refuge in underwater or underground dens during severe cold periods. However, radiotelemetry studies have shown that these two species move into shallow water and position themselves with their nostrils exposed above the surface ice. They are incapable of lowering their metabolism sufficiently to depend entirely on anaerobic metabolism, and hence must breathe during these periods. They have even been found with their snouts frozen into surface ice.

The two species of *Paleosuchus* (dwarf caimans) may be found in rainforests some distance from water. *P. palpebrosus* more often occurs in rivers and lakes than *P. trigonatus*, which prefers small streams (Magnusson et al. 1987). These species are nocturnal, and little is known of their natural history. Diets sometimes include substantial numbers of terrestrial vertebrates compared with the diets of other sympatric crocodylians (Magnusson et al. 1987). Because *Paleosuchus* live in deep forest, they cannot rely on heat from the sun to warm eggs for hatching. *P. trigonatus* lays eggs in mounds of earth or vegetation that are usually constructed adjacent to termite mounds in the forest. The metabolic heat generated by the termites warms the eggs (Magnusson et al. 1985).

Classification, distribution, and conservation 4 genera (*Alligator, Caiman, Melanosuchus, Paleosuchus*), 8 species. All genera except *Alligator* are restricted to Central and South America (**Figure 4.70B**). The IUCN lists 1 species (*Alligator sinensis*) as Critically Endangered, due largely to habitat destruction.

Systematics references Brazaitis (1973), Gatesy and Amato (2008), Hrbek et al. (2008), Oaks (2011).

Crocodylidae • Crocodiles

In crocodylids the fourth tooth in the lower jaw is accommodated in a notch in the upper jaw and is visible when the mouth is closed. The saltwater crocodile (*Crocodylus porosus*; **Figure 4.71A**) grows to more than 7 m in total length and is the largest extant crocodylian. The West African dwarf crocodile (*Osteolaemus tetraspis*) is the smallest crocodylian and reaches only 2 m in total length. *Osteolaemus* inhabits small streams in rainforests and savannas and is similar to the dwarf caiman *Paleosuchus* (Alligatoridae). Dwarf crocodiles construct burrows under riverbanks and lay eggs in mound nests.

Figure 4.71 Crocodylidae. (A) Saltwater crocodile, *Crocodylus porosus*. (B) Distribution. (Photograph © Madeleine Hall/ Alamy.)





Crocodylus porosus has the widest distribution of all crocodylians, from India to Australia and perhaps as far as Fiji in the southwest Pacific Ocean. It has been observed in open ocean far from land and has colonized small islands nearly 1,000 km from the nearest land. This species and the Nile crocodile (*Crocodylus niloticus*) are almost exclusively responsible for crocodiles' reputation for eating humans, and for these two species—the reputation is well deserved.

Classification, distribution, and conservation 3 genera (*Crocodylus, Mecistops, Osteolaemus*), 15 species. They inhabit southern Mexico to northern South America (Orinoco River basin), the West Indies and southern tip of Florida, coastal Madagascar and nearly all of Africa, southern Asia from Iran east throughout India, Southeast Asia, and the Indo-Australian Archipelago to New Guinea and northern Australia (**Figure 4.71B**).

Systematics references Meganathan et al. (2010), Man et al. (2011), Meredith et al. (2011), Oaks (2011), Brochu and Storrs (2012), Shirley et al. (2014).

Gavialidae • Gharial and False Gharial

Gavialis gangeticus and *Tomistoma schlegelii* reach total lengths of about 6.5 m and 4 m, respectively. Both have an elongate, narrow snout formed by a long extension of the mandibular symphasis (**Figure 4.72A**). *Gavialis gangeticus* is possibly the most aquatic of extant crocodylians, has relatively weak limbs, and lives in fast-flowing rivers. Its diet consists mostly of fish, which it snaps up with sideways sweeps with its long narrow snout. Male *Gavialis* are easily recognized by the enlarged bulblike structure called a boss at the end of the rostrum. The boss grows with age, and although its function is not precisely known, its presence only in males suggests it is used in territorial defense or sound communication. *Gavialis gangeticus* nests in holes in sandbanks along rivers,

Tomistoma schlegelii is phenotypically similar to *G. gangeticus*, but males lack the boss. The diet of *T. schlegelii* includes both fish and other animals in water and along the shoreline. Females construct a mound nest. In Borneo, this species characteristically inhabits peat swamps.

Classification, distribution, and conservation 2 genera, 2 species: *Gavialis gangeticus* historically inhabited northern India, Pakistan, Nepal, Bangladesh, and Bhutan, east to Myanmar (Burma). *Tomistoma schlegelii* inhabits southern Thailand and Malaysia, Sumatra, Borneo, and Java (**Figure 4.72B**). The IUCN lists *G. gangeticus* as Critically Endangered, the result of past hunting and current habitat loss; fewer than 200 individuals are estimated to remain in the wild. The IUCN lists *T. schlegelii* as Endangered, with fewer than 2,500 individuals remaining in the wild.

Systematics references None.

(B) Gavialis gangeticus Tomistoma schlegelii Malay Peninsula Gavialidae Gavialidae Cavialidae Cavialidae Cavialidae

Figure 4.72 Gavialidae. (A) Indian gharial, *Gavialis gangeticus* (also called the gavial and fish-eating crocodile). (B) Distribution. (Photograph © Nazzu/Shutterstock.)

4.7 Testudines: Turtles

Turtles are among the longest-lived vertebrates. There are documented records of captive tortoises living more than 150 years, although longevity in natural populations is probably less. The shell that encases the body of a turtle is unique among vertebrates, and this makes them among the most distinctive and recognizable of all organisms.

Many of the peculiar features of turtles are also derived characters of Testudines (Gaffney and Meylan 1988; Gaffney 1990; Lee 1995). These features include the shell and its association with vertebrae, ribs, and girdles; the medial position of the girdles relative to the ribs; the absence of teeth and their replacement by a keratinous beak (palatine and vomerine teeth are present in some early fossils); and the unusual configuration of the jaw adductor musculature (see discussion of the trochlea, below). Other derived char-



(A)



acters of the turtle skeleton include loss of the pineal foramen and loss of certain skull bones. Because of the unique structural features of turtles, their monophyly has never been challenged. The term Testudines is often used for all turtles, including both extant crown and extinct stem lineages. The alternative term Chelonia is widely used for the extant crown clade only. For simplicity, we use Testudines.

The turtle skeleton

The embryonic origin of the turtle shell has been debated, with competing hypotheses proposing that it is derived from dermal bone (like osteoderms) or from elements of endochondral bone that form the axial skeleton and long bones of tetrapods. Recent embryonic development analysis of *Pelodiscus sinensis* (Trionychidae) has shown that a majority of the shell is composed of expansions of endochondral bone of the axial skeleton, most notably from developing ribs (Hirasawa et al. 2013, 2014). The final shell is therefore a fusion of the vertebral column and laterally expanded ribs, with some other dermal elements incorporated as the shell develops.

Turtles are also unique in that their pectoral and pelvic girdles are within the rib under the vertebrae (Figure 4.73). The shoulder girdle of other tetrapods (including humans) essentially sits on top of the rib cage. Because the vertebrae of turtles, except for those of the neck and tail, are completely fused into the shell, no movement occurs in much of the axial skeleton.

The turtle shell

The turtle shell has two parts—a dorsal **carapace** and a **ventral plastron**—which are joined laterally by a bridge (**Figure 4.74**). The shell is covered externally by keratinous scutes (see Figure 4.1B,C). The scutes do not have the same alignment as the underlying bony elements, and this misalignment of sutures in the bony and keratinous portions of the shell adds strength akin the the alternation of bricks in a

wall. The limbs, tail, neck, and head protrude from anterior and posterior openings. The plastron of some groups of turtles is solid, whereas others have a set of loosely articulated or separate bony elements. The overall shell shape varies greatly, with a relatively high dome being characteristic of many terrestrial turtles, and a relatively flat, streamlined form characteristic of aquatic and marine turtles. Three lineages of aquatic and marine turtles (Trionychidae, Dermochelyidae, Carettochelyidae) are covered by leathery skin instead of a bony shell. The shell of the turtle protects against predation, and this protections is enhanced by the ability of most turtles to retract their head inside the shell when threatened (see Figure 4.76).



Figure 4.74 Components of the turtle carapace. In this dorsal view, bony components of the carapace are shown on the left; the right side shows the surface with its overlying epidermal scutes. A similar relationship between dermal and epidermal components exists in the plastron. (After Pritchard and Trebbau 1984.)

In most turtles, both the carapace and the plastron are rigid structures, but several lineages have independently evolved the ability to close the body within the shell. In most cases there is a hinge on the front or rear lobe of the plastron, as seen in North American box turtles (Terrapene; Emydidae) and mud turtles (Kinosternon; Kinosternidae) and the Asian box turtle (Cuora amboinensis; Geoemvdidae). However, African testudinids of the genus Kinixys draw the posterior portion of the carapace downward to protect the rear end, and trionychids of the genus Lissemys have anterior and posterior plastral hinges that close both ends. Shell reduction has occurred in some turtles, perhaps most peculiarly in the African tortoise Malacochersus (Testudinidae). Unlike most land tortoises, this turtle has a very flat shell and the carapace is reduced to a series of bony rings surrounding large vacuities. Both the carapace and the plastron are soft and flexible. This turtle inhabits rocky outcrops in African savannas and wedges itself into crevices by inflating its body with air.

Turtle skulls differ from those of other extant reptiles in lacking temporal fenestrae and hence have an anapsid condition. As discussed in Section 2.7, this condition is secondarily derived, since turtles are phylogenetically nested within Diapsida. Despite having an anapsid condition, the skulls of many turtles are greatly emarginated (notched) from the posterior end, resulting in rather open temporal and posterior regions of the skull (**Figure 4.75**). Teeth are completely absent in extant turtles, although they are present in some fossil specimens. In extant lineages, the teeth have been replaced by a tough, keratinous beak. Moreover,



Figure 4.75 Turtle skulls show variation in structure. All turtles are anapsid, lacking temporal fenestrae. However, their skulls are emarginated (notched) to varying degrees. The diagrams show lateral views of the temporal regions of (A) an Atlantic ridley sea turtle (*Lepidochelys kempi*, Cheloniidae) and (B) the Nile soft-shelled turtle (*Trionyx triunguis*, Trionychidae). The skull of *Lepidochelys* is only shallowly emarginated, whereas that of *Trionyx* is extensively emarginated. (After Gaffney 1979.)

the orientation of the jaw adductor muscles to the braincase in turtles is unique among tetrapods, although this character is modified in distinctive ways in the two lineages of extant turtles, Pleurodira and Cryptodira (Gaffney 1975). In each case, the muscles pass over a prominence, the trochlea, in passing from the lower jaw to the skull, thus forming a sharp angle in the orientation of the muscle fibers (see Chapter 11). In other tetrapods the orientation of the jaw adductors is relatively straight because there is no trochlea to reorient the muscle fibers.

Locomotion and reproduction

The structure of turtle limbs is highly variable, reflecting the environment and mode of locomotion of different species. Marine species and the freshwater turtle *Carettochelys* (in the monotypic family Carettochelyidae) have flippers with extremely elongated digits that are not independently movable. Most aquatic species have webbing between the digits, which still retain some independent mobility. Terrestrial turtles (e.g., tortoises and a few others such as box turtles of the genus *Terrapene*) generally have stout clublike limbs capable of lifting their heavy bodies off the substrate. Their digits are usually reduced, and the feet are equipped with thickened pads.

All turtles are oviparous and lay eggs in a nest dug in the ground or on the surface with no nest (e.g., the testudinid Geochelone denticulata). Fertilization is internal via the male penis which is an outgrowth of the cloacal wall. It contains erectile tissue and a groove in the dorsal surface through which sperm flows during copulation. Courtship in turtles is often elaborate, involving prolonged interaction between the sexes before copulation (see Chapter 14). Embryonic development is arrested during late gastrula in the oviduct and resumes after oviposition. Some turtles also exhibit one of several forms of embryonic diapause after oviposition. For example, clutches of the North American kinosternid Kinosternon baurii laid during the fall undergo a diapause over the winter and resume development the next spring with the onset of warmer weather. Most turtles with such a diapause are warm temperate or subtropical species of Chelidae, Kinosternidae, Emydidae, Testudinidae, and Trionychidae (Ewert and Wilson 1996). In general, turtles provide no parental care.

Temperature-dependent sex determination (see Figure 9.3) is probably the only mode of sex determination in the **Testudinidae**, Chelydridae, Kinosternidae (except *Stauro-typus*), Dermatemydidae, Cheloniidae, Dermochelyidae, Carettochelyidae, Pelomedusidae, and Podocnemidae (Janzen and Paukstis 1991). Temperature-dependent sex determination also occurs in most emydids and geomydids. Genotypic sex determination is probably the rule in Trionychidae and Chelidae (Sarre et al. 2011).

Fossil record

Turtles have the most complete fossil record of any extant reptiles, owing in part to their heavy, bony skeletons and their aquatic or marine habits. The earliest-known turtle fossils are from the Late Triassic (~220–210 mya) and include *Odontochelys* from China (Li et al. 2008), *Proganochelys* from Germany (Gaffney 1990; Rougier et al. 1995), and *Palaeochersis* from South America (Sterli et al. 2007). However, the earliest ancestors of modern turtle lineages (crown Testudines) arose in the Middle Jurassic (Joyce et al. 2013).

Odontochelys is particularly important for understanding the evolution of turtles; it has teeth like other early turtles, and although it has a plastron, it does not have a carapace that surrounds the entire dorsal portion of the body. The absence of a full carapace in this early turtle suggests that the plastron evolved before the carapace. More important, the carapace resembles that of an embryonic turtle in that the ribs are laterally expanded, but they are not fused to form a complete shell. Thus, *Odontochelys* is a well-preserved example of an intermediate step in the evolution from the ancestral reptile body type to the highly modified body plan of extant turtles.

The oldest cryptodire, *Kayentachelys aprix*, is known from the Early Jurassic Kayenta Formation of Arizona (Gaffney et al. 1987; but see Joyce and Sterli 2012). The oldest pleurodire is the Late Triassic *Proterochersis* (Gaffney et al. 2006), although this taxon could instead be a stem chelonian (Joyce et al. 2013). A gap in the fossil record of pleurodies extends through the Early and Middle Jurassic (Gaffney et al. 2006). Thus, both major extant clades are known from relatively early in the recorded history of Testudines. Extant families were once more widespread than their present distributions (Carroll 1988). The controversy over the phylogenetic placement of turtles among reptiles was summarized in Chapter 2. Recent analyses of the relationships of fossil turtles include Joyce (2007), Joyce and Sterli (2012), and Anquetin (2012).

Systematics and Phylogeny of Turtles

All extant turtles belong to one of two clades, the Pleurodira and Cryptodira. Pleurodira includes the extant freshwater families Chelidae, Pelomedusidae, and Podocnemidae. All other turtles are cryptodires, which may be freshwater, marine, or terrestrial. Although both clades are supported by numerous skeletal characters (Gaffney 1975), they are most easily identified by their mode of neck retraction. Extant members of both clades retract their head into their shell as an antipredator defense, but the mode of neck retraction differs and is based on the form of the cervical vertebrae that permits bending of the vertebral column in either the horizontal or vertical plane (Williams 1950). Pleurodires (from the Greek pleura, "side," + dira, "neck") fold their long, snakelike neck along the side of their body, protecting it within the overhanging projections of the carapace (Figure 4.76A), whereas most cryptodires (from the Greek cryptos, "hidden,") can fully retract the neck and head linearly into their shell (Figure 4.76B). Early fossil members of both

(A)



(B)



Figure 4.76 Neck retraction by turtles. (A) Pleurodire turtles such as the South American flat-headed turtle (*Platemys platycephala*, Chelidae), withdraw their head laterally (to the side), where it is covered by the outer margins of the carapace. (B) Crypotodires ("hidden neck") turtles such as the South African mountain tortoise (*Geochelone pardalis*, Testudinidae) can retract their necks linearly (straight back) so that the head is fully protected inside the shell. (Photographs: A, © Pete Oxford/Minden Pictures/Corbis; B, © EcoPrint/Shutterstock.)

of these clades lack the retraction mechanisms typical of later members but are characterized by numerous derived characters of the vertebrae and skull (Gaffney and Meylan 1988). Some cryptodires, such as sea turtles (Cheloniidae and Dermochelyidae) and snapping turtles (Chelydridae), have lost the ability to retract their neck completely.

Recent molecular phylogenetic analyses of turtles have largely supported, or at least not strongly disagreed with, the phylogeny in Figure 4.76 (Fujita et al. 2004; Krenz et al. 2005; Barley et al. 2010; Thomson and Shaffer 2009; Lourenço et al. 2012; Joyce et al. 2013; Crawford et al. 2015). Many studies have examined the phylogenetic history of both fossil and extant turtle groups using morphological data; particularly relevant papers include Gaffney (1975), Gaffney and Meylan (1988), Shaffer et al. (1997), Thomson et al. (2008), and Brinkman et al. (2009).

Figure 4.77 Phylogenetic relationships of Testudines based on DNA data.

Phylogenies based on molecular and morphological characters disagree in some respects, especially with the placement of Trionychidae (softshells) and Chelvdridae (snappers). Morphological data place trionychids in a clade with Kinosternidae (musk turtles) and Dermatemydidae (Central American river turtle), and Chelydridae + Platysternidae (big-headed turtles) as the sister lineage to all other cryptodires. Molecular data place Platysternidae as the sister lineage to Emydidae (pond turtles) and, curiously, exactly swap the placement of Chelydridae and Trionychidae, with the former placed in the Kinosternidae + Dermatemydidae clade and the latter being the sister lineage to all cryptodires (Figure 4.77).

Classification, distribution, and conservation The 14 extant turtle families contain approximately 341 species. They are cosmopolitan in terrestrial, freshwater, and marine habitats except at extremely high latitudes and elevations. Regions of exceptionally high diversity are the southeastern United States (primarily Emydidae) and Southeast Asia (primarily Geoemydidae). The IUCN lists 75 species (>33%) as Critically Endangered or Endangered and 7 species as extinct in the wild.

Systematics references See van Dijk et al. (2011) for systematic summaries of the world's turtle species.

PLEURODIRA

Pleurodires typically have a very long neck that they retract sideways, and thus they are sometimes called snake-necked or side-necked turtles. They are distinguished from cryptodires by their mode of neck retraction and other osteological characters (Gaffney et al. 1991). Extant pleurodires have a strictly Gondwanan distribution, being found in the Australo-Papuan region, Madagascar, and South America.

Chelidae • Austro-American Side-Necked Turtles

Chelids are aquatic turtles that range in size from about 15 cm in carapace length (*Pseudemydura umbrina*) to nearly 50 cm (*Chelodina expansa*). Most species inhabit swamps or slow-moving fresh water, although *Chelodina siebenrocki* (**Figure 4.78A**) also occurs in brackish water. Chelids are characterized by unusually extensive emargination of the cheekbones, so that only a parietal-squamosal bar remains.

The South American matamata (*Chelus fimbriatus*) is one of the strangest-looking turtles. Its shell is broad and



flat, with three keels produced by the strongly protuberant costal and vertebral plates. The shell is often camouflaged by a thick coating of algae. Like *Chelodina* and *Hydromedusa*, *Chelus* has a very long neck, and the skin of the head and neck has many cutaneous flaps that may serve a tactile function or be sensitive to water currents. The snout has a fleshy proboscis. The mandibles are reduced to slender bony struts and fail to meet at the midline. *Chelus* uses suction feeding to capture fish and aquatic invertebrates (Formanowicz et al. 1989.).

The Australian chelid *Chelodina rugosa* has an unusual reproductive strategy (Kennett et al. 1993). This turtle inhabits a region with sharply defined wet and dry seasons. Nests are constructed under mud in shallows of seasonally flooded waterholes. Embryonic development is arrested while the eggs are in the oviducts, and after the eggs are deposited, development does not resume until the dry season when the substrate dries and the eggs are exposed to air. Emergence of hatchlings coincides with flooding in the following wet season. Both the eggs and individuals of this species have diverse physiological mechanisms to survive in a highly seasonal environment (Kennett 1999).

Classification, distribution, and conservation 16 genera, 56 species. Representative genera include *Acanthochelys, Chelodina, Chelus, Elseya, Emydura, Mesoclemmys, Phrynops,*



and *Platemys*. Chelids inhabit South America, Australia, and New Guinea (Figure 4.78B). The IUCN lists 7 species as Critically Endangered or Endangered and 6 species as Vulnerable.

Systematics references Gaffney (1977), Seddon et al. (1997), Georges et al. (1998), Le et al. (2013), Todd et al. (2014).

Pelomedusidae • African Mud Turtles

Pelomedusids inhabit lakes, rivers, swamps, and marshes. Pelusios inhabit permanent waters of forests or savannas, whereas Pelomedusa subrufa (Figure 4.79A) inhabits temporary waters of African savannas and survives dry seasons by burying into mud and estivating. Pelomedusids live in slow-moving water and are bottom-walkers (similar to North American kinosternids) rather than strong swimmers. The smallest species, the African dwarf mud turtle (Pelusios nanus), attains a carapace length of 12 cm, and the largest pelomedusid can reach over 50 cm carapace length (Pelusios sinuatus). Pelusios are mostly carnivorous, but Pelomedusa subrufa is omnivorus. The hinged plastron of Pelusios allows the turtles to close the anterior part of the shell. Pelomedusa subrufa has a large distribution across sub-Saharan Africa, the western Arabian Peninsula, and Madagascar. Genetic evidence suggests it may include multiple species and that Madagascan populations are the result of human introduction within the past 2,000 years (Vargas-Ramírez 2010; Wong et al. 2010).

Classification, distribution, and conservation 2 genera (*Pelomedusa, Pelusios*), 27 species. They inhabit Africa, Madagascar, and the Seychelles Islands (**Figure 4.79C**). The IUCN lists 1 species (*Pelusios broadleyi*) as Vulnerable.

Systematics references Georges et al. (1998), Vargas-Ramírez et al. (2010), Fritz et al. (2011).

Podocnemidae Madagascan and South American River Turtles

Extant podocnemids inhabit lakes and rivers and are active swimmers with a flat shell, but some fossil podocnemids were marine. The largest podocnemid (and also the largest extant pleurodire) is *Podocnemis expansa* of the Amazon and Orinoco river systems of South America. Females reach nearly 90 cm in carapace length (Pritchard and Trebbau 1984). However, the podocnemid *Stupendemys* from the Late Tertiary (<5 mya) of Venezuela reached at least 2.3 m (A) Pelomedusidae



(B) Podocnemidae





Figure 4.79 Pelomedusidae and Podocnemidae. (A) African helmeted turtle, Pelomedusa subrufa. (B) Madagascan big-headed turtle, Erymnochelys madagascariensis. (C) Distribution. These two species' ranges overlap (green) in western Madagascar. (Photographs: A © blickwinkel/Alamy; B © Ryan M. Bolton/Shutterstock.)

P. unifilis, have been harvested for food for more than a century, as first reported by the Amazon explorer and naturalist Henry Walter Bates (1876). Management of these two species is of concern in several countries because of overexploitation.

in carapace length and is possibly the largest turtle ever to have lived (Wood 1976).

Podocnemids are mainly herbivores. *Podocnemis expansa* forages in rivers and flooded forests, and its diet is principally the fruits and flowers of forest trees that fall into the water (Soini 1984). The nesting behavior of *P. expansa* is similar in many ways to that of sea turtles. Females nest en masse on sandy beaches of islands within the rivers they inhabit. Nests are constructed at night and consist of a body pit, within which the nest hole is dug and up to 100 eggs are deposited. Populations of *P. expansa* in the Amazon basin are highly differentiated genetically. Even within short segments of major rivers, population subdivision occurs, which may indicate natal philopatry similar to that of sea turtles (Valenzuela 2001).

All but one podocnemid species are South American. The critically endangered *Erymnochelys madagascariensis* (**Figure 4.79B**) is endemic to slow-moving rivers and lakes in western Madagascar.

Classification, distribution, and conservation 3 genera (*Erymnochelys, Podocnemis, Peltocephalus*), 8 species. They inhabit northern South America and Madagascar (**Figure 4.79C**). The IUCN lists 2 species as Critically Endangered or Endangered and 4 species as Vulnerable. The eggs of several species of *Podocnemis*, particularly *P. expansa* and **Systematics references** Williams (1954), Vargas-Ramírez et al. (2008), Gaffney et al. (2011).

CRYPTODIRA

Cryptodires represent the majority of turtle diversity. They are characterized by the derived mode of neck retraction, being able to fully retract their neck and head into the protection of the carapace (see Figure 4.76B) and numerous other osteological characters (Gaffney 1975, 1979, 1990).

Trionychidae • Softshell Turtles

Trionychids have a flattened body and reduced bony portions of the shell. The carapace lacks the peripheral series of bones (except in *Lissemys*, which has them only posteriorly), and the costal bones that form the major portion of the carapace are reduced distally in most species. The bones of the plastron are not fused at the midline. The bony plates of the shell are covered with leathery skin that has no keratinous scutes and is soft to the touch. The snout bears a fleshy proboscis, and the jaws are covered with fleshy lips rather than a keratinous beak. Trionychids have a long neck, and their limbs are extensively webbed (**Figure 4.80A**). Species of Cyclanorbinae have cutaneous femoral flaps on the plastron that cover the hindlimbs when they are withdrawn into the shell. Sizes range from relatively small (25 cm carapace length for *Lissemys punctata* and *Pelodiscus sinensis*) to 1.1 m and 140 kg for the critically endangered *Rafetus swinhoei*, the largest freshwater turtle in the world. Trionychids are sexually dimorphic, with females being larger than males.

Trionychids are fully aquatic and are strong swimmers, yet they spend a majority of their time buried in substrate. They are carnivorous and primarily ambush predators. Trionychids can remain submerged for extended periods of time and can exchange gases via the skin, cloaca, and by ventilating their highly vascularized buccopharyngeal cavity with water (Dunson 1960; Wang et al. 1989). They can also extend their long neck to project the snout above the water surface to breathe.

Classification, distribution, and conservation 13 genera, 31 species. 2 subfamilies: Cyclanorbinae (*Cyclanorbis, Cycloderma, Lissemys*) in Africa, the Indian subcontinent, and Burma, and Trionychinae (representative genera *Apalone, Cyclanorbinae, Pelodiscus, Rafetus, Trionyx*) in North Amer-

(A)



ica, Africa, the Middle East, Southeast Asia, and islands of the Sunda Shelf (**Figure 4.80B**). The IUCN lists 7 species as Critically Endangered or Endangered, primarily due to harvesting for human consumption. The Yangtze giant softshell turtle (*Rafetus swinhoei*) is on the brink of extinction with only 5 known individuals remaining in captivity or the wild.

Systematics references Meylan (1987), Weisrock and Janzen (2000), Engstrom et al. (2004).

Carettochelyidae • Pig-Nosed Turtle

Carettochelyidae contains a single species, *Carettochelys insculpta* (Figure 4.81A). It resembles Trionychidae but retains a bony carapace and plastron. Large individuals reach about 70 cm in carapace length. The species inhabits fresh waters of rivers, waterholes, and lagoons and also enters brackish estuaries. *Carettochelys insculpta* is primarily herbivorous and eats aquatic plants, algae, flowers, and fruits that drop into the water; it also eats aquatic crustaceans and insects. Females lay two clutches of approximately 10 eggs about 40 days apart every other year (Doody et al. 2003). Eggs are laid at night on high sandbanks during the dry season (Georges and Kennett 1989). In Australia, fully developed embryos become dormant within the eggs until rising river waters flood the nests. Sexual maturity takes 14–16 years for males and 20–22 years for females.

The bony carapace of *C. insculpta* is covered with soft skin like that of trionychids. A fleshy proboscis at the tip of the snout is a derived character shared with trionychids.

Figure 4.80 Trionychidae. (A) North American spiny softshell turtle, *Apalone spinifera*. (B) Distribution. (Photograph courtesy of Wayne Van Devender.)



(A)





Figure 4.81 Carettochelyidae. Pig-nosed turtle, *Carettochelys insculpta*. (B) Distribution. (Photograph © Universal Images Group Limited/Alamy.)

As in sea turtles, the limbs are elongate paddles, and they are clawed.

Classification, distribution, and conservation 1 species, *Carettochelys insculpta*. It inhabits southern New Guinea and extreme northern Australia (Figure 4.81B). The IUCN lists it as Vulnerable.

Systematics references Engstrom et al. (2004), Li et al. (2013).

Platysternidae • Big-Headed Turtle

The single platysternid species (*Platysternon megacephalum*; **Figure 4.82A**) reaches about 18 cm in carapace length and has a tail nearly the length of the carapace. It has a large head, flattened carapace, and well-developed plastron and inhabits cool montane rocky streams. This turtle is apparently a nocturnal carnivore and seldom basks, although it may forage short distances from water. It is a superb climber in vegetation. One or 2 eggs are laid per clutch.

Classification, distribution, and conservation 1 species, *Platysternon megacephalum*. It inhabits southeastern China





Figure 4.82 Platysternidae. (A) Chinese big-headed turtle, *Platysternon megacephalum*. (B) Distribution. (Photograph © Chris Johnson/Alamy.)

to Burma and Thailand (Figure 4.82B). The IUCN lists it as Endangered.

Systematics references Ernst and Laemmerzahl (2002), Parham et al. (2006).

Emydidae • Pond and Box Turtles

Most emydids are freshwater or semiaquatic turtles. However, *Malaclemys terrapin* inhabits brackish marshes and coastal marine habitats. *Terrapene* species are terrestrial except for the aquatic box turtle (*T. coahuila*). Sizes range from relatively small, such as *Clemmys guttata* and *Glyptemys muhlenbergi* (12 cm in carapace length), to the relatively large *Trachemys scripta* (up to 60 cm in carapace length). Most emydids are omnivorous as adults, but *Emydoidea* and *Deirochelys* are primarily carnivorous. The plastrons of *Emys, Emydoidea*, and *Terrapene* are hinged, and *Terrapene* can completely enclose itself in its shell when disturbed. All other emydids have solid plastrons. Because of their relative abundance and ease of study, several emydids have been the subjects of long-term ecological studies (e.g., Dodd 2001; Daszak et al. 2005). Trachemys scripta, the red-eared slider turtle, is a notoriously invasive species that has been introduced worldwide due to its popularity in the pet trade and human consumption (see Chapter 17).

Classification, distribution, and conservation 12 genera, 52 species. 2 subfamilies: Emydinae (Actinemys, Clemmys, Emydoidea, Emys, Glyptemys, Terrapene) (Figure 4.83A) and Deirochelyinae (Chrysemys, Deirochelys, Graptemys, Malaclemys, Pseudemys, Trachemys) (Figure 4.83B). All genera are restricted to North America (to northern Mexico) except Trachemys (North, Central, and South America and the West Indies) and Emys (Europe, western Asia, and northwest Africa) (Figure 4.83C). The IUCN lists 11 species as Endangered or Critically Endangered and 11 species as Vulnerable.

Systematics references Feldman and Parham (2002), Spinks and Shafer (2009), Spinks et al. (2009), Wiens et al. (2010d), Fritz et al. (2011).

Geoemydidae

Formerly known as Bataguridae, geoemydids are ecologically similar to emydids. Most species are freshwater aquatic to semiaquatic, but some occur in brackish water-Callagur borneoensis even nests on sea beaches with nesting sea turtles. Pyxidea mouhotii and two species of Heosemys are terrestrial, and Heosemys silvatica uses burrows in the ground as refuges. Many species are herbivorous or omnivorous, but Malayemys subtrijuga eats predominantly snails, and species of Mauremys are highly carnivorous. Hardella thurjii is notable because females lay their eggs submerged in water rather than in a terrestrial nest.

Sizes of geoemydids range from small (carapace length 12-14 cm in several species of Cuora and in Heosemys silvatica) to relatively large (carapace length 50-60 cm in Hieremys, Kachuga, Callagur, and Orlitia). Callagur borneoensis and Orlitia borneensis attain 75-80 cm in carapace length.

(A) Emydinae



(B) Deirochelvinae

(A) European pond turtle, Emys orbicularis (Emydinae). (B) Red-eared slider, Trachemys scripta (Deirochelyinae). (C) Distribution. (Photographs: A © Dennis Jacobsen/Shutterstock; B courtesy



Classification, distribution, and conservation 19 genera, 69 species. A single New World genus, *Rhinoclemmys* (**Figure 4.84A**) occurs from northwestern Mexico to northern South America. The remaining genera (representatives *Batagur, Cuora, Cyclemys, Geoclemys, Hardella, Mauremys, Sacalia*) inhabit northwest Africa, Europe to western Asia and the Middle East, and across southern Asia to China, Japan, the Philippines, and islands of the Sunda Shelf (**Figure 4.84B**). The greatest diversity is in southern Asia. Many species are imminently threatened with extinction because of overharvesting for food, traditional medicines, and the pet trade.

Systematics references Spinks et al. (2004), Sasaki et al. (2006), Praschag et al. (2007), Lourenço et al. (2012).

Testudinidae • Tortoises

Testudinidae are terrestrial and usually have a high, domed shell (**Figure 4.85A**). The limbs are stout, the feet are unwebbed, and the digits contain no more than two phalanges. The head and limbs can be fully withdrawn into the shell, with the heavily scaled limbs forming an effective

protective barrier to the outside. Plastrons are hinged in *Testudo* and *Pyxis*. Unique among extant turtles, tortoises in the genus *Kinixys* have a hinged carapace that can be lowered over the hindquarters. Unlike other tortoises, *Malacochersus* has a flattened shell with a reduced bony component. Terrestriality has evolved repeatedly and independently many times in the history of turtles; testudinids are merely a recent and diverse example. (Box turtles of the genus *Terrapene* [Emydidae] are another recent example of the evolution of terrestriality by turtles, and box turtles have converged on testudinids in some aspects of limb and shell structure.) Extant testudinids range in size from about 10 cm to 1.3 m in carapace length.

The shells of some testudinids may provide protection from predators because shell height exceeds the gape of many potential predators. For example, the shells of many large individuals of the South American yellow-footed tortoise (*Geochelone denticulata*) bear tooth marks as evidence of unsuccessful attacks by jaguars, which are apparently incapable of extracting a tortoise from either end of the shell. Jaguars can break open the top of the carapace of smaller individuals (Emmons 1989) and can crush the relatively flat shells of much larger *Podocnemis* (Podocnemidae). These observations lend credence to the hypothesis that the domed shell of tortoises can provide effective defense against some predators.

Gigantism has evolved independently in many oceanic island populations of testudinids. The most notable examples are the Galápagos tortoise (*Chelonoidis nigra*) and Aldabra giant tortoise (*Aldabrachelys gigantea*; **Figure 4.85B**) from the Aldabra atoll in the Seychelles, both of which can weigh up to 250 kg. Many such island populations became extinct with the arrival of Europeans. Extant continental species are smaller than island species, but some fossil giant tortoises are known from continental areas (Arnold 1979).

Most testudinids are herbivores or omnivores. They inhabit environments ranging from extremely arid deserts to wet rainforests. Species of *Gopherus* construct deep burrows for refuge using spadelike front feet. Most tortoises have

Figure 4.85 Testudinidae. (A) Hermann's tortoise, *Testudo hermanni.* (B) Aldabra giant tortoise, *Aldabrachelys gigantea*, Aldabra atoll, Seychelles. (C) Distribution. (Photographs: A © xpixel/Shutterstock; B © Craig Dingle/istock.)

(A)

relatively small clutch sizes (in many species only 1–2 eggs). The largest clutch sizes are reported for the Asian testudinid *Manouria emys*, which can lay up to 50 eggs. The eggs of testudinids may be laid in holes dug in the ground, as in many other turtles, but *M. emys* constructs a large mound nest of decaying vegetation and may remain with the nest for several days. *Geochelone denticulata* often does not construct a nest at all but deposits its eggs either singly or in small clusters in the leaf litter of the forest floor.

Classification, distribution, and conservation 15 genera, 57 species. Representative genera include *Aldabrachelys, Astrochelys, Chelonoidis, Geochelone, Gopherus, Testudo,* and *Stigmochelys.* Testudinids inhabit southern North America, most of South America, southern Eurasia and Africa, Madagascar, and oceanic islands, including the Galápagos and Aldabra Islands (**Figure 4.85C**). The IUCN lists at least 10 species as Endangered or Critically Endangered and many





(B)





Figure 4.86 Dermatemydidae.

(A) Central American river turtle, *Dermatemys mawii*. (B) Distribution. (Photograph courtesy of Wayne Van Devender.)

more as Vulnerable. Eight species have become extinct in the wild since 1500, primarily due to hunting.

Systematics references Le et al. (2006), Parham et al. (2006), Lourenço et al. (2012).

Dermatemydidae • Central American River Turtle

The single dermatemydid species, *Dermatemys mawii* (Figure 4.86A), reaches a carapace length of about 65 cm and is totally aquatic. It is herbivourous and inhabits large rivers, lakes, and temporary pools where there is aquatic vegetation. It also enters brackish water. Surfacing only rarely, *D. mawii* apparently uses the buccopharyngeal lining for gas exchange, as in the Trionychidae. Captive individuals continually take water in through the mouth and expel it from the nostrils (Ernst and Barbour 1989).

Classification, distribution, and conservation 1 species, *Dermatemys mawii*. It occurs from southern Mexico to northern Honduras (Figure 4.86B). The IUCN lists it as Critically Endangered, due to harvesting of meat and eggs for human consumption.

Systematics references González-Porter et al. (2011).

Kinosternidae • American Mud and Musk Turtles

This family includes the smallest turtles in North America (11-15 cm carapace length), commonly called mud and musk turtles (Figure 4.87A). Although primarily semiaquatic, they inhabit a wide variety of habitats, including deserts, forests, and grasslands. The tropical species of Kinosternon and Staurotypus are larger, ranging from 25 cm to nearly 40 cm in carapace length. The shells are elongate. The plastron may be very reduced, and it is singly or doubly hinged in some species (e.g., Kinosternon subrubrum and K. minor). These turtles release a foul-smelling musk from glands in the cloaca, hence the common name stinkpot for Sternotherus odorata. Like chelvdrids, kinosternids are mostly bottom-walkers rather than strong swimmers and live in slow-moving water, often with much vegetation. Sternotherus minor can respire via buccopharyngeal respiration like Carretochelvidae, Dermatemydidae, and Trionychidae (Belkin 1968). Clutch sizes range from 2 to 10 eggs. All species are carnivorous.

Classification, distribution, and conservation 5 genera, 25 species. 2 subfamilies: Kinosterninae (*Cryptochelys, Kinosternon, Sternotherus*) and Staurotypinae (*Claudius,*



Figure 4.87 Kinosternidae.

(A) Central American white-lipped mud turtle, *Kinosternon leucostomum*. (B) Distribution. (Photograph courtesy of Todd W. Pierson.) *Staurotypus*). They inhabit eastern North America from southern Canada south through Mexico, Central America, and South America (**Figure 4.87B**). The IUCN lists 1 species (*Sternotherus depressus*) as Critically Endangered and 4 species as Near Threatened or Vulnerable.

Systematics references Iverson (1991), Iverson et al. (2013), Spinks et al. (2014).

Chelydridae • Snapping Turtles

Chelydrids are large-headed freshwater turtles with powerful jaws. Their plastron is reduced, which prevents the head, neck, and limbs from being retracted fully within the shell. In ventral view, this gives snapping turtles the appearance of being stuffed into an undersize swimsuit. These turtles are not strong swimmers, and they move mainly by walking on the bottom of water bodies. *Chelydra* (Figure 4.88A) inhabit a wide variety of freshwater and brackish habitats, usually with abundant aquatic vegetation. They are omnivorous, seemingly eating almost anything they can swallow. Eggs are laid in nests that are often constructed some



Figure 4.88 Chelydridae. (A) North American snapping turtle, *Chelydra serpentina*. (B) Distribution. (Photograph courtesy of Wayne Van Devender.)

distance from water. *Chelydra* exhibit an unusual defensive posture (shared with the chelid *Chelus*) in which the head and anterior body are lowered while the hindlimbs are extended maximally, thus exposing the dorsal surface of the shell toward a potential threat (Dodd and Brodie 1975). Although typically not aggressive, *Chelydra* can deliver a powerful bite if handled.

The alligator snapping turtle (*Macrochelys temminckii*) is almost completely aquatic and is one of the world's heaviest freshwater turtle species, growing to nearly 70 cm in carapace length and weighing more than 80 kg. It inhabits deep-water rivers, lakes, and swamps where there is abundant vegetation. A bifurcate fleshy projection on the tongue is used to lure fish into the open mouth as the turtle rests on the bottom. However, alligator snappers also forage actively, and their diet includes frogs, snakes, molluscs, crustaceans, aquatic plants, and other turtles.

Classification, distribution, and conservation 2 genera (*Chelydra, Macrochelys*), 6 species. They inhabit eastern North America from southern Canada south through Central America to western Ecuador (**Figure 4.88B**). The IUCN lists 1 species (*Macrochelys temminckii*) as Vulnerable.

Systematics references Shaffer et al. (2008), Chandler and Janzen (2009), Echelle et al. (2010).

Cheloniidae • Sea Turtles

Cheloniidae and Dermochelyidae, collectively called sea turtles, are sister clades, and many aspects of their biology are similar. Their strongly developed forelimbs are modified into elongate, fully webbed paddles. Sea turtles are totally marine except that females come ashore to lay eggs. The limbs cannot support the body off the substrate, and nesting females use their forelimbs to pull themselves along, sliding on their plastron. Cheloniid carapace length ranges in size from about 70 cm (*Lepidochelys*) to about 1.5 m (*Chelonia mydas* and *Caretta caretta*). Virtually all cheloniids feed on plants or animals that are on or attached to the substrate. *Chelonia mydas* is herbivorous, while other cheloniids are carnivores or omnivores. *Eretmochelys* is largely a spongivore, and *Caretta* consumes primarily molluscs and crustaceans.

Outside the breeding season, many sea turtles move widely throughout temperate and tropical seas, but for all species egg laying occurs only on tropical or (for *Caretta*) on warm temperate beaches. All sea turtles undergo extensive migrations, navigating by using cues from Earth's electromagnetic field (see Figure 12.22). They are also extremely faithful to particular breeding areas, which are probably their natal areas (Bowen et al. 1992, 1993). Most species nest at night, although *Lepidochelys* nests during the day.

Female sea turtles dig nest holes in beach sand and deposit 100 or more eggs, covering them with sand. After 2–3 months, the eggs hatch and the neonates scramble to the ocean, suffering massive predation along the way from



(B) Dermochelvidae



Figure 4.89 Cheloniidae and Dermochelyidae

(A) Hawksbill turtle, *Eretmochelys imbricata* (Cheloniidae), in Red Sea. (B) A female leatherback turtle, *Dermochelys coriacea* (Dermochelyidae) returning to sea after laying eggs on the beach. (C) Distribution. (Photographs: A © orlandin/Shutterstock; B © FLPA/Alamy.)

birds, crabs, and other predators. Individual females do not reproduce every year, although several large clutches of eggs are usually laid within one breeding season. **Classification, distribution, and conservation** 5 genera (*Caretta, Chelonia, Eretmochelys, Lepidochelys, Natator*), 6 species. They inhabit worldwide temperate and tropical oceans (**Figure 4.89C**). The IUCN lists all species of cheloniids as Endangered or Vulnerable, primarily due to human consumption (especially of the eggs) and commercial fishing bycatch.

Systematics references Bowen and Karl (2007), Naro-Maciel et al. (2008).

Dermochelyidae • Leatherback Sea Turtle

Dermochelys coriacea (Figure 4.89B) is by far the largest extant turtle, with a carapace length up to 2–2.5 m and a mass of 700 kg. It is unique among extant turtles in that the carapace is composed of thousands of polygonal osteoderms embedded in the leathery skin, giving rise to the species' common name.

Rows of enlarged osteoderms form seven longitudinal keels on the carapace. Between the keels the carapace is only 3–4 mm thick, the thinnest of all turtles. The plastron consists only of a thin outer ring of bone. Claws are absent from the tips of the flippers, unlike in the Cheloniidae. The skeleton of *D. coriacea* is composed primarily of cartilage that does not ossify as it does in all other turtles. Molecular genetic studies suggest that extant *D. coriacea* populations radiated within the last 1 million years. Populations from different nesting areas are genetically distinct, supporting the hypothesis that individuals return to their natal beaches to mate and lay eggs (Dutton et al. 1999).

Dermochelys coriacea and Cheloniidae share many characters but differ behaviorly in that *D. coriacea* is totally pelagic and feeds primarily in the water column on jellyfish. Its jaws are weak and incapable of crushing hard-bodied prey. The large body size of *D. coriacea* allows it to maintain its body temperature well above ambient sea temperature, which may explain in part its extension farther north into colder oceans than any other sea turtle.

Classification, distribution, and conservation 1 species, *Dermochelys coriacea.* It inhabits worldwide temperate and tropical oceans (**Figure 4.89C**). The IUCN lists it as Vulnerable, primarily due to human consumption and anthropogenic pollution. The resemblance of floating plastic bags to jellyfish creates a hazard for *Dermochelys*, which ingests the bags, often with fatal results (Mrosovsky 1981; Mrosovsky et al. 2009).

Systematics references Wood et al. (1996), Dutton et al. (1999), Duchene et al. (2012).

SUMMARY

■ Extant reptiles, including Rhynchocephalia (tuatara), Squamata (lizards and snakes), Crocodylia (alligators, crocodiles, and gharials), Testudines (turtles), and Aves (birds), include more than 20,000 extant species and countless fossil forms. About half of these species are birds.

Reptilian skin is thicker than amphibian skin, contains few glands, and is toughened by the presence of the protein keratin. Scales are thickened layers of epidermal and dermal tissues, and are supplied with mechanoreceptors in most squamates and crocodylians. Lepidosaurs (Squamata and Rhyncocephalia) are unique in shedding their skin in large pieces simultaneously.

Reptiles rely to varying degrees on the senses common to most tetrapods:

- Reptiles have a single sound-transmitting bone in the inner ear—the columella—rather than the three bones that form the ossicular chain of mammals. Despite the absence of a tympanum, snakes can detect low-frequency sounds (50–1,000 Hz). The outer end of the sound-transmitting bone, the columella, is attached by a ligament to the quadrate bone of the lower jaw and transmits vibrations in the substrate, water, or air to the inner ear.
- Reptile chemosensation (smell and taste) is via the nose, taste buds, and vomeronasal organ and is employed during foraging, orientation, and courtship and other social interactions.
- Scleral ossicles (thin plates of bone) are found in the sclera of the eyes of most reptiles. The ciliary

muscles, which change the shape of the lens during focusing, originate in part on the scleral ossicles.

• The retinal cone cells of most reptiles contain droplets of lipid that channel light to the photosensitive pigments. Some of the lipids are pigmented and act as filters, allowing only some wavelengths to pass through.

The eyes of snakes differ from those of lizards in several respects, probably because snakes passed through a fossorial stage during their evolution. Distinctive features of the visual systems of snakes include the spectacle, a transparent scale that covers the eye; the absence of cilliary muscles and sclerial ossicles; and the presence of colorless microdroplets of lipids in the cone cells and of an amber-colored lens that filters incoming light. Snakes rely primarily on moving the lens to focus the eye. They change the size of the pupil to regulate the amount of light reaching the photosensitive cells, but cannot change the depth of those cells in the pigmented retina.

Heat-sensitive pit organs on the face have evolved independently in some snakes in the families Boidae, Pythonidae, and Viperidae. These organs sense infrared radiation and relay a thermal image to the optic region of the brain.

Lepidosauria includes the rhynchocephalians (tuatara) and squamates (lizards and snakes).

Lepidosaurs are characterized by a transverse cloacal slit, regular cycles of skin shedding, and many skeletal features.

Rhynchocephalians arose in the Middle Triassic and were once distributed across the supercontinent Pangaea. However, they became extinct by the Late Cretaceous except for a single genus of tuatara (*Sphenodon*) living on offshore islands in New Zealand.

Rhynchocephalians superficially resemble lizards, but their skull is more robust and lacks cranial kinesis. *Sphenodon* has heterodont dentition, and its premaxillary teeth have been replaced by downgrowths of bone.

Squamates comprise the vast majority of non-avian reptile diversity, with over 9,600 described species. They are distributed worldwide and are morphologically, behaviorally, and ecologically diverse.

Although snakes are derived from within lizard lineages, the two groups are so distinct in their biology and natural history that they are usually treated separately.

Squamates have paired copulatory organs called hemipenes that are often ornamented with spines and ridges. The male inserts one of the two hemipenes into the female to transfer sperm.

Squamates exhibit two distinct types of dentition. In the acrodont pattern, teeth are permanently attached on the crest of the tooth-bearing bones. In the pleurodont pattern, teeth only have a bony attachment to the lingual (inner) side of the tooth-bearing bone and are replaced continually. Snakes have a modified type of pleurodonty in which the base of each tooth sits in a rudimentary socket.

Many squamates lose their tail (caudal autotomy) as a defense mechanism, and this breakage occurs via two mechanisms. Species with intravertebral autotomy have specialized fracture planes in the vertebrae that allow for easy separation. Autotomy is under voluntary control for these species, and the tail regrows. In species with intervertebral tail breakage (pseudoautotomy), the tail breaks between vertebrae. This event is not under voluntary control and the tail does not regenerate.

Reproduction and sex determination in squamates are complex. Approximately 20% of squamate species are viviparous (live-bearing), some with a relatively elaborate placenta and significant mother-to-embryo transfer of nutrients. Parthenogenesis, the ability to produce offspring without mating, occurs in several lizard families and in a few species of snakes.

A striking morphological trend in squamates is the repeated independent evolution of limb reduction. A completely limbless, snakelike body form has evolved at least 25 separate times. Many limbed species have reduced digits.

The phylogenetic relationships of squamates based on morphological versus molecular data are drastically different, with molecular data becoming increasingly accepted as the basis for squamate evolutionary relationships.

Extant lizard lineages account for more than 60% of all known squamate species.

Approximately 25% of lizard species are geckos (Gekkota). Geckos typically are recognizable by the presence of wide adhesive toe pads on their hands and feet that allow them to climb vertical surfaces. However, this trait has been secondarily lost multiple times. Most geckos are nocturnal.

Another approximately 25% of lizard species are iguanians (Iguania). Iguanians include two major clades. Acrodonta includes Agamidae and Chamelonidae, which have acrodont dentition. All other iguanians (e.g., iguanas, horned lizards, anoles) have pleurodont dentition and constitute the clade Pleurodonta.

About 25% of lizard species are skinks (Scincidae). Skinks have smooth, shiny scales underlain by osteoderms that give the body a hard exterior. Skinks may be small (35 mm SVL) to large (800 mm SVL) and range in form from the typical lizardlike body to elongate and snakelike.

The remaining 25% of lizard species are spread throughout the squamate phylogeny and include wellknown groups such as worm lizards (Amphisbaenia), the Gila monster (Helodermatidae), wall lizards (Lacertidae), monitors and goannas (Varanidae), and more obscure groups such as Dibamidae, Shinisauridae, and Xenosauridae.

Snakes have numerous morphological features that distinguish them from other squamates, including other limbless taxa.

Snakes have an extremely flexible skull, due to the loss or modification of several bones. The jaws of snakes have been modified by natural selection into remarkable extremes adapted for consuming prey ranging from ant pupae to deer (the latter usually intact).

Typical snake teeth are long, slender, and slightly curved, but have been highly modified in some lineages into hollow fangs with a venom canal (vipers, elapids, and atractaspidines).

The fossil record of snakes extends back to 167–143 mya. Five genera of snakes with hindlimbs, one of which has a hindlimb that articulates with a pelvic girdle (*Najash*), have been discovered in geological deposits dating to about 95 mya. Snakes became widespread in the Late Cretaceous, with fossils of the most diverse groups (colubroids) appearing in the Eocene and Oligocene.

There is some disagreement between morphologybased and increasingly accepted DNA-based phylogenies of snakes. The most notable difference is that morphological data support a clade composed of all species with a large gape, called Macrostomata. No phylogenetic analysis of DNA supports this clade; instead, molecular data support the hypothesis that the macrostomate condition evolved multiple times or was secondarily lost in several lineages.

Blindsnakes (Scolecophidia) are small (<100 cm total length) snakes that specialize on eating ant or termite pupae, larvae, and eggs. Leptotyphlopids and typhlopids feed by raking pupae and larvae into their mouths using their dentary (leptotyphlopids) or maxilla (typhlopids) bones like a pair of swinging doors.

All other snakes belong in the Alethinophidia, which includes well-known groups such as boas, colubrids, pythons, vipers, and elapids, as well as lesser-known groups such as Bolyeriidae, Pareatidae, and Uropeltidae.

Most colubroid snakes (colubrids, elapids, vipers, etc.) have glands that produce venom. Snake venom is a mixture of proteins with numerous functions, and venoms of different species differ in the presence or abundance of various proteins.

Crocodylia includes alligators, crocodiles, and gharials. They are highly aquatic, heavily armored predators.

All species are aquatic to varying degrees and have numerous adaptations to their aquatic lifestyle. The nostrils are dorsally located at the tip of the snout and are closed by valves during diving. A secondary palate separates the buccal and respiratory passages, which allows crocodylians to inhale while holding prey in the mouth.

All crocodylians are oviparous and fertilize their eggs via internal fertilization. They lay their eggs either in mound nests constructed from vegetation or directly in soil on beaches or other exposed areas. Temperaturedependent sex determination occurs in all species examined.

Unlike most turtles and squamates, crocodylians exhibit parental care. Parents guard the nest, and in some species remain with the young for weeks or months. The social behavior of crocodylians is complex and includes vocalizations in a variety of social contexts, including territorial bellowing during the breeding season and aggressive warnings to intruders. Body postures and head-slapping at the water surface are often used as dominance advertisements.

Extant Testudines (turtles) originated in the Triassic and are distributed worldwide, but with about 341 species they comprise only about 3% of all non-avian reptiles.

Turtles are the only vertebrates with a bony shell (some turtles have secondarily evolved a leathery shell). The shell is composed of a dorsal carapace and ventral plastron. Developmental evidence suggests that the shell develops from the lateral expansion of the ribs during embryonic development.

Turtles are also unique in that their pectoral and pelvic girdles are essentially within the rib cage.

Most turtles can retract their head into their shell, but this mechanism differs between the two major clades. Pleurodires retract their neck by curving it along the lateral side of the body, but within a protected space formed by overhang parts of the carapace and plastron. Cryptodires retract their neck linearly, straight back into the shell.

Turtles have an anaspid skull (i.e., no temporal fenestrae), but some species have a highly emarginated skull that makes space for jaw muscles similar to temporal fenestrae. Turtles have a structure called the trochlea that redirects jaw muscle fibers from moving laterally to dorsoventrally, thereby providing a strong bite force.

All turtles are oviparous and lay eggs in a nest dug in the ground or on the surface with no nest. Fertilization is internal via the male penis which is an outgrowth of the cloacal wall. Most turtles have temperature-dependent sex determination.

The molecular phylogeny of turtles has been relatively stable across studies.

Go to the *Herpetology* Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

5 The Biogeography of Amphibians and Reptiles

In the preceding chapters we examined the phylogenetic relationships and distributions of amphibians and reptiles. In this chapter we explore the geography of their evolution—their **biogeography**. What are the common patterns of species distributions, and what evolutionary processes have produced them? We do not cover the entire scope of biogeographical studies of amphibians and reptiles, but instead provide an overview of major patterns and processes at large and small scales, both temporal and geographic.

Biogeography combines information about natural history, phylogeny, geology, and climate to interpret the past and present distributions of taxa. It describes patterns of occurrence and to understand the forces that create and maintain them. For example, how did continental movements during the Mesozoic and Cenozoic affect the patterns of biodiversity we see today? What proportion of Australian amphibians and reptiles is derived from Gondwanan and Laurasian lineages? What were the effects of Pleistocene glaciation and associated sea level and climate changes on species distributions, and how will species respond to future climate change?

5.1 Biogeographic Analysis

Three kinds of data contribute to biogeographic analysis:

- Information about the organisms themselves: distributions, species diversity, habitat preferences, and dispersal abilities.
- 2. Information about Earth's history: past continental movements and other geologic events, such as the origins of islands, rivers, and mountain ranges, as well as changes in climate and sea level.
- Information about the phylogenies of the organisms and the estimated times of their divergence in the past.

Having established a correspondence between a phylogeny of organisms and their distributions, we can examine the events that produced this correspondence. Phylogenetic relationships tell us about the branching pattern and relative timing of speciation events in a clade; these patterns can sometimes be explained by specific events in Earth's history. In recent decades, molecular phylogenetics and the development of sophisticated molecular clock methods have allowed us to estimate when lineages in a phylogeny diverged. These estimates can then be compared with geological or climatic conditions in Earth's past to infer how those conditions affected species distributions.

Fossil data are invaluable for the study of biogeography because they establish the location of the ancestors of modern lineages. Fossils of many lineages occur on one continent while all extant species of that same lineage now live on another continent. For example, fossil evidence shows that varanid lizards, now found only in Africa and Australasia, once occurred in North America (Sullivan and Lucas 1988). Similarly, gharials now occur exclusively in South and Southeast Asia, but fossil gharials have been discovered in South America and Puerto Rico (Brochu and Rincón 2004; Vélez-Juarbe et al. 2007).

Two mechanisms—dispersal and vicariance—are responsible for the geographic distributions of organisms:

- 1. Organisms move via **dispersal** to their present locations, by walking, swimming, flying, drifting, or being transported by another organism (often humans).
- 2. Vicariance occurs when a new barrier fragments what had been a continuous geographic distribution of organisms into two or more discontinuous distributions. The separation of South America from Africa in the Mesozoic is a large-scale example of vicariance, whereas a change in the course of a river is a vicariant event on a smaller scale.
Prior to the acceptance of the theory of plate tectonics 1950s, biogeographers assumed that dispersal was the dominant mechanism by which lineages became distributed worldwide. But with improved knowledge of Earth's history and the development of cladistic methods and population genetics, it is now apparent that both vicariance and dispersal play roles in shaping biogeographic patterns.

5.2 Dispersal

Amphibians and reptiles can disperse actively (by walking, hopping, slithering, or swimming) or passively (e.g., by floating on a raft of vegetation, or traveling in vehicles, ships, or airplanes, either as cargo or as stowaways).

Transoceanic dispersal

Many amphibian and reptile groups originated on one continent and dispersed over the ocean to other continents. Transoceanic dispersal of amphibians is comparatively rare, possibly because of the osmotic stress caused by submersion in seawater. Nonetheless, there are some examples. Phylogenetic evidence shows that during the fragmentation of Gondwana, ptychadenid, rhacophorid, dicroglossid, and ranid frogs dispersed from Madagascar to the Indian subcontinent before its collision with Asia (Vences et al. 2004; Bossyut et al. 2006). Moreover, hyperoliid frogs made two hops, dispersing from Africa to Madagascar, and then from Madagascar to the Seychelles Islands (Vences et al. 2003; Pyron 2014).

Reptilian dispersal is more impressive in terms of distance traveled. Amphisbaenians (Vidal et al. 2008), mabuyine skinks (Carranza and Arnold 2003; Whiting et al. 2006), crocodiles (Meredith et al. 2011), and phyllodactylid geckos (Gamble et al. 2011) dispersed from Africa to the New World via the Atlantic Ocean, and chameleons dispersed from Madagascar to the Seychelles (Townsend et al. 2009, 2011c; Tolley et al. 2013).

These reptiles almost certainly did not swim across the ocean. Rather, they probably floated on rafts of vegetation that were washed to sea during storms and carried by ocean currents. After a hurricane in 1995, a group of 15 green iguanas (*Iguana iguana*) floated on a mat of vegetation that washed ashore on the Caribbean island of Anguilla. Genetic testing determined that these iguanas originated on the island of Guadalupe, meaning they had rafted more than 300 km (Censky et al. 1998) after the storm. Over millions of years, such events must have happened countless times worldwide.

The giant tortoises found on oceanic islands provide a special case of rafting. Tortoises are terrestrial and only clumsy swimmers; however, they are good floaters because their lungs lie in the upper portion of their domed shells. Tortoises on the Seychelles go down to the shore and even walk out onto the surrounding reef to forage at low tide, and occasionally a tortoise is caught by the incoming tide (J. Gerlach pers. comm.). In December 2004, an adult Aldabra giant tortoise (*Aldabrachelys gigantea*) walked out of the surf on the shore of Tanzania after a journey of nearly 750 km from Aldabra Atoll (**Figure 5.1**). She was emaciated and dehydrated, and had barnacles on her limbs and shell, but she was alive. The size of the barnacles suggested that the tortoise had been in the sea for 6 or 7 weeks (Gerlach et al. 2006). Additional evidence of open-water crossings by tortoises is provided by a molecular analysis of interisland dispersals of Galápagos tortoises (*Chelonoidis*) (Poulakakis et al. 2012).

The saltwater crocodile (*Crocodylus porosus*) is an excellent swimmer with a satellite-recorded movement of 589 km in 25 days (see Figure 12.11) (Campbell et al. 2010). It is highly likely that the current range of this species, which extends from coastal India through the Indo-Australian Archipelago to the western islands of the South Pacific, is the result of ancestors of modern *C. porosus* swimming across open ocean.



Figure 5.1 Rafting by an Aldabra giant tortoise (Aldab*rachelys gigantea*). The tortoise that landed on the beach at Kimbiji, Tanzania, had probably drifted from Aldabra Atoll, carried initially by the South Equatorial Current and then by the north-flowing branch of the East African Coastal Current. The adult in the photograph was seen swimming in the sea off Alphonse Island in December 2005. The tortoise was swimming strongly, but with its head only a few centimeters above the water surface it probably could not see land. (After Gerlach 2006 and J. Gerlach, pers. comm; photograph by Justin Gerlach.)

Transcontinental dispersal

Ever since the breakup of the supercontinent Pangaea (from the Greek pan, "all," + Gaia, "Mother Earth"), ephemeral connections have joined some continents that were previously isolated (Figure 5.2). These land bridges allowed exchange of organisms between continents. The best studied of these is the Bering land bridge, or Beringia, which connected Eurasia and North America several times during the Cenozoic or earlier. Although this connection was stable for periods spanning millions of years, the climate and habitat of Beringia were not always hospitable to amphibians and reptiles. Biogeographic analysis of the skink genus Plestiodon using molecular clock methods estimated that this genus dispersed from eastern Asia to North America between 30 and 18 mya (Brandley et al. 2011). This interval coincided with a time when Beringia connected the two landmasses and, even more important, was warm enough to sustain a belt of forest (Wolfe 1975, 1978; Tiffney 1985; Zachos et al. 2001). Other amphibians and reptiles that dispersed across Beringia include lampropeltine rat snakes (Burbrink and Lawson 2007), anguid lizards (Macey et al. 1999), geckos (Gamble et al. 2008), and frogs of the genus Rana (Macey et al. 2006).

Figure 5.2 also shows the de Geer (~71–63 mya) and Thulean (~56 mya) land bridges that connected North America and Europe across what is modern-day Greenland (Brikiatis 2014). Because Beringia was also connected during some of this time, it is often difficult to determine whether a taxon dispersed between North America and Eurasia via the eastern or western route. However, given their present-day distribution, phylogeny, and age of the clades, it is clear that

plethodontid and salamandrid salamanders, as well as anguid, gekkotan, and perhaps dibamid lizards, took one or both routes between these landmasses (Macey et al. 1999, Vences et al. 2007; Gamble et al. 2008; Zhang et al. 2008; Townsend et al. 2011c).

Human-mediated dispersal

Humans have provided extraordinarily efficient means of dispersal for amphibians and reptiles. These movements may be deliberate, as when animals are transported for food or as pets, or accidental, as with stowaways on cargo ships or in soil around plants. Invasive species have dispersed to locations where they are now creating problems, and five species of amphibians or

Figure 5.2 Beringia and transatlantic land

bridges. At least three land bridges connected North America and Eurasia during the Tertiary, facilitating dispersal of amphibians and reptiles throughout the Holarctic. Although all three land bridges are shown here, they existed at different times. Present-day land masses are indicated by the green outline.

reptiles are included on the IUCN's list of the world's "100 Worst Invasive Species" (Lowe et al. 2000):

- Three of these species—the red-eared slider turtle (*Trachemys scripta*), American bullfrog (*Rana catesbeiana*), and cane toad (*Rhinella marina*)—were introduced intentionally and are outcompeting, eating, poisoning, and transmitting pathogens to native species.
- A fourth species, the brown tree snake (Boiga irregularis), occurs naturally in parts of Australasia and the Pacific islands and was accidentally introduced to Guam. Using phylogenetic analysis of DNA, Richmond et al. (2014) infer that Boiga was accidentally transported to Guam shortly after World War II from Manus, an island 1,899 km to the south that was one of numerous staging grounds for the movement of military cargo. Brown tree snakes have decimated most of the native birds and lizards on Guam and have begun to prey on other invasive species, such as the greenhouse frog (Eleutherodactylus planirostris) (Mathies et al. 2012).
- The Puerto Rican coquí frog (*Eleutherodactylus coqui*) was accidentally transported in plant shipments to Hawaii. Unlike most invasive species, the coquí has not had a direct biological impact, probably because Hawaii has no native amphibians (Beard and Pitt 2005; Sin et al. 2008). However, the high-pitched calls of coquís annoy humans, and on the "big island" of Hawaii, an official complaint of a coquí within 800 m lowers the value of a residential property (Kaiser and Burnett 2006).





The patterns and mechanisms of human-mediated dispersal can be inferred from faunal surveys and historical data. The gecko Hemidactylus turcicus is native to the Mediterranean region but has been introduced to all continents except Australia and Antarctica. In both its native and introduced ranges, H. turcicus is nocturnal and prefers human dwellings, especially those that are well lit and thus attract moths that the gecko feeds on. Traveling with returning military cargo, geckos are presumed to have entered the United States at Brownsville, Texas, at the end of World War II. Historical records indicate that populations of geckos had become established at fruit and vegetable markets in Houston and San Antonio by the early 1950s. By the 1970s, the geckos' range had expanded north along major highways (Figure 5.3). These data suggest that produce trucks were the mechanism of dispersal (Davis 1974); the species has since established populations throughout southeast Texas and beyond (Rödder and Lötters 2009).

Human transport of amphibians and reptiles is not limited to modern times. Genetic diversity patterns in the turtle Dermatemys mawii indicate that its present geographical distribution was shaped, in part, by human transport by Middle American cultures over the past 2,000 years (González-Porter et al. 2011). In the Pacific, Polynesians and

Figure 5.3 Human-mediated dispersal of the Mediterranean house gecko (Hemidactylus turcicus).

Soon after its probable introduction to Brownsville, Texas at the end of World War II, the range of H. turcicus expanded north to the cities of San Antonio and Houston-destinations for fruit and vegetable trucks from southern Texas. Populations became established at small towns and truck stops along major highways that connected these cities. Arrows show the different dispersal routes and the hypothetical order (1-4) in which they occurred. (After Davis 1974; photograph © blickwinkel/Alamy.)

Melanesians inadvertently introduced geckos and skinks throughout much of the region during their extensive ocean travels throughout the past 4,000 years (Case and Bolger 1991; Austin 1999).

5.3 Vicariance

Recall that vicariance is the process by which lineages are split when barriers to gene flow arise, and this isolation results in the evolution of unique fauna on both sides of the barrier over time. Vicariance due to the continental fragmentation of Pangaea shaped the earliest history of both amphibians and reptiles. Our discussion concentrates on the distributions and relationships of extant species of amphibians and reptiles without extensive consideration of fossils.

Fossils record the presence of a taxon in an area where it does not occur today, and a lack of fossils makes distinguishing between vicariance and extinction difficult. The development and use of molecular clock methods has greatly aided biogeographic reconstruction when fossils are unavailable (reviewed by Rannala and Yang 2013). Distinguishing between vicariance and dispersal hypotheses for modern biogeographic distributions is relatively straightforward if the time of divergence between two lineages can be estimated. For example, New World amphisbaenians are derived from African lineages, and molecular clock estimates show that New World amphisbaenians split from their African relatives about 40 mya, which is 60 million years later than the separation of South America from Africa (Vidal et al. 2008). Because no physical connection existed between the two continents 40 mya, the most plausible explanation for this biogeographic pattern is that the ancestor of New World amphisbaenians dispersed from Africa to the New World by traversing the Atlantic Ocean.

Pangaea and the Mesozoic origin of modern amphibians and reptiles

Terrestrial vertebrates first appeared in the Late Devonian, about 360 mya. The presence of *Triadobatrachus* and *Czat-kobatrachus* in the Early Triassic (~230 mya) marks the first occurrence of animals belonging to an extant clade (Salien-

tia) of amphibians or reptiles. This is evidence that all three modern amphibian clades were present on the single continent Pangaea (**Figure 5.4A**), a conclusion that is also supported by molecular clock analyses (Roelants and Bossuyt 2005; San Mauro et al. 2005; Pyron 2014). The Pangaean origin of modern reptiles is also supported by fossils and molecular clock analyses (e.g., Jones et al. 2013). Thus, the



movement of the continents. (A) Earth in the Late Triassic consisted of a single supercontinent, Pangaea. Members of extant amphibian and reptilian clades were present at this time. (B) By the Late Jurassic, Laurasia and Gondwana had separated, with the latter beginning to fragment into the present-day continents. (C) In the Middle Cretaceous, epicontinental seas separated eastern and western North America, Euramerica, and

single landmass, as did Antarctica and Australia. (D) At the Cretaceous-Tertiary (K/T) boundary, the Gondwanan continents had largely separated and the Indian Plate was drifting northward, leaving the granitic Seychelles in its wake. (E) By the Eocene, Australia and Antarctica were isolated and India had begun its collision with Eurasia. (F) Present-day positions of the continents. portion of Earth's history most germane to the biogeography of extant amphibians and reptiles begins on Pangaea in the late Paleozoic.

Pangaea remained intact through the Triassic, but its fragmentation into the northern supercontinent of Laurasia and southern Gondwana had begun by the Jurassic. During the Late Jurassic (~135 mya), Gondwana and Laurasia were separated by a westward extension of the Tethys Sea, and rotation of Laurasia away from Gondwana resulted in separation of North America from South America and the opening of the Atlantic Ocean (Figure 5.4B). By the Middle Cretaceous, Laurasia and Gondwana were completely separate and the Tethys Sea formed a continuous seaway near the Equator.

Shallow epicontinental seas also expanded across the continents during the Mesozoic and caused additional fragmentation of Laurasia. Early in the Jurassic, the Turgai Sea extended southward from the Arctic region to split Laurasia, separating most of Asia from Europe and North America (Euramerica). By the Middle Cretaceous (~100 mya) another epicontinental sea separated eastern and western North America, forming three landmasses-western North America, Euramerica, and eastern Asia (Figure 5.4C). Toward the end of the Cretaceous (~75 mya) the Bering land bridge (Beringia) was established between eastern Asia and western North America and lasted (with some interruptions) through most of the Cenozoic, allowing intermittent biotic interchange between eastern Asia and western North America. Eastern North America and Europe were continuous, but they were separated from both Asia and western North America by the epicontinental seas. However, these continents were connected at least twice via the de Geer and Thulean land bridges (see Figure 5.2) (Brikiatis 2014).

Laurasian and Gondwanan origins of extant amphibians and reptiles

Salamanders provide the best example of modern clades with a Laurasian origin. All clades of extant salamanders inhabit the Holarctic; only bolitoglossine plethodontids and hynobiids have secondarily dispersed to more southern latitudes. All salamander families except hynobiids are represented in North America, strongly suggesting that modern salamander lineages originated on this continent. Although most frog groups have a Gondwanan origin, pelobatoid frogs (Pelobatoidea: Megophryidae, Pelobatidae, Pelodytidae, Scaphiopodidae) probably originated in Laurasia (Table 5.1) (Pyron 2014).

> Most modern reptile groups originated in Gondwana, but the Holarctic distribution of many anguid and lacertid lizards as well as emydid turtles strongly suggests Laurasian origins for these lineages. Finally, phylogenetic and biogeographical reconstruction analyses suggest a North American origin of Crocodylia (Salisbury et al. 2006) and pleurodont iguanians (Townsend et al. 2011). The latter pattern is remarkable as it is one of the few examples of a Laurasian clade that subsequently colonized multiple Gondwanan fragments, including South America and Madagascar.

> Gondwana began rifting in the Early Jurassic (~180 mya), ultimately separating about 160 mya into West Gondwana (now Africa and South America) and East Gondwana (now Madagascar, India, the Seychelles, Australia, New Guinea, Antarctica, and New Zealand). By about 130 mya, Madagascar + India was separated from Antarctica + Australia, and rifting had begun to separate Africa from South America. Approximately 100 mya, Australia + New Guinea + New Zealand began to separate from Antarctica, and sea-

TABLE 5.1 Examples of amphibian and reptile taxa with disjunct distributions in former Laurasian continents

Taxon	Present-day distribution	
Salamanders		
Cryptobranchidae (pp. 46–47)ª	Eastern North America, China, Japan	
Salamandridae (pp. 48–49)	North America, western Europe, eastern Asia	
Proteidae (p. 51)	Eastern North America, southern Europe	
Hydromantes (Plethodontidae; pp. 53–55)	California, southern Europe	
Frogs		
Pelobatoidea (pp. 64–66)	North America, Eurasia	
Lizards		
Dibamidae (pp. 122–123)	Southern North America, Southeast Asia	
Anguidae (pp. 139–140)	North American, Eurasia (South America) ^b	
Crocodylians	and the second se	
Alligator (Alligatoridae) (pp. 182–183)	Eastern North America, eastern China	
Turtles		
Platysternidae (p. 192)	Eastern North America, eastern Asia	
Emys (Emydidae) (pp. 192–193)	North America, western Eurasia	
See the page numbers cited for taxonomic	descriptions and distribution maps	

^b The Gondwanan continent of South America, indicated in parentheses, was presumably reached by dispersal (see text).

floor spreading dispersed all of the Gondwana remnants. By about 92 mya a continuous seaway (the South Atlantic Ocean) was present between Africa and South America, although these two continents had a long period of relative proximity, potentially allowing dispersal of organisms between the continents.

By the end of the Cretaceous, most of the major fragments of Gondwana were well separated (Figure 5.4D). However, dinosaur faunas shared by Madagascar, India, and South America indicate that these landmasses were still in contact via Antarctica, though isolated from Africa (Sampson et al. 1998). Likewise, a similar route of exchange between South America and Australia probably explains the shared presence of marsupials, and possibly other biota, on those continents (Woodburne and Case 1996).

Some contact between former Laurasian and Gondwanan landmasses occurred during the late Mesozoic, permitting exchange between North and South America and between Africa and Eurasia. Once it was freed of its connection with South America, Africa rotated clockwise and became more closely associated with Eurasia. A brief connection between the two landmasses probably existed in the Late Cretaceous and Early Cenozoic (Rage 1988; Gheerbrant 1990), as well as a permanent connection established later in the Cenozoic (Oligocene to Early Miocene, 30-25 mya). Continental movements set in motion during the late Mesozoic continued during the Cenozoic. The Tethys Sea was briefly closed during the Late Cretaceous or Early Paleocene but still separated Eurasia from Africa until the late Oligocene or Early Miocene (30-25 mya), when it closed and formed the precursor of the modern Mediterranean Sea.

India and Madagascar-regions of Gondwana that were originally attached to eastern Africa-have a more complex history (Krause et al. 1997). After first drifting away from Africa and Antarctica/Australia, the Madagascar + India + Seychelles microcontinent split during the Late Cretaceous and Early Cenozoic (~87-60 mya) (Storey et al. 1995). Madagascar drifted southeastward relative to Africa to its present position. India, on a newly formed Indian Plate, drifted northward, leaving the Seychelles in its wake and ultimately colliding with the southern edge of Asia early in the Eocene (~40 mya; Figure 5.4E), pushing up the Himalayas (Beck et al. 1995). This collision of the Indian Plate with southern Asia had two biogeographic consequences: it introduced Gondwanan elements to that region of Laurasia, and it caused the tectonic uplift of the Himalayan Plateau that fragmented the ranges of formerly widespread Asian taxa, leading to the diversification of numerous clades of amphibians and reptiles.

Africa and faunal exchange with southern Europe

The major biomes of Africa—including the Sahara desert, high-elevation plateaus, and tropical rainforests—have shaped the biogeography of the amphibians and reptiles of those regions. Biogeographic reconstructions of worldwide amphibian taxa suggest that ranoid frogs, which represent approximately one-third of extant frog diversity, originated in the African tropics in the Early to Middle Cretaceous (Pyron 2014).

Both East and West Africa are home to tropical rainforests inhabited by a diversity of amphibians and reptiles (Lovett and Wasser 2008; Penner et al. 2011), especially arthroleptid, conrauid, and ptychadenid frogs, herpelid caecilians, and calabariine boid and grayiine colubrid snakes. These tropical forests were contiguous up until about 1 mya, when climate change separated the forests in West-Central Africa from those in East Africa (Lovett 1993; Trauth et al. 2009). This isolation can be seen in the phylogenetic history of multiple caecilian clades (Loader et al. 2007).

Many anurans were confined to small, separate areas in the highlands of East Africa, especially the Eastern Arc Mountains, during the Pleistocene, thereby promoting speciation (Lovett et al. 2005; Fjeldså and Bowie 2008). Examples of this phenomenon include the extant frogs *Arthrolepis xenodactyloides* (Blackburn and Measey 2009) and *Hyperolius substriatus* (Lawson 2013).

The land that became the Arabian Peninsula was geologically part of Africa but collided with Eurasia about 19 mya. This collision formed a land bridge that allowed a dispersal corridor for reptiles between Africa and Eurasia, including *Echis* snakes (Arnold et al. 2009; Pook et al. 2009), *Pelomedusa* turtles (Vargas-Ramírez et al. 2010; Wong et al. 2010), *Chamaeleo* (Macey et al. 2008) and *Uromastyx* (Amer and Kumazawa 2005) lizards, and the ancestors of *Eumeces*, *Scincopus*, and *Scincus* lizards (Carranza et al. 2008). However, during this time the Red Sea was forming, eventually splitting the Arabian Peninsula from Africa and becoming a barrier to gene flow, although *Varanus* (Portik and Papenfuss 2012) and *Chalcides* lizards (Lavin and Papenfuss 2011) may have crossed this barrier.

Finally, the Mediterranean Sea was largely dry for more than 600,000 years in the Late Miocene (~5.9-5.3 mya), resulting in direct connections between North Africa and southern Europe and allowing dispersal of amphibians and reptiles between those continents (Husemann et al. 2014). Filling the Mediterranean Basin separated lineages that were distributed in both Europe and North Africa, causing them to diversify in isolation (e.g., pelodytid frogs). Declining sea levels in the Pliocene and Pleistocene exposed some of the continental shelves, thereby facilitating dispersal between the landmasses for amphibians such as Alytes frogs (Martínez-Solano et al. 2004) and Salamandra salamanders (Steinfartz et al. 2000), in addition to reptiles, including Mauremys (Fritz et al. 2006) and Testudo (Gracía et al. 2013) turtles and Chalcides (Carranza et al. 2008) and Psammodromus (Carranza et al. 2006) lizards.

Madagascar: An ancient continental fragment

The amphibian and reptile fauna of Madagascar is typical of a large, topographically complex island with only ancient connections to other landmasses. It has high species diversity, but these species are descendants of only a few major lineages (reviewed by Vences et al. 2009; Gehring et al. 2011). Nearly all species are **endemic** (restricted to that region) and the non-endemics are mostly shared with the nearby Comoro Islands. Approximately 250 species of amphibians (all frogs) and almost 400 species of reptiles have been described, but surveys of genetic diversity indicate that hundreds of reptiles and frogs are yet to be described (Vietes et al. 2009; Nagy et al. 2012).

Excluding introduced species, Madagascar's amphibians and reptiles comprise several endemic frog taxa, including Mantellidae, some Microhylidae (subfamilies Cophylinae, Dyscophinae, and Scaphiophryninae), an endemic genus of hyperoliid frog (*Heterixalus*), plus a non-endemic ptychadenid frog (*Ptychadena*). Lizard taxa include Chamaeleonidae, Gekkonidae, and Gerrhosauridae and the endemic family Opluridae. The snake fauna consists of the endemic taxa Xenotyphlopidae and Sanziniinae (Boidae) in addition to colubrid species. Other reptiles include tortoises (Testudinidae, Pelomedusidae, Podocnemidae) and the Nile crocodile (*Crocodylus niloticus*).

Madagascar's fauna is as interesting for what it lacks as for what it has. Many Gondwanan taxa found in Africa, such as the frog families Pipidae, Bufonidae, and several ranoid groups (Arthroleptidae, Petropedetidae, Rhacophoridae, Hemisotidae), are absent from Madagascar. The snake clades Viperidae, Elapidae, and pythonine boids, and the lizard families Cordylidae, Lacertidae, and Varanidae, are widespread in Africa but absent from Madagascar. These families radiated after the split between Africa and Madagascar, and their absence from Madagascar is evidence that there has been very little dispersal to Madagascar from Africa since the two land masses separated.

The Seychelles Islands: Endemism on a microarchipelago

The present Seychelles Islands comprise relatively young coral islands as well as ancient granitic islands. The granitic islands are remnants of Gondwana that were originally connected to the Indian landmass when it separated from Africa and began moving northward toward Asia (see Figure 5.4D). Thus, this tiny archipelago harbors endemic lineages that are more than 65 million years old (Collier et al. 2008). Although the granitic islands of the Sevchelles are currently separated by 50-60 km of open ocean, all of the islands were connected up until 10,000-16,000 years ago (Davies 1968). Discounting introduced species, the reptile fauna includes two species of colubrid snakes (Lamprophis geometricus and Lycognathophis seychellensis), several genera of skinks and geckos, and a small radiation of the gekkonid genus Phelsuma. The amphibian fauna comprises six species of caecilians and five species of frogs, all restricted to the granitic Seychelles. The endemic frogs include all four species of the endemic frog family Sooglossidae and an endemic hyperoliid frog, Tachycnemis seychellensis.

The Indian subcontinent: Gondwanan elements rafting to southern Asia

After the fragmentation of Gondwana, the Indian subcontinent harbored a complex residual Gondwanan fauna that evolved in isolation for tens of millions of years before its collision with Asia some 40 mya. Today the Indian subcontinent harbors many relict endemic lineages, including the frog families Micrixalidae, Nasikabatrachidae, Nyctibatrachidae, and Ranixalidae, the caecilian family Chikilidae, the snake family Urotyphlopidae, and numerous other genera in other families. Most of these endemic taxa inhabit the Western Ghats mountain range in southwest India. These mountains are a fascinating living museum that preserves ancient Gondwanan lineages of plants and animals (Gunawardene et al. 2007).

India's collision with Asia about 40 mya introduced Gondwanan lineages into Laurasia some 130 million years after the breakup of the two supercontinents in the Jurassic. Many of these lineages subsequently dispersed to regions outside India, including Southeast Asia (Bossuyt and Milinkovich 2001; Datta-Roy and Karanth 2009). This out-of-India scenario explains the distribution of many amphibians, including the frog families Bufonidae (Van Bocxler et al. 2009), Dicroglossidae (Bossuyt et al. 2006), Ranidae (Bossuyt and Milinkovitch 2001; Bossuyt et al. 2006), and Rhacophoridae (Li et al. 2013), and the caecilian family Ichthyophidae (Gower et al. 2002; Nishikawa et al. 2012; San Mauro et al. 2014).

The Australian Plate: Mixed Gondwanan and Laurasian elements

After the separation of Australia, Antarctica, New Guinea, and New Zealand from the rest of East Gondwana in the Cretaceous (see Figure 5.4C,D), Australia and New Zealand were still connected to eastern Antarctica, which also formed a land bridge to South America. New Zealand separated from these landmasses approximately 80-90 mya and rapidly moved eastward. Australia maintained a land bridge to South America via Antarctica until the early Paleocene, which may have permitted dispersal between these continents (Noonan and Chippendale 2006). Australia and Antarctica severed their connection between 55 and 32 mya. Thereafter, Australia was completely isolated through much of the Cenzoic until it contacted the Asian Sunda Shelf in the early Miocene (~15-20 mya), when periodic sea level changes exposed more of the continental shelf and thereby facilitated dispersal (Hall and Blundell 1996; Voris 2000; Lohman et al. 2011).

Clades in Australia can be sorted into two units reflecting this history: ancient clades that are generally shared with one or more Gondwanan landmasses, and a group of clades that entered Australia only after connection between the Australian and Asian Plates in the early Miocene. Given Australia's geological history, hypotheses about Gondwana and Asian origins are relatively easy to test using molecular clock analyses of DNA. Australia was isolated from all other Gondwana fragments by about 32 mya, when it finally split from Antarctica. Therefore, if the divergence between an Australian taxon and its closest non-Australian relative is older than 32 million years, it is best explained by Gondwanan vicariance (i.e., the common ancestor once inhabited East Gondwana before Australia became isolated). However, if the split between Australian and non-Australian lineages is younger than this age, we can infer that the common ancestor of the Australian lineage dispersed from another continent.

At least one amphibian and two reptilian Australian lineages have unambiguous Gondwanan origins:

- 1. The endemic Australian frog family Myobatrachidae shares a common ancestor with its sister lineage, the South American Calyptocephalellidae, of more than 110 mya—a period when South America was still in close proximity to East Gondwana (Bossuyt and Roelants 2009; Pyron 2014). This date suggests that the myobatrachid lineage became isolated on Australia during the Gondwanan fragmentation.
- 2. The Australian endemic diplodactyloid geckos (Carphodactylidae, Diplodactylidae, and Pygopodidae) split from their common ancestor about 70 mya, well before the isolation of Australia from other parts of Gondwana (Oliver and Sanders 2009).
- 3. South American and Australian chelid turtles share a common ancestor of 65 mya or more, during a time when Australia and South America shared a connec-

tion to Antarctica (Near et al. 2005; Dornburg et al. 2011; Joyce et al. 2013).

Dispersal from Asia explains the distribution of a majority of Australia's amphibian and reptile fauna (Table 5.2). The ancestor of Australian microhylid frogs inhabited Asia and dispersed to Australia about 25 mya (Kurabayashi et al. 2011). Varanid lizards dispersed to Australia from Asia between 39 and 26 mya (Vidal et al. 2012). Although this time frame includes ages when Australia was connected to Antarctica, we can nonetheless rule out a Gondwanan origin of Australian varanids because the oldest lineages of this family inhabit Asia. The ancestors of Australian agamid (Hugall et al. 2008) and lygosomine scincid lizards (Skinner et al. 2011), and of acrochordid (Sanders et al. 2010), pythonid (Rawlings et al. 2008), and colubrid snakes, also dispersed to Australia about 30 mya or later. The diversity of Australian hydrophiline snakes and crocodylians is particularly young, as these groups dispersed from Asia and radiated 15-19 mya (Sanders and Lee 2008; Sanders et al. 2008. 2013: Oaks 2011).

South America

The separation of Laurasia and Gondwana began in the Jurassic when a seaway opened between North and South America, and the two continents were separated by the Middle Cretaceous (~110 mya). The southern boundary of the North American Plate corresponds to what is now southern Mexico to northern Guatemala. In the Middle Cretaceous the Caribbean Plate formed as part of the

TABLE 5.2	Clade age and biogeographical	origin for major	radiations of terr	estrial Australian
squamates				

Time to most recent common ancestor (mya)	Biogeographical origin	Number of Australian species (approx.)
The second second	ALL AND A	
10	Asian	102
35	Asia	13
Unknown	Asia (multiple invasions)	10
Unknown	Uncertain	42
23	Asia	71
Unknown	Asia	27
25–30	Asia	232
Unknown	Uncertain	120
Unknown	Uncertain Uncertain	45
Unknown	Asia/Africa (multiple invasions)	28
71	Gondwanan	121
	Time to most recent common ancestor (mya) 10 35 Unknown Unknown 23 Unknown 25–30 Unknown Unknown Unknown Unknown 71	Time to most recent common ancestor (mya)Biogeographical originBiogeographical origin1010Asian35AsiaUnknownAsia (multiple invasions)UnknownUncertain23AsiaUnknownAsia25–30AsiaUnknownUncertainUnknownUncertainUnknownSia10Asia25–30Asia10Uncertain10Uncertain10Asia/Africa (multiple invasions)71Gondwanan

Data from Oliver and Sanders 2009.

Pacific Plate about 1,000 km west of present-day Central America. This small plate moved eastward through the gap between North and South America. Southern parts of the North American Plate were subducted beneath the Caribbean Plate. Volcanic islands formed along the eastern margin of the Caribbean Plate as it moved, creating the Proto-Antilles, which would become the foundation of the Greater Antilles in the West Indies. In the Late Cretaceous, the Proto-Antilles were between North and South America in approximately the position of presentday Central America, forming a possible route between the two continents. This connection was severed by rising sea levels early in the Cenozoic. However, the Proto-Antilles continued their eastward movement and were in more or less their current position by the Eocene (~38 mva). Subsequent evolution of the West Indies is very complex and has been modulated by fragmentation and coalescence of some of the original Proto-Antilles and by changing sea levels throughout the Cenozoic (Pindell et al. 1988; Perfit and Wiliams 1989).

North and South America were separated by a water gap from the Late Cretaceous/Early Paleocene until the Isthmus of Panama was completed to form the continuous land connection existing today. Much of the land forming presentday Central America had its origin as an archipelago on the western edge of the Caribbean Plate. Moving eastward, this archipelago reached approximately its current position in the Early Miocene (~22 mya) to form the foundation of Central America. Subsequent formation of a land connection between Central and South America was long dated at ~3.5 mya, but a new study placed the connection between 13 and 15 mya (Montes et al. 2015). Completion of the Panamanian isthmus initiated a series of biogeographic exchanges known as the Great American Biotic Interchange, which we describe later in this section.

The isolation of South America promoted the evolution of unique amphibian and reptile faunas. Perhaps the most notable amphibian clade with South American origins is Hyloidea, which diverged from other frogs in the Late Jurassic or Early Cretaceous. Hyloids are a hyperdiverse assemblage that includes more than 40% of the recognized species of frogs, including the families Hylidae, Craugastoridae, Dendrobatidae, Eleutherodactylidae, Leptodactylidae, and others (see Figure 3.22). Similarly, the toad lineage (Bufonidae) originated in South America about 105 mya and later dispersed worldwide except to Australia and Madagascar (Pramuk et al. 2008; Pyron 2014). As we will discuss, dispersal from South America to Central and North America explains much of the present-day diversity of amphibians in those areas.

Origin of Central American assemblages

Many researchers have recognized that Central America has a characteristic amphibian and reptile fauna that is distinct from that of North and South America (e.g., Savage 1982, 2002; Cadle 1985; Duellman 2001). These assemblages are thought to comprise lineages that differentiated in response to historical biogeographic events affecting Central and South America during the Late Cretaceous and Cenozoic. Jay Savage (1982, 2002) identified three historical elements that today comprise significant portions of Neotropical amphibians and reptiles. These elements can be thought of as complex assemblages in which individual species or clades share a common temporal and geographic origin.

- 1. *Middle American element:* Derivatives of a generalized Neotropical amphibian and reptile fauna that evolved in isolation in tropical North and Central America during most of the Cenozoic. Mid-Cenozoic climate changes in the north gradually restricted these elements to tropical Central America. These taxa include some phyllomedusine and hyline frogs, microhylid frogs, corytophanid lizards, and some boiid genera (*Boa, Exiliboa*).
- 2. South American element: Derivatives of a generalized Neotropical amphibian and reptile fauna that evolved in isolation in South America during most of the Cenozoic. The affinities of lineages in this component are Gondwanan and include numerous hylid genera and species groups, caecilid caecilians, hoplocercid and gymnophthalmid lizards, and boiid and dipsadine colubrid snakes.
- 3. Old Northern Element: Lineages with long-term Laurasian affinities, primarily extratropical in origin. These lineages were incorporated into the evolving tropical assemblage of Central America as increased cooling and drying during the Early Tertiary forced the species southward from North America. Examples include bolitoglossine plethodontid salamanders, the skink genera *Plestiodon* and *Scincella*, colubrine snakes, and kinosternid, chelydrid, and emydid turtles.

Species from all three elements make up the modern amphibian and reptile fauna of Central America. In reality, only a few taxa in these historical units have been subjected to phylogenetic analysis, and they have been recognized primarily on the basis of patterns of endemism and diversity in the Neotropics.

Merging faunas: The Great American Biotic Interchange

North, Central, and South America each developed highly distinctive assemblages of amphibians and reptiles during their long isolation in the Cenozoic. The absence of a Panamanian Isthmus land bridge would not have eliminated dispersal between the continents, especially because the ocean between pre-Pliocene North and South America contained a series of stepping-stone islands (Coates and Obando 1996). Many analyses indicate that dispersal before the closure of the Isthmus of Panama was an important factor in shaping the biogeography of amphibian and reptile taxa north and south of the isthmus. For example, the ancestors of extant *Pristimantis* frogs, *Rhinella marina* species complex toads, eleutherodactylid frogs, *Lachesis* snakes, and *Apalone, Rhynoclemmys*, and kinosternid turtles, dispersed between continents in the Miocene (Za-mudio and Greene 1997, Head et al. 2006, Mulcahy et al. 2006, Heineke et al. 2007, Le and McCord 2008, Vallinoto et al. 2010, Pinto-Sánchez et al. 2012, Iverson et al. 2013). However, the movement of bolitoglossine salamanders from North America to Central and South America probably occurred no more recently than the Miocene (Vietes et al. 2007; Elmer et al. 2013).

The closure of the Panamanian isthmus initiated a series of dispersal events that were so momentous for the composition of the biotas of North, Central, and South America that it is known as the **Great American Biotic Interchange** (**GABI**) (reviewed by Vanzolini and Heyer 1985; Cody et al. 2010). The GABI is documented primarily from its mammalian component because mammals are represented by well-studied and extensive fossil deposits during the relevant time interval (Leigh et al. 2014). However, the GABI included all groups of plants and animals throughout the Americas.

The Indo-Australian Archipelago and the Philippines

The Indo-Australian Archipelago (IAA) stretches from the Malay Peninsula and Sumatra in the west to New Guinea and northern Australia in the east (**Figure 5.5**). The IAA is one of the most diverse places on earth, harboring an

estimated 25% of Earth's terrestrial species (Corlett 2009). This diversity is due in part to the complex geological history of the region and the effects of Pliocene–Pleistocene climate change (reviewed by Lohman et al. 2011). Indeed, the IAA is an encapsulation of the biogeographic principles discussed thus far. In general, the biogeographic patterns seen among species or higher taxonomic levels are the result of vicariance due to creation and submergence of islands, and to the movement of these islands and continents during the last 45 million years or so (Lohman et al. 2011). Mechanisms that affected the distributions of species populations include movement of landmasses due to tectonic activity, and changes in sea levels that exposed terrestrial connections among islands.

The rich history of species diversification across the IAA was critically important in the development of many of our most famous theories in evolution and biogeography. One of the most famous biogeographic patterns on our planet is **Wallace's Line**, named after Alfred Russel Wallace, who is widely recognized as the "father of biogeography." It was during expeditions throughout the IAA that Wallace observed that, despite the geographic proximity of the islands of Bali and Lombok (<40 km; see Figure 5.5), the two islands had very different fauna, with Bali inhabited by relatives of Asian taxa and Lombok by relatives of Australo-Papuan taxa. The situation was similar between Borneo and Sulawesi to its east. The explanation for this phenomenon is that the present-day islands were much farther apart in geological history and developed their unique faunas before



Figure 5.5 The Indo-Australian archipelago (IAA). Light blue areas show the extent of exposed land during periods of low sea level during the Pleistocene glacial periods. The two boundaries between major floral and faunal assemblages discussed in the text, Wallace's and Huxley's Lines, are indicated. tectonic activity brought the islands into close contact (Hall 1996, 2002; Holloway and Hall 1998).

Although Wallace's Line marks dramatic faunal contrasts, faunal separation east and west of the line is not complete. For example, multiple clades of fanged frogs of the genus *Limnonectes*, sailfin lizards of the genus *Hydrosaurus*, and forest frogs of the genus *Platymantis* have dispersed across the deep ocean barriers between Borneo, Sulawesi, the Philippines, and the Pacific islands since the Miocene (Evans et al. 2003; Siler et al. 2014; Brown et al. 2015).

The western half of the IAA is formed by the Sunda Shelf (see Figure 5.5A). Since its formation began about 65 mya, this continental shelf has always maintained a geological connection to Asia, but terrestrial connections among islands varied with the cyclical nature of sea level oscillations in this region that connected islands separated by shallow seas. However, during glacial periods, when sea levels were lower, this region was a contiguous promontory of land. The eastern half of the IAA contains Wallacea and the Sahul Shelf. For brevity, we will focus our discussion on Wallacea. Unlike the Sunda Shelf, Wallacea is isolated from all nearby continents by deep ocean trenches and therefore has higher endemism than Sunda Shelf taxa. Isolation promotes species diversity because gene flow is restricted among island populations, leading to the evolution of characters unique to each population (see also Section 5.4).

The Wallacean island of Sulawesi is particularly interesting because it contains seven areas of endemism (AOEs) that are reflected in species phylogenies (**Figure 5.6**) (Evans et al. 2003, 2008). The Celebes toad (*Ingerophrynus* [formerly *Bufo*] *celebensis*) inhabits the entire island of Sulawesi, yet phylogenetic analyses demonstrate that each AOE is home to at least one endemic clade, although there is some evidence of gene flow among AOEs (e.g., the NC and WC clades in Figure 5.6). However, that the genetic history of Sulawesi *I. celebensis* is so closely tied to each AOE demonstrates there are factors limiting dispersal of this species, and determining those factors is an area of active research.

Tectonic activity and Pleistocene glaciation also heavily influenced the biogeography of the Philippines (reviewed by Brown et al. 2013). Philippine amphibian and reptile species diversity is high, with 80% of the 111 amphibian species and 74% of the 270 reptile species endemic to the archipelago, and new species being discovered every year. The fauna of

Figure 5.6 Areas of endemism on Sulawesi. (A) Circles represent samples used in a phylogeographic analysis of the Celebes toad (*Ingerophrynus celebensis*), colored to show membership in nine toad clades. Clade distribution corresponds to the seven major areas of endemism (AOEs) on Sulawesi. Name abbreviations are directional (NE = northeast, NC = northcentral, etc.) (B) An intraspecific phylogeny of *I. celebensis* clades shows general congruence between the phylogeny and AOEs. Congruence is not complete, however, as there exist examples of range overlap (vertical lines) between clades at their peripheral distributions. (After Evans et al. 2008; photograph courtesy of Sean Reilly.)



the western island of Palawan has characteristics of both the IAA west of Wallace's Line and the Philippines (Esselstyn et al. 2010); indeed, Huxley (1868) later modified Wallace's Line to include the Philippines (see Figure 5.5). The Palawan microcontinent split from the Asian continent some 30 mya and collided with the developing Philippine islands between



16 and 20 mya. Phylogenetic and molecular dating evidence suggest that this movement of Palawan from Asia to the Philippines brought with it a comparatively old assemblage of amphibians and reptiles. This Palawan Ark hypothesis has been implicated to explain the origin and endemic radiation of several clades, including bombinatorid frogs (Black-

burn et al. 2010) and Philippine members of the genus *Gekko* (Siler et al. 2012).

More recent abiotic processes, especially changes in sea level due to glaciation during the Pleistocene, have also affected Philippine amphibian and reptile distributions. The Philippines comprises more than 7,100 islands, but these islands can be grouped into larger island units that are linked only during periods of low sea levels. These Pleistocene aggregate island complexes (PAICs; **Figure 5.7A**) are areas of high endemism, suggesting that many of the organisms distributed across each PAIC

Figure 5.7 PAICs and colonization routes of three genera of amphibians and reptiles.

(A) The map shows the extent of exposed land (light blue) during different periods of low sea level during the Pleistocene glacial periods and the five Philippine Pleistocene aggregate island complexes (PAICs).
(B) Two Philippine frog lineages, *Hylarana* and *Limnonectes*, invaded multiple PAICs from Borneo along the routes indicated with arrows. Arrows also indicate the historical reciprocal exchange of *Limnonectes* between Mindanao (Philippines) and Sulawesi (Indonesia).
(C) Repeated back-and-forth dispersal of *Brachymeles* skinks between multiple PAICs. (After Brown et al. 2013.)



have evolved in isolation and demonstrate little gene flow with other PAICs. However, there are numerous examples of taxa that are distributed across PAICs, including skinks of the genera *Brachymeles* and *Sphenomorphus* (Linkem et al. 2010, 2011; Siler et al. 2011), *Cyrtodactylus* geckos (Siler et al. 2010, 2014), and some species of rhacophorid frogs (Brown et al. 2010).

Pleistocene sea level changes also aided dispersal from Borneo and the Sunda Shelf to the Philippines by bringing the islands in closer geographic proximity. Indeed, recent phylogenetic evidence has shown that the Sunda Shelf, especially the geographically proximate Borneo, is the source of numerous amphibian and reptile lineages in the Philippines, including Philippine species of *Limnonectes* (Setiadi et al. 2011) and *Hylarana* (Brown and Siler 2014) frogs and *Brachymeles* skinks (Siler et al. 2011) (**Figure 5.7B,C**). Because so much of the amphibian and reptile diversity of the



IAA and the Philippines has yet to be discovered, it will remain a fruitful area for continued herpetological research.

5.4 ■ Phylogeography: Biogeography of the Recent Past

Phylogeography studies factors that have shaped the geographic distribution of lineages over the past few million, or even the past several thousand, years. A goal of many phylogeographic studies is to determine what historical factors lead to **speciation**—the splitting of a single lineage into two lineages we recognize as distinct species (see Coyne and Orr 2004).

Phylogeography blends elements of population genetics with phylogenetics to study historical population expansions and contractions, hybridization, barriers to gene

flow, and how those relatively recent phenomena shaped current distributions of species or populations. Phylogeographers are particularly interested in mechanisms that create barriers to gene flow between populations of a species, such as changes in the courses of rivers or rising sea levels that inundate low areas, creating isolated island populations.

Climate change, isolation, and refugia

Habitat change is the largest factor that shapes where a population can live, and climate change can fragment suitable habitat into separate **refugia**—locations where species have persisted while becoming extinct elsewhere—and lead to long-term isolation of populations. If the severity of climate change increases, these refugia could shrink until no habitable environment for a species remains, thereby leading to its extinction.

Figure 5.8 Ocillating climate changes during the Pleistocene. (A) Antarctic temperatures between 800,000 and 170 years before present estimated from the Dome C ice core. Temperatures are relative to 170 years before present (= 0° C). (B) Maximum extent of Northern Hemisphere glaciation during the Pleistocene. (A after Jouzel et al. 2007; B after Ehlers and Gibbard 2007.)

An example of the refugium concept can be seen among central and eastern Australian amphibians and reptiles. Australia was once covered by moist forests and was home to the ancestors of many extant reptile groups, including Heteronotia geckos (Fujita et al. 2010), Lampropholis skinks (Chapple et al. 2011), Rhamphotyphlops snakes (Marin et al. 2013b), and Uperoleia frogs (Catullo and Keogh 2014). However, climate change in the mid-Miocene (~17 mya) led to significant drying of central Australia, and the distribution of moisture-adapted lineages contracted to the much-reduced mesic and monsoonal forest refugia, where these lineages subsequently diversified into multiple species (reviewed by Byrne et al. 2008, 2011).

Changes in climate can also be brief (in geological terms), with climates returning to their original state after tens or hundreds of thousands of years. As the climate returns to its previous condition, the descendants of species confined to refugia disperse to fill expanding suitable habitat. Periodic episodes of drastic global cooling and glaciation that occurred every 40,000 to 100,000 years during the Pleistocene (Figure 5.8A) strongly affected the genetic structure and distribution of Holarctic amphibians and reptiles. North America, Europe, and parts of Asia were covered by ice sheets more than 3 km thick (Figure 5.8B), while the southern end of South America was covered by an expansion of the Antarctic ice sheet. Sea levels dropped by 140 m, exposing large portions of the continental shelf and connecting continental islands to the mainland.

The contraction and postglacial expansion and dispersal of North American taxa can be traced by analyzing changes in a species' DNA (reviewed by Zeisset and Beebee 2008).

For example, today there are two major clades of the upland chorus frog (Pseudacris feriarum) in the United States (Lemmon et al. 2007a,b; Lemmon and Lemmon 2008). An inland clade inhabits areas south and west of the Appalachian Mountains, and a coastal clade inhabits the East Coast from the Appalachian foothills of eastern Tennessee north to New Jersey. During glacial periods, ice sheets covered the northern portion of North America, extending as far south as the Ohio River. The resulting climate change isolated the original P. feriarum population into two separate refugia in the southern United States (Figure 5.9A). As the glaciers receded, both clades dispersed to fill newly habitable land, eventually achieving their present-day distributions (Figure 5.9B). Similar glaciation patterns can be seen among European amphibians and reptiles, which retreated to the southern Iberian, Italian, and Balkan peninsulas and numerous areas of Asia (Zeisset and Beebee 2008; Zhang et al. 2008; Zheng et al. 2009).

Figure 5.9 Population contraction and expansion of upland chorus frogs (Pseudacris feriarum) during Pleistocene glaciations. (A) As ice sheets expanded and the climate cooled, suitable habitat for upland chorus frogs contracted, resulting in separate refugia on either side of the Appalachian Mountains. (B) As the glaciers receded and global temperatures rose, P. feriarum populations extended north and south, filling newly available habitat. These patterns of contraction and expansion are reflected in the phylogenetic history of the species (lower right). (After Lemmon et al. 2007a,b; Lemmon and Lemmon 2008; photograph © Rvan M. Bolton/Shutterstock.)

(A)



Sky islands

Amphibians and reptiles that inhabit mountains provide a special case of range contraction into refugia. Climate change may contract livable habitat to higher elevations to the point where connectivity between mountains is severed, and populations in these mountaintop sky islands evolve in isolation without gene flow from other mountaintops, much as happens with oceanic islands (see Section 5.4). If subsequent climate change extends livable habitat to lower elevations and restores the connections between mountaintops, formerly isolated populations can once again come into contact. The Ouachita Mountains of eastern Oklahoma and western Arkansas are home to multiple species of Plethodon salamanders. Plethodon ouachitae inhabits cool, wet habitats on the northern slopes at elevations above 450 m. Phylogenetic evidence indicates that each mountain peak harbors an endemic clade, suggesting that there is very little current or recent gene flow among the populations on the peaks (Figure 5.10A,B) (Shepard and Burbrink 2008). The peaks were probably colonized in a stepwise fashion throughout the middle Pleistocene, beginning with Kiamichi and Round peaks and then the northern peaks. Periods of Pleistocene glaciation probably aided dispersal by expanding suitable cooler habitat to lower elevations (Figure 5.10C). Other examples of the sky island phenomenon for amphibians and reptiles are described by Tennesson and Zamudio (2008), Leaché et al. (2013), and Zhang et al. (2014).

Tropical plethodontids (all of which are bolitoglossines; see Figure 3.16), show a geographical pattern typical of many tropical vertebrates: they are a very species-rich

Figure 5.10 Phylogeography of Plethodon ouachitae in the Ouachita Mountain sky island system. (A) The present-day suitable habitat of Plethodon ouachitae in the Ouachita Mountains of eastern Oklahoma and western Arkansas exists on isolated mountain peaks above 450 m elevation. (B) The intraspecific phylogeny of P. ouachitae populations shows that each mountain peak harbors an endemic clade. This suggests little or no current or recent gene flow among populations (since in the absence of gene flow, each peak's population evolves a unique genetic identity). (C) During periods of cooler global temperatures, suitable habitat for P. ouachitae expanded to lower elevations, as can be seen from the >400 and >300 m elevation slices of the Ouachita Mountains. Under these cooler conditions, populations from formerly isolated peaks would have come into contact and exchanged genes. A return to previous global temperatures would once again isolate P. ouachitae on each peak. (After Shepard and Burbrink 2008; photograph courtesy of Todd W. Pierson.)



group, but individual species are restricted in geographic and elevational distribution. Most species are rare where they occur, and extreme genetic differentiation on a local scale is common (García-París et al. 2000; Rovito et al. 2012a,b). For example, 18 species of bolitoglossines are found on a single elevational transect (1,100-3,500 m) in Costa Rica, the highest known salamander diversity along such a transect. Despite the high species diversity, all Costa Rican salamanders belong to three genera: Nototriton, which are small, secretive, moss-dwelling species; Oedipina, which are fossorial or semifossorial; and Bolitoglossa, which are terrestrial to arboreal. Thus, tropical salamander communities are characterized by high species diversity within a few clades, strong local genetic differentiation of populations, narrow elevational ranges of species, and habitat specialization. Many previously unrecognized species await description based on new genetic evidence.

5.4 Island Biogeography

Because of the unique ecological and evolutionary dynamics of insular plants and animals, island biogeography is often treated as a distinct subdiscipline of biogeography. Island biological communities are often unique because they evolve in isolation, with little gene flow from other landmasses. Thus islands are natural laboratories where we can study how biological communities evolve given different ecological conditions and founding populations. Because islands are typically easy to date geologically, we can also estimate how quickly characteristics of fauna on the islands evolved.

Islands are classified as continental or oceanic in origin. **Continental islands** have a geologic connection to a landmass, and terrestrial connections between continental islands and the mainland can emerge and submerge as sea level changes. Thus, intermittent gene flow can occur between island and mainland populations.

Oceanic islands are usually either uplifted limestone or volcanic islands that do not form terrestrial connections to the mainland, even during periods of low sea levels. Researchers can therefore witness the long-term effects of national selection in isolation. Oceanic islands are particularly interesting to biologists because the entire floral and faunal composition of an island is descended from just a few colonizing species (Heaney 2007). Different ecological communities evolve on different island simply because each island was initially colonized by different species.

Island gigantism and dwarfism

Populations composed of individuals that are dramatically larger or smaller than their mainland counterparts are common phenomena on islands. Tiger snakes (*Notechis*) inhabit the southern mainland and offshore islands of Australia that are no more than 10,000 years old. Insular populations of these snakes differ markedly in body size, including both dwarf and giant populations. Phylogenetic analyses show that these body sizes evolve multiple times, perhaps in response to the size of prey that inhabit each island (Keogh et al. 2005).

Four-lined rat snakes (*Elaphe quadrivirgata*) inhabit mainland Japan and most of the offshore Izu islands, yet the body size and coloration of island populations differ dramatically from mainland populations and from each other (Hasegawa 2003). Most Izu Island *E. quadrivirgata* consume lizards, but lizards are rare on the island of Tadanae, and the large body size in this population is probably an adaption to instead consume the large eggs of nesting seabirds (Kuriyama et al. 2010). Similar patterns are seen in frogs (e.g., Lampert et al. 2007; Montesinos et al. 2012), lizards (e.g., Barahona et al. 2000; Carranza et al. 2001), and turtles (Jaffe et al. 2011).

An analysis of 11 populations of speckled rattlesnakes (*Crotalus mitchellii*) on islands in the Sea of Cortez and off the Pacific coast of Baja California revealed gigantism on one island, various degrees of dwarfism on eight other islands, and one island on which the snakes were the same size as on the mainland (Meik et al. 2010, 2012). Snakes from Ángel de la Guarda Island are substantially larger than mainland snakes, whereas snakes from eight other islands are smaller (**Figure 5.11A,B**). The average weight of the smallest snakes, those from El Muerto, Cabeza de Caballo, and El Piojo islands, is about one-third that of snakes from the mainland (J. Meik pers. comm.).

Statistical analysis showed that the mean snout-vent length of snakes correlates strongly with the size of islands, whereas the ages of the islands and their distance from the mainland have little effect (**Figure 5.11C**). Diversion of resources from growth to reproduction may explain the evolution of dwarfism in the face of intense intraspecific competition on small, resource-poor islands. That is, once a snake reaches reproductive maturity, it can maximize its fitness by using energy for reproduction rather than for additional growth.

The giant speckled rattlesnakes on Ángel de la Guarda, which are 50% longer and three times heavier than the mainland snakes, are especially interesting because that island is also home to a giant species of chuckwalla (Sauromalus hispidus) and a dwarf form of the red diamond rattlesnake (Crotalus ruber). Meik and his colleagues have proposed that these three species on Angel de la Guarda became isolated from mainland populations about 1.5 mya when the island was separated from the peninsular mainland. In contrast, all islands harboring dwarfed forms were isolated less than 15,000 years ago as sea levels rose following the last glacial maximum. Crotalus mitchellii has a proportionately larger head than C. ruber, and may have been predisposed to feed on chuckwallas, which are large lizards. Thus, the gigantism of C. mitchellii on Ángel de la Guarda may partly be a consequence of tracking evolution of gigantism in their prey. In contrast, C. ruber on Ángel de



Figure 5.11 Gigantism and dwarfism among island populations of speckled rattlesnakes (Crotalus mitchellii). An island giant from Ángel de la Guarda (A) and a dwarf from Cabeza de Caballo (B) are shown at their correct relative sizes. (C) The mean SVLs of snakes are closely linked to the size of the islands on which they occur. The star marks the mean length of mainland snakes. Only snakes from Ángel de la Guarda (area 930 km²) are larger than the mainland snakes. The smallest snakes are found on the three smallest islands, El Piojo (0.55 km²), Cabeza de Caballo (0.77 km²), and El Muerto (1.33 km²). (After Meik et al. 2012 and J. Meik, pers. comm; photographs by Jesse Meik.)

la Guarda may have avoided competition with *C. mitchellii* by specializing on smaller prey.

Adaptive radiations on islands

The diversity of Anolis lizards on Cuba, Jamaica, Puerto Rico, and Hispaniola provides a remarkable example of adaptive radiation and convergence in ecology, morphology, and behavior (summarized by Williams 1983; Langerhans et al. 2006; Losos 2009). Each island is home to several species of Anolis, and five or six species often occur in the same area, with each species occupying a different microhabitat. Sixty-four species of Anolis occur on Cuba, with as many as 11 species at the same site (J. Losos, pers. comm.). Perch height is one way that species of Anolis divide the habitat (Figure 5.12). On Puerto Rico A. cooki, A. cristatellus, and A. gundlachi live on the lower parts of tree trunks, A. evermanni and A. stratulus live high on tree trunks, A. occulatus lives on twigs, and A. cuvieri lives in the crowns of trees. Three other species, A. krugi, A. poncensis, and A. pulchellus, live in grass and low bushes.

These different forms of *Anolis* are called **ecomorphs** species that have independently evolved similar morphology, habitat use, and behavior (Williams 1983; Losos 2009). Ecomorphs of *Anolis* differ not only in size and in their selection of perch diameters and microhabitats, but also in body proportions, scalation, locomotor ability, and predatory behavior (Irschick and Losos 1998,1999; Cooper 2005;



(B)



Rodríguez-Robles et al. 2005; Johnson et al. 2008; Wegener et al. 2014). Jonathan Losos (2009) summarizes:

- Trunk-ground and grass-bush ecomorphs have long hindlegs and most often run or jump. They make few spontaneous movements, instead resting motionless until they see a moving prey item, and then jumping and running to capture it. These species sprint well on broad, flat surfaces (tree trunks, branches, and leaves) but are slowed by narrow surfaces and lose their balance frequently.
- Crown giant, trunk-crown, and twig ecomorphs have short legs and are walkers. They make twice as many spontaneous movements as trunk-ground and grass-bush species and locate prey by searching. They sprint more slowly than trunk-ground and grass-bush species on all perch diameters, but they are more sure-footed on narrow perches.
- 3. Trunk ecomorphs fall between the other two groups in leg length. They are the most active of the ecomorphs, running up and down the tree trunk to capture ants, which make up a substantial part of their diets.

Anolis also divide the habitat in terms of sun and moisture (Rand 1964; Williams 1983; Leal and Fleischman 2002).

(B)



Figure 5.12 Adaptive radiation of *Anolis* **lizards on Caribbean Islands.** *Anolis* divide the habitat in terms of the body size of the lizard (size axis), perch height (perch axis), and levels of sun and humidity (microclimate axis). (A) The size axis is particularly evident for species that live in the canopy: a small species lives on twigs at the outer edge of the canopy, larger species are found closer to the trunk, and a giant species lives in the crown of the canopy. The perch axis includes differences in habitat vegetation (trees, bushes, and grasses). The microclimate axis reflects variation in the proportion of sun and shade, extending from species that live in full sun to those living in perpetual shade beneath the forest canopy. (B) The morphologi-

For example, *A. evermanni* and *A. stratulus* are trunk–crown species, but *A. evermanni* occurs in deep shade whereas *A. stratulus* lives in open shade (Figure 5.13). Two trunk–ground species. *A. gundlachi* and *A. cristatellus*, display a similar shade–sun separation, as do two grass–bush species, *A. krugi* and *A. pulchellus*.

The most striking feature of the diversification of *Anolis* on Caribbean islands is its repeatability (summarized by Losos 2009). The same ecomorphs with the same ecological, morphological, and behavioral characteristics are found on island after island. Furthermore, the different ecomorphs on each island are generally more closely related to each other than to any species on another island, indicating that the ecomorphs on each island evolved from a different founder species (**Figure 5.14A**). Thus, *Anolis* on



Grass-bush (GB

Crown-giant (CG)

Trunk-crown (TC)

Trunk (TR)

each island independently evolved similar body plans in response to similar natural selection pressures, although the sequence in which the ecomorphs evolved differs among islands (Figure 5.14B). Unfortunately it has not been possible to identify the ecomorph of the founding species, but it is likely that different ecomorphs have been the starting points for radiations on different islands (Losos 2009).

Island paleoendemism

In addition to providing opportunities for new radiations, islands can preserve genetic diversity of relict lineages, a phenomenon known as **paleoendemism**. We saw in our discussion of rhynchocephalians in Chapters 2 and 4 that these reptiles once had a nearly worldwide distribution in

(A)

Shady and moist



Figure 5.13 Microhabitat separation of Puerto Rican Anolis. The six species of Anolis that occur at Maricao in the



mountains of western Puerto Rico divide the habitat by height and by microclimate. (Data from Rand 1964.)



Figure 5.14 Evolution of Anolis ecomorphs. (A) On Puerto Rico, the *cristatellus* lineage of *Anolis* diversified into three ecomorphs. Each pair of sister species differs in its selection of sunny or shady microhabitats. (The crown giant ecomorph present on Puerto Rico is a member of a different lineage and thus does not appear on this cladogram.) (B) Similar ecomorphs evolved independently on different Caribbean islands but the sequence in which they evolved differed. On Cuba, for example, the trunk–crown and twig ecomorphs are sister species, whereas on Hispaniola the crown giant and trunk–ground ecomorphs are sisters. (Data from Rand 1964; Losos et al. 1998; Leal and Fleischman 2002; Losos 2009.)



the Triassic but today exist on only a handful of islands off the coast of New Zealand (although they inhabited the main islands of New Zealand before the arrival of humans). Thus, these islands preserve a lineage of vertebrates that is some 250–240 million years old (Jones et al. 2013). A similar example is leiopelmatid frogs, which represent one of the earliest divergences in frog phylogeny, and almost certainly had a larger range than today. However, over evolutionary time, leiopelmatids became extinct with the exception of a 250-million-year-old lineage in New Zealand that has survived to the present day.

Examples of paleoendemism are not limited to ancient lineages. Lying some 1,000 km east of North America, the island of Bermuda was formed within the last 2 million years with no direct connection to any continent. The island is home to a single species of lizard, *Plestiodon longirostris*. Because North America is home to at least 27 other species of *Plestiodon*, including multiple species that inhabit the east coast of the continent, a reasonable hypothesis explaining the presence of *P. longirostris* on Bermuda is that ancestors of one of these east coast species dispersed to Bermuda within the past 2 million years. However, phylogenetic and molecular divergence analyses support a much more interesting scenario. Instead of a species that is closely related to the east coast species, *P. longirostris* instead represents the earliest split in North American *Plestiodon*, thereby making this species' lineage between 19.8 and 11.5 million years old (Brandley et al. 2010).

What could explain the presence of such an old lineage on an island that is only 2 million years old? The available data suggest that the *P. longirostris* lineage once inhabited North America, eventually dispersed to Bermuda, and subsequently became extinct on the mainland. Because this species is critically endangered, the discovery that *P. longirostris* preserves ancient genetic diversity adds to the importance of conservation efforts.

SUMMARY

■ Biogeography is the study of the geographic distributions of organisms in the past and present, and of the evolutionary and ecological processes that caused these distributions.

Biogeography uses data from natural history, present geographic distribution, phylogenetics, geologic history, and climate.

Biogeography includes numerous subdisciplines, among them island biogeography and phylogeography.

Organisms may become distributed in disjunct areas by two mechanisms: dispersal or vicariance.

A geographic distribution created by dispersal indicates that organisms have migrated across preexisting barriers to create their present distribution.

Dispersal may occur over long distances and over thousands to millions of years (e.g., transcontinental dispersal between North America and Asia via the Bering land bridge).

Overwater dispersal over short distances is a common explanation for species distributions, and there are a handful of examples of transoceanic dispersal across both the Pacific and Atlantic Oceans.

Vicariance occurs by formation of barriers that physically fragment ancestral ranges of organisms, such as mountains, rivers, and fragmentation of continents.

Humans have introduced many species of amphibians and reptiles to non-native habitats throughout the world. These introductions may be intentional (e.g., food for human consumption, pets) but are usually accidental (e.g., stowaways on cargo ships). ■ The breakup of Pangaea into Laurasia and Gondwana, and of Gondwana into multiple continents in the Southern Hemisphere during the Jurassic and Cretaceous, shaped the worldwide distribution of major amphibian and reptile clades.

Fewer amphibian and reptile clades originated in Holarctic Laurasia than in Gondwana. However, several lineages have Holoarctic origins:

- The common ancestor to all extant salamanders and the ancestors of most salamander families inhabited North America.
- Reptile groups that probably originated in Laurasia include anguid, lacertid, and pleurodont iguanian lizards, emydid turtles, and Crocodylia.

Ephemeral historical connections via Beringia and other transatlantic land bridges were important dispersal corridors between North America and Eurasia.

Gondwana began rifting in the Early Jurassic (~180 mya), ultimately separating into West Gondwana (now Africa and South America) and East Gondwana (now Madagascar, India, the Seychelles Islands, Australia, New Guinea, Antarctica, and New Zealand).

Madagascar is topographically complex and has been isolated from Africa for some 160 million years, resulting in both high species diversity and endemism.

India and the Seychelles rifted away from Madagascar approximately 87–60 mya. The Seychelles preserves ancient phylogenetic diversity, including endemic lineages of caecilians and frogs. The collision of the Indian subcontinent into Asia approximately 40 mya introduced Indian fauna to South and Southeast Asia. The Western Ghats mountain range in southwest India preserves many relict endemic lineages that originated long before this collision.

The amphibians and reptiles of Australia and New Guinea include ancient Gondwanan clades and relatively recent colonists from Asia that dispersed during times of low sea level via the Sunda Shelf.

South America is home to a diverse assemblage of amphibians and reptiles. Many lineages, including hyloid frogs and bufonid toads, originated in South America and subsequently dispersed nearly worldwide.

The Central American amphibians and reptiles are a mixture of North and South American lineages. Their dispersal, known as the Great American Biotic Interchange, was greatly aided by the closing of the Isthmus of Panama.

Phylogeography is the study of the biogeography of the recent past and incorporates elements of population genetics to determine what factors shaped the current and past distributions of species or populations.

Pleistocene climate change due to periods of glaciation is one of the most important factors that shaped species distributions in the Holarctic. Periods of drastic climate change shrink the distributions of amphibians and reptiles to smaller areas of suitable habitat called refugia. As the climate returns to its previous state, the species disperse from these refugia to newly available habitat.

Climate change may push suitable habitat for highelevation, cool-adapted species to mountaintops, thereby creating isolated "sky islands" in which these populations evolve in isolation or become extinct.

Islands are particularly interesting to biogeographers because their isolation promotes phylogenetic and morphological diversity.

Continental islands typically have terrestrial connections to the mainland that are exposed when sea levels are low. By contrast, oceanic islands are usually uplifted limestone or volcanic islands and almost never have a direct connection to the mainland.

Islands provide opportunities for specialization (e.g., dwarfism and gigantism), adaptive radiations (e.g., *Anolis* on islands in the Caribbean), and may preserve ancient lineages of organisms that are extinct on the mainland (paleoendemism).

Go to the *Herpetology* Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

PART II How Do They Work?

CHAPTER 6 Water and Temperature Relations

CHAPTER 7 Energetics and Performance

CHAPTER 8 Reproduction and Life Histories of Amphibians

CHAPTER 9 Reproduction and Life Histories of Reptiles

CHAPTER 10 Body Support and Locomotion

CHAPTER 11 Feeding





6

Water and Temperature Relations

A nimals are mostly water. Water makes up between 65% and 75% of the body mass of reptiles and some 75% to 85% of the body mass of amphibians (Shoemaker and Nagy 1977; Hillman et al. 2009). Cells swell or shrink as the volume of water in them increases or decreases, and those changes alter the concentrations of dissolved substances within the cells as well as the configuration of intracellular structures. Blood becomes more viscous as its water content drops, flowing more sluggishly and requiring more effort from the heart to move it. Thus, any departure from an animal's normal water and salt content upsets the balance of its biochemical and physiological processes and may limit its ability to engage in normal behaviors, such as locomotion or capturing prey.

The effect of body temperature is equally profound. The rates of many biochemical reactions approximately double when the temperature increases by 10°C and fall to half the original rate when the temperature decreases by 10°C. This phenomenon is known as the Q_{10} effect. If the rate of a reaction doubles with a temperature change of 10°C, the Q_{10} value is 2, and if the rate decreases by half, the Q_{10} value is 0.5. Not all reactions have the same temperature sensitivity, and Q_{10} values of biochemical reactions extend from 1 (no change in reaction rate as temperature changes) to 3 (tripling of reaction rate) or occasionally even more.

Viewed from a biochemical perspective, an organism is a series of linked chemical reactions, and the product of each reaction is the substrate for the next reaction in the series. If each reaction has a different Q_{10} value, you can imagine what havoc a variable body temperature causes with the integration of cellular processes. To complicate the situation still further, these reactions take place in a cellular environment that also changes with temperature. As temperature increases, the viscosity of cytoplasm decreases, the lipid membranes of cells and cell organelles become more permeable, the rate at which electrical impulses travel along nerve axons increases, and the speed and force of muscular contractions increase. How could an animal function in the face of such chaos? The solution is for an animal to regulate its body temperature and water content so as to minimize the disruptive effects of variation.

The study of how animals exchange heat and water with their environments is known as **biophysical ecology**, and reptiles and amphibians have been especially important in the development of this field because interaction with the physical environment is such a conspicuous part of their lives. Early studies of temperature regulation focused on lizards and were carried out in the Soviet Union and North America (Sergeyev 1939; Cowles and Bogert 1944), and our knowledge has increased greatly since then (reviewed by Angilleta 2009; Hillman et al. 2009). Although water balance and temperature regulation are closely intertwined, we will discuss them separately for the sake of clarity.

6.1 Water Uptake and Loss

Regulating the amount of water in the body requires balancing gain and loss. In a steady state (i.e., no change in body water content), the total intake of water must equal the total water loss, and each side of the water-balance equation has several components:

Gain (liquid water + preformed water + metabolic water) = *Loss* (evaporation + urine + feces + salt glands)

This is a general equation that fits terrestrial or aquatic amphibians or reptiles, but some of the details of water movement apply only to particular situations or certain kinds of animals.

Routes of water gain

All of the water an organism needs for its metabolic processes and to replenish water lost by evaporation or in the feces, urine, and salt glands enters through the mouth or across the skin, and some amphibians and reptiles have structures and behaviors that enhance collection of water. Three sources of water are available to animals: liquid water, preformed water, and metabolic water.

LIQUID WATER Liquid water is what you normally think of as water—that is, enough water molecules collected in one place to form a pool, puddle, drop, or at least a film of water on the surface of a rock or leaf. Amphibians and reptiles make use of all those sources of water.

Many reptiles drink from pools or puddles, just as birds and mammals do. More intriguing are the ways some reptiles have of obtaining liquid water in habitats where puddles rarely form. In deserts, water can disappear into the soil as quickly as it falls, and some reptiles catch water droplets before they reach the ground.

In the Namib Desert of southern Africa, the small lacertid lizard *Meroles anchietae* and the viper *Bitis peringueyi* collect droplets of fog that form when moist air from the sea blows across the cold Benguella Current (Louw 1972; Hen-

(A) Ambush posture



(B) Rain-collecting posture



schel and Seely 2008). The lizard drinks droplets of water that collect on vegetation and can consume nearly 15% of its body mass in 3 minutes. The snake uses its own body surface to collect water, flattening to present a large surface area. The skin of the viper, like that of most snakes, is hydrophobic (i.e., it repels water, much as a freshly waxed car does), and small droplets of water on the skin flow together to form large drops. The snake moves its head along the length of its body, swallowing the water it has collected. *M. anchietae* and *B. peringueyi* occur only in the fog belt of the Namib, suggesting that the collection of water from fog plays a critical role in their overall water balance.

Foggy deserts are limited to coastal locations, but some reptiles and amphibians from inland habitats collect rain (Comanns et al. 2011). The Australian thorny devil (*Moloch horridus*) and several other species of agamid lizards, as well as some species of North American horned lizards (*Phrynosoma*), and several species of vipers harvest rain (Sherbrooke 1990, 1993, 2002, 2004; Vesley and Modry 2002; Glaudas 2009). The rain-harvesting behavior of the Mohave rattlesnake (*Crotalus scutulatus*) has been described by Michael Cardwell (2006). This species normally rests in an ambush posture with the anterior portion of the body lying on the posterior part and the head and neck held in an Sshaped striking position (**Figure 6.1A**). During rainstorms,

> the snake repositions its body like a coiled garden hose, maximizing the area exposed to rain and allowing water to collect between the coils; the head is then inserted between the coils and the snake imbibes the collected water (Figure 6.1B). Like the fog-collecting mechanisms of the Namib reptiles described above, this water-collection mechanism is based on the hydrophobic properties of the scales, which cause water droplets to bead up on the body surface and flow into channels formed between coils of the body.

> In contrast, the water-collection mechanisms of several agamid and iguanid lizards are based on scale surfaces to which water adheres. Many of these lizards adopt a distinctive humpbacked water-collecting posture when they are sprayed with water. Hinges of the scales of *Moloch horridus* and the Texas horned lizard (*Phrynosoma cornutum*) form semienclosed channels that con-

 Head between coils (drinking position)

 Body flattened, channeling water into valleys

Figure 6.1 Rain-harvesting behavior of the Mohave rattlesnake (*Crotalus scutulatus*).

(A) Resting snake in ambush posture. The body is rounded and the head rests over the posterior in a striking position. (B) When it rains, the snake coils and flattens its body, maximizing the area exposed to rainfall and drinking the water that collects between the coils. (From Cardwell 2006; photographs by Michael D. Cardwell.)





(C) Top view



(B)





Figure 6.2 Water transport by lizard skin. (A,B) Both the Australian thorny devil (*Moloch horridus;* A) and the Texas horned lizard (*Phrynosoma cornutum;* B) harvest rain, although *Moloch* lacks a stereotyped rain-harvesting stance. (C) Capillary flow carries the harvested water through a network of channels formed by hinge joints between the scales. Rainwater flows down between the scales into a network of interconnected hinge-joint channels. Capillary flow moves water through the channels. Each jaw movement pulls a little water from the channels into the lizard's mouth and moves water further away in the channel system closer to the mouth. (After Sherbrooke et al. 2007 and Wade C. Sherbrooke, pers. comm.)

duct water to specialized scales at the corners of the mouth (**Figure 6.2**). Soon after a lizard's dorsal surface has been wetted, it begins to open and close its jaws rhythmically with swallowing movements that draw water into the mouth, thereby maintaining the flow of water through the scale channels (Sherbrooke 2004; Sherbrooke et al. 2007).

Condensation of water vapor on the body surface (i.e., the formation of dew) is another potential source of water (Comanns et al. 2011). The body temperatures of nocturnally active amphibians and reptiles can drop below the temperatures in their retreats. If an animal's temperature is below the dew point of the air in its retreat, water vapor may condense on its skin and in its respiratory passages when it returns to its retreat. Condensation equivalent to nearly 1% of an animal's body mass has been measured for a species of gecko and three species of anurans (Lasiewski and Bartholomew 1969; Tracy et al. 2011).

The marginal scutes of some species of turtles curve upward to form a structure rather like a gutter that extends around the margin of the carapace. These turtles adopt a rain-collecting posture, extending their hindlegs to raise the posterior end of the shell and stretching their forelegs parallel to their extended necks (Figure 6.3). Rain runs off the carapace into the gutters formed by the marginal scutes and flows to the front of the shell, where the forelegs channel it to the turtle's mouth. Other turtles, such as the desert tortoises Gopherus agassizii and G. morafkai, build basins to catch water at the bottoms of slopes. The tortoises move to the basins after a rain and drink enough water to increase their body mass by an average of 9.2% (Medica et al. 1980).

Amphibians do not drink; instead, they absorb water through their skin. In general, terrestrial species of amphibians have more permeable skin than do aquatic and arboreal species

(Boutilier et al. 1992; Shoemaker et al. 1992; Hillman et al. 2009). The amphibian hormone arginine vasotocin, or AVT, is closely related to mammalian antidiuretic hormone (ADH). AVT is produced by the posterior lobe of the pituitary (the neurohypophysis) and plays a major role in water balance of semiaquatic and terrestrial amphibians by stimulating the uptake of water through the skin. AVT also reduces water loss by reducing the rate at which urine is produced and increasing reabsorption of water from the bladder.

Most terrestrial anurans have an area of skin called the pelvic patch that is the primary site of cutaneous water absorption. The skin of the pelvic patch is relatively thin and is underlain by a dense network of capillaries. When a dehydrated frog is on a moist surface, it splays its hindlegs, presses its pelvic patch against the substrate, and absorbs water. Permeability of the pelvic patch is controlled by AVT, which initiates a sequence of intracellular processes that culminates with insertion of aquaporins (water conducting channels) into the plasma membranes of the cells.

Spadefoot toads (*Scaphiopus* and *Spea*) make particularly dramatic use of the ability to absorb water through the skin (Ruibal et al. 1969; Shoemaker et al. 1969; McClanahan 1972). These anurans, which inhabit dry desert regions in the American Southwest, spend about 9 months of the year in burrows they construct by digging with the hindlimbs. A western spadefoot (*Spea hammondi*) that is fully hydrated when it burrows into the ground in September or October has a bladder filled with dilute urine—about 100 millimoles per kilogram of water (100 mmol/kg H₂O)—and a blood plasma concentration of about 300 mmol/kg H₂O. From September through March the concentration of urea and the osmolalities* of urine and plasma remain stable, even

Direction of water flow



Figure 6.3 Water-collecting posture of the African hinge-back tortoise (*Kinixys homeana***).** During rainfall events, the tortoise raises the rear of its carapace and extends its neck and forelegs. The marginal scutes of the carapace form a gutter and the forelimbs direct the water to the tortoise's mouth. (After Auffenberg 1963.)

though urea is being produced by metabolism of protein. The lack of change in fluid concentrations during these 7 months indicates that the toads are absorbing water from the surrounding soil.

Between March and June the situation changes and the concentration of urea rises in both the plasma and urine. As urea accumulates, the osmolalities of plasma and urine increase in parallel, with the plasma remaining more concentrated than the urine by about 200 mmol/kg H_2O . By June, just before the summer rains begin, urea concentrations in urine can exceed 300 mmol/kg H_2O and plasma osmolality can reach 500–600 mmol/kg H_2O . These high internal osmolalities may allow the toads to continue to absorb water from the nearly dry soil. The urine, which is always dilute compared with the plasma, provides a source of water to limit the increase in plasma osmolality.

When they are in fresh water, amphibians face an osmotic influx of water. The body fluids of amphibians have an osmolality of about 250 mmol/kg H_2O , whereas the osmolality of fresh water is often as low as 1–2 mmol/kg H_2O . That difference establishes a steep gradient for inward water flow, and the high permeability of amphibian skin means that there is little resistance to the inward movement of water. Excess water is eliminated by producing a large volume of dilute urine. Concentrations of salts inside the body are higher than those in fresh water, so ions diffuse outward. These losses are counteracted by active uptake of ions from the water via the skin and through gills when they are present.

Salt water is a difficult environment for an amphibian, and only a dozen species of salamanders and 61 species of anurans inhabit (or at least tolerate) brackish conditions (Balinsky 1981). These species raise their internal osmolalities by accumulating inorganic and organic solutes in the body fluids. The green toad (*Bufo viridis*) ventures into

^{*} Osmolality, measured in millimoles of solute per kilogram of water (mmol/kg H₂O), refers to the concentration of small molecules or ions in solution.

brackish lakes, maintaining an internal osmolality above that of its environment. Concentrations of sodium, chloride, and urea increase in the blood plasma, but in muscle, free amino acids account for most of the change in osmotic activity. Some populations of salamanders in the genus *Batrachoseps* live on the margins of beaches, where ocean spray deposits salt. Both coastal and inland populations of these salamanders tolerate high environmental salt concentrations by increasing plasma concentrations of sodium and urea.

PREFORMED WATER Most of the food that animals eat contains large amounts of water, so food is a source of **pre-formed water** as well as a source of energy and nutrients. Some 70 to 80% of the body mass of most vertebrates is water, and many insects are in the same range. Plants are more variable in their water content, and the water content of some plant tissues changes seasonally or even from day to night. For example, the plants eaten by chuckwallas (*Sauromalus obesus*) contain 72% water in early May, but by late May the water content falls to 51%. When their food contains less than 63% water, chuckwallas lose more water in their urine and feces than they gain from their food, and they stop eating when the water content of their food plants drops below that level (Nagy 1972).

Because animals generally have more stable water contents than plants, you would think that carnivorous animals could use water from their prey to balance their own water budgets, but that is not always the case. Digesting prey requires an increase in a predator's metabolic rate, and that increases the predator's respiratory water loss. The predator loses still more water in urine and feces as the waste products of the meal are excreted. As a result, a meal can result in a net loss of water. For example, free-ranging Gila monsters (*Heloderma suspectum*) have elevated plasma osmolality in summer, and a meal increases their internal concentration still further (Davis and DeNardo 2010; Wright et al. 2013). Similarly, consumption of fish by sea snakes can produce a net increase in plasma osmolality (Lillywhite et al. 2008).

METABOLIC WATER Metabolic water is the least obvious source of water in the diet of an animal, because it is not in the form of water molecules until hydrogen from chemicals in the food is combined with oxygen to form water. The water formed by cellular metabolism can be substantial: 1 g of starch yields 0.556 g of water, and 1 g of fat produces 1.071 g of water. The amount of water derived from the oxidation of protein depends on whether the end product of protein metabolism is urea or uric acid. Metabolism of protein to urea produces 0.396 g of water per 1 g of protein. Uric acid contains fewer hydrogen atoms per nitrogen atom than does urea, so more hydrogen is converted to water, and the yield is 0.499 g of water from 1 g of protein.

Routes of water loss

An amphibian or reptile can use behavioral and physiological mechanisms to control the magnitude of its water loss and, to some extent, the routes by which water leaves the body.

EVAPORATION Evaporation from the skin is the major route of water loss for most terrestrial amphibians, but reptilian skin has low permeability and cutaneous water loss plays a relatively small role in the water balance of most reptiles (Lillywhite and Maderson 1982, 1988; Shoemaker et al. 1992; Lillywhite 2006; Hillman et al. 2009). The stratum corneum (Latin, "horny layer") is the outermost layer of the skin and is formed by dead cells that contain the protein keratin. The stratum corneum of amphibians is only a single cell layer thick and contains little keratin, whereas the stratum corneum of reptiles consists of multiple layers of a lipid-keratin complex. In terrestrial amphibians, a wet film of fluid secreted by mucus glands protects the epidermis from dehydration, but it evaporates water rapidly. A few amphibians apply a waxy layer of lipids over the stratum corneum to reduce water loss. In the skin of all reptiles and mammals a lipid-keratin complex in the stratum corneum reduces the permeability of the epidermis (Figure 6.4).

Most amphibians lose water rapidly by cutaneous evaporation, but arboreal frogs have rates of evaporative water loss that are only one-half to one-third those of typical amphibians. Cutaneous resistance is measured as the time water takes to diffuse through the skin and is expressed as seconds per centimeter (s/cm) of skin thickness. On this scale, low numbers mean rapid diffusion and permeable skin, whereas high numbers indicate slow diffusion and impermeable skin.

A comparison of skin resistances among amphibians suggests that there are three groups with different skin permeability (Lillywhite 2006; Wells 2007):

- 1. Terrestrial and aquatic amphibians have very low cutaneous resistances (0.05–10 s/cm), and these species evaporate water essentially as rapidly as a free water surface.
- 2. A second group, mostly arboreal hylids and rhacophorids, have cutaneous resistances of 10–120 s/cm.
- 3. Waterproof frogs (many species of *Chiromantis* and *Phyllomedusa*) have cutaneous resistances of 200–900 s/cm.

To provide comparison, a free water surface has a resistance of 0 s/cm, most birds and mammals have resistances between 200 and 400 s/cm, and the highest cutaneous resistances—more than 1,000 s/cm—are found among desertdwelling squamates.

The basis of high resistance to water loss among amphibians is best understood for arboreal hylids, such as the waxy leaf frog (*Phyllomedusa sauvagii*). This large South American frog lives in seasonally arid regions and spends the day perched in bushes exposed to the wind. Its skin contains an abundance of small glands that secrete a mixture of wax esters, triglycerides, free fatty acids, hydrocarbons, and cholesterol. When a frog assumes its resting posture, it wipes its



Epidermis

corneum

Dermis

Figure 0.4 Skin structure and permeability. Simplified cross sections of skin show the barriers to water movement. (A) Amphibian stratum corneum consists of a single layer of cells. The skin surface of terrestrial amphibians is covered by a layer of watery mucus secreted by mucus glands located in the dermis. (B) Lipid glands in the dermis of some arboreal frogs secrete a waxy mixture of compounds that the frog wipes over the stratum corneum (see Figure 6.5), creating a barrier to water loss. (C) Reptile epidermis consists of layers of stratified mature β keratin with stratified mature α keratin below. Mesos layers contain keratin and lipids that form a barrier to water loss. When the outer generation (OG) cells are shed, the inner generation (IG) cells become the outer generation and a new inner generation forms. (After Lillywhite 2004, 2006.)

body with its forelimbs and hindlimbs (Figure 6.5). Wiping stimulates mucus glands, and the frog spreads the waxy fluid over its entire body (Blaylock et al. 1976; McClanahan et al. 1978). Two rhacophorid frogs (*Chiromantis petersi* and *Polypedates maculatus*) and several species of hylid treefrogs engage in similar wiping behavior (Barbeau and Lillywhite 2005). Lipids from cutaneous glands are probably respon-

OG

IG

sible for the high resistance to water loss of other arboreal species of anurans in environments that pose a risk of dehydration (Lillywhite 2006).

Cocooning is another way that amphibians reduce cutaneous water loss. Several species of anurans as well as the salamander *Siren intermedia* that live in seasonally arid habitats bury themselves in soil and form a cocoon. Co-

Figure 6.5 Wiping behavior of the waxy leaf frog (*Phyl-lomedusa sauvagii*). The wiping behavior is highly stereotyped. (A) Both hindfeet are simultaneously wiped forward from the vent, across the parotoid glands, and (B) down across the sides, forelimbs, ventrolateral surfaces of the body, and finally over the hindlimbs and the dorsal surfaces of the hindfeet. (C) The forelimbs are used sequentially, each wiping forward from the parotoid gland across the eyes to the snout, down the throat, and across the ventral body surface. Wiping takes about 4 minutes, after which the frog remains motionless on its perch with its eyes closed and limbs drawn against its body. (Photographs courtesy of Rodolfo Ruibal.)







Figure 6.6 Cocoons formed by shed skin cells and mucus reduce the rate of cutaneous water loss.

(A) An empty cocoon of the African bullfrog *Pyxicephalus adspersus*. (B) A cross section of the cocoon of the South American frog *Lepidobatrachus llanensis* reveals its layered structure. (Photographs: A, © Image Quest Marine/Alamy; B, courtesy of Rodolfo Ruibal.)

coons are formed by layers of shed skin or mucus (Figure 6.6), and their resistance to water loss increases with time. Fully formed cocoons have water loss resistances that are as much as 50 times higher than skin resistance (Lillywhite 2006). The primary function of cocoons is probably to reduce the rate of water loss to dry soil (Reynolds et al. 2010).

Reptilian skin is relatively impermeable to water and ions (Lillywhite and Maderson 1982; Lillywhite 2006). Lipids in the skin form the primary barrier to water movement, and removal of lipids from shed skins by treatment with organic solvents increases permeability as much as 30-fold (Roberts and Lillywhite 1980, 1983). Cutaneous permeability is high in hatchling reptiles and falls to adult levels after the first shed, when the embryonic skin is replaced by adult skin with a different lipid composition (Lillywhite 2004). Some snakes wipe lipids on their skins; for example, a lamprophiid snake, *Malpolon monspessulanus*, wipes lipid-containing secretions from its nasal gland over its body (Dunson et al. 1978). These lipids may reduce cutaneous evaporation, but lipid-based pheromones are also important sex attractants for some snakes (Lillywhite 2004).

RESPIRATORY WATER LOSS The gas exchange surfaces of the lungs are delicate and would dry out if they were exposed to dry air. Evaporation of water from the nasal passages raises the humidity of inhaled air, and by the time this air reaches the lungs the air is saturated with water vapor. Some of the water used to humidify the inhaled air is recovered as water condenses on the surfaces of the nasal passages during exhalation, but exhaled air normally contains more water than inhaled air. The difference in water content between exhaled and inhaled air is respiratory water loss.

Both amphibians and reptiles experience respiratory water loss, but the low rates of cutaneous water loss of reptiles make respiratory water loss a larger part of total water loss for these animals than for amphibians. Generalizations about the magnitude of respiratory water loss are difficult, however, because respiratory rates of both amphibians and reptiles increase as their body temperatures increase, and respiratory water loss shows a corresponding increase. Furthermore, rates of both cutaneous and respiratory water loss change as the humidity of the air around an animal changes. The air in a burrow or tree hollow is normally more humid than air outside the shelter, and an animal can change its rates of evaporative water loss behaviorally by moving between sheltered and exposed locations.

URINE AND FECES Urine is a fluid that contains nitrogenous waste products plus ions—mostly sodium, potassium, chloride, and bicarbonate. It is produced in the kidney in a structure called the glomerulus, where blood pressure forces water and small molecules out through the capillary wall. This filtrate of the blood flows through the kidney tubules, where it can be modified by reabsorption of water and reabsorption or excretion of ions and small molecules. Ultimately the urine is gathered by the collecting duct, which empties either into the bladder or directly into the cloaca (Latin for "sewer"; the *cloaca maxima* was the main sewer of ancient Rome).

Nitrogenous wastes are produced when amino groups are removed from proteins in the process of digestion and metabolism. Some of the nitrogen is used to synthesize new protein, and the rest is excreted. Depending on the primary form of the excreted nitrogenous waste, species are described as **ammonotelic**, **ureotelic**, or **uricotelic**. The suffix *-tele* is from a Greek root meaning "end"; hence these terms indicate, respectively, that ammonia, urea, or uric acid is the end product of nitrogen metabolism. The three end products are found in varying proportions in the urine of amphibians and reptiles.

Ammonia (NH₃) is the chemical produced by the removal of an amino group from a protein, and it is very soluble in water. It doesn't require energetically expensive biochemical synthesis, and its solubility means that a lot of nitrogen can be excreted in a small volume of urine. Ammonia has a serious drawback as a waste product, however, because it is extremely toxic and must be excreted rapidly. Aquatic species do this; ammonia leaves the body across the skin and gills as well as in urine, but ammonotely is not an option for terrestrial vertebrates.

A biochemical pathway called the urea cycle converts ammonia to urea (CH₁ON₂), consuming 4 moles of adenosine triphosphate (ATP) per mole of urea produced. Thus, ureotely requires more energy than ammonotely, but urea is even more soluble in water than ammonia and is only slightly toxic. Thus, terrestrial vertebrates can excrete urine with high concentrations of urea.

Reptiles excrete uric acid (C₅H₄O₂N₄), although ammonia and urea are also present and the proportions of the three compounds shift in relation to the availability of water (Dantzler and Bradshaw 2009). Excretion of uric acid has also been described for two genera of frogs, Phyllomedusa (Hylidae) and Chiromantis (Rhacophoridae).

Uric acid is a purine that is synthesized via several interlocking pathways and requires 24 moles of ATP per mole of uric acid produced. Unlike ammonia and urea, uric acid is very insoluble in water. Urine in the reptilian kidney tubule is dilute, so the uric acid remains in solution. When the urine enters the bladder or the cloaca, water is reabsorbed, concentrating the solution, and some of the uric acid precipitates. This precipitation reduces the concentration of the fluid, allowing more water to be reabsorbed, which causes additional precipitation of uric acid. The result of this cycle of reabsorption of water and precipitation of uric acid is a white or gray semisolid material containing salts of uric acid, and enough water to give it a pasty consistency. Thus, the insolubility of uric acid, combined with precipitation in the bladder or cloaca, allows nitrogen to be excreted with relatively little water.

The semisolid urine produced by reptiles is a complex chemical mixture of uric acid, ions, and other compounds (Minnich 1972; Minnich and Piehl 1972). The potassium salt of uric acid (potassium urate) is an important component of this mixture, and many reptiles excrete a substantial portion of their excess potassium as potassium urate. Indeed, excretion of potassium actually competes with protein synthesis for the nitrogen in a reptile's diet. Mohave

desert tortoises (Gopherus agassizii) eating food with a high potassium concentration were unable to retain nitrogen, even on high-nitrogen diets (Oftedal et al. 1994). A tortoise needs 1.3 g of nitrogen for each 1 g of potassium simply to excrete the potassium it eats.

Urine and feces are excreted together through the cloaca. Thus, excretory products of reptiles emerge as a semisolid mixture of white or gray salts of uric acid and dark fecal material. That color combination will be familiar to anyone who has ever parked a car under a tree where birds roost.

Amphibians produce large volumes of dilute urine, and this urine is stored in a bladder that can be astonishingly large, especially among anurans. These animals use their urine as a source of water that can be reabsorbed if it is needed, and the size of the bladder is related to how terrestrial a species is and how arid its habitat is. Aquatic anurans and salamanders such as Xenopus, Triturus, and Necturus have bladders that hold a volume of urine equivalent to 1-5% of the body mass of the frog (i.e., 1-5 g of urine for a frog that weighs 100 g), whereas terrestrial anurans have bladders that can hold a volume of urine equivalent to 20-60% of the frog's mass (Hillman et al. 2009). Australian aborigines use water-holding frogs, Cyclorana, as a water source during the dry season. They dig the frogs from their burrows and squeeze them, emptying their bladders. An adult frog can produce half a glass of clear, tasteless urine. Of course, that's the death knell for the frog, which counts on the urine in its bladder to survive until the next rainy season.

SALT GLANDS Many reptiles have a step in the process of urine formation that appears paradoxical: they reabsorb potassium and sodium ions from urine after it has passed into the bladder or cloaca. Transporting ions across cell membranes against an electrochemical gradient requires ATP. What makes that process peculiar is that the ions that are reabsorbed were already in the urine ready to be excreted. The animal used energy (via the blood pressure in the glomerulus of the kidney) to get those ions into the urine—why is it now using more energy to bring those ions back into the blood?

The solution of this paradox lies in the presence of an extrarenal (i.e., outside the kidney) route of salt excretion-

TABLE 6.1 Reptilian salt glands				
n <u>alu=n</u> ä	Lineages	Salt-secreting gland		
Lizards	Agamidae, Cordylidae, Crotaphytidae, Dactyloidae, Iguanidae, Lacertidae, Phrynosomatidae, Scincidae, Teiidae, Troganophidae, Varanidae, Xantusiidae	Nasal gland		
Snakes	Acrochordidae, Hydrophiinae, <i>Laticauda</i> Homalopsidae (<i>Cerberus</i>)	Posterior sublingual gland Premaxillary gland		
Turtles	Cheloniidae, Dermochelyidae, Malaclemys terrapin	Orbital gland		
Crocodylians	Probably all Crocodylidae, but not Alligatoridae or Gavialidae	Lingual glands		

Source: Babonis and Brischoux 2012.

a salt gland (**Table 6.1**). Sea turtles and sea snakes have specialized glands that excrete sodium and chloride at high concentrations (Dunson 1976; Minnich 1982). Insects and plants—the dietary staples of many lizard species—contain high levels potassium and bicarbonate, and the salt glands of lizards are more versatile: in addition to excreting sodium and chloride, the nasal salt glands of lizards also excrete potassium and bicarbonate (Hazard 2004). The proportions of ions in gland secretions probably reflect their relative abundance in the diet of an animal, and can be altered by changing the ratio of the ions in the



diet (Hazard 2001, 2004; Hazard et al. 2010). Using the salt gland instead of the kidney to excrete ions saves water, because the total concentrations of salt gland secretions can be greater than 2,000 mmol/kg H_2O , which is about seven times the maximum osmolal concentration of urine (Figure 6.7).

The locations and embryonic origins of reptilian salt glands are diverse despite their similarity in function. Many lizards secrete salt from glands that empty into the nasal passages, and sea snakes have a salt-secreting gland on the tongue sheath (**Figure 6.8A,B**). Sea turtles and the diamondback terrapin (*Malaclemys terrapin*) have a saltsecreting gland in the orbit of the eye (**Figure 6.8C**). (Desert tortoises do not have salt glands and depend on their kidneys to excrete salts; that is why the nitrogen:potassium ratio of their food plants is so critical.) All species of croco**Figure 6.7 Secretory characteristics of some reptilian salt glands.** Because the plants and insects they eat contain more potassium than the vertebrate body does, the salt gland secretions of herbivorous and insectivorous terrestrial lizards, such as the desert iguana (*Dipsosaurus dorsalis*) and the fringe-footed lizard (*Uma scoparia*), contain concentrations of potassium ions (K⁺) more than 100 times greater than plasma concentrations of K⁺. In contrast, sodium (Na⁺) and chloride (Cl⁻) are the major ions excreted by the salt glands of marine reptiles (yellow-bellied sea snake, *Hydrophis platurus*; loggerhead sea turtle, *Caretta caretta*; and saltwater crocodile, *Crocodylus porosus*). Their salt gland secretions contain these ions at concentrations 3 to 8 times higher than the plasma.



Figure 6.8 Locations of reptilian salt glands. Salt-secreting glands have evolved independently in different lineages of reptiles. (A) The nasal gland, which extends from the nasal region posteriorly over the eye, is the salt-secreting gland of lizards. A desert iguana is shown here. (B) In file snakes and sea snakes, such as the vellow-bellied sea snake, the posterior sublingual gland secretes salt. (C) The lacrymal gland of sea turtles such as the loggerhead secretes salt. The fluid is released via the tear ducts and is the source of the tears that can often be seen on the faces of nesting sea turtles. (D) Saltwater crocodiles have multiple small salt-secreting glands on the surface of the tongue.

diles that have been studied have salt-secreting glands on the surface of the tongue (**Figure 6.8D**). The diversity in the salt glands of extant reptiles and the patterns of presence and absence of salt glands indicate that salt glands were evolved, lost, and evolved anew several times during the phylogenetic history of the lineages.

6.2 ■ Water and the Ecology of Amphibians and Reptiles

The availability of water in an animal's habitat and the behavioral and physiological mechanisms the animal uses to obtain water can play a profound role in shaping its daily life. Any driver in a rural area has observed that amphibians are likely to be out on the roads on wet nights, and these nights are also when nocturnal species of frogs and salamanders are foraging most actively. The eastern redbacked salamander (*Plethodon cinereus*) emerges from the leaf litter on the forest floor on wet nights and searches for prey on the stems of plants. Plants appear to be good places to forage—salamanders collected on plants have significantly more prey items in their stomachs than do those sampled foraging in the leaf litter—but only on wet nights can salamanders climb plants to reach those prey items (Jaeger 1978).

When you remember that most amphibians have skin that provides little barrier to evaporative water loss, it's not surprising that their water balance is often in a state of flux. Most amphibians appear to balance their water budgets on a time scale of hours to days, and they use a variety of behavioral and physiological mechanisms to do this. Reptile skin is less permeable than that of amphibians, and water flux is slower for most reptiles than for most amphibians. Some reptiles balance their water budgets on time scales extending from days and weeks to months. A few reptiles appear to be out of water balance for such long periods that it may be more useful to think of them as having inherently variable salt and water concentrations rather than a set concentration from which they deviate.

Short-term water balance

The costs and benefits of adjusting behavior to control water loss on a daily basis can be seen in the night-to-night activities of the Puerto Rican coquí (*Eleutherodactylus coqui*) (Pough et al. 1983). This small arboreal frog spends the day in a sheltered retreat in the understory vegetation of the forest. Soon after dusk, male coquís emerge and move to their calling stations, which are tree trunks or leaves only a meter or two from their retreat sites. Up to this point the behavior of the frogs is nearly independent of the weather; male frogs move to their calling stations soon after dusk on both wet and dry nights.

The subsequent behavior of the frogs, however, does depend on the weather, and especially on the availability of water in the forest understory (Figure 6.9). During the rainy season in Puerto Rico, thunderclouds build through the morning and early afternoon, and by late afternoon and early evening it is often raining heavily. The rain penetrates the forest canopy and wets the frogs' calling sites in the understory vegetation. The rain usually stops in late afternoon, but the forest is still wet at dusk. On nights like this a male coquí stands in the high-alert posture with its legs extended, holding its trunk above the substrate (see Figure 6.9D). A frog in this position is exposing nearly its entire surface area to the atmosphere—only the soles of its feet are in contact with the substrate. Furthermore, each time the frog calls (see Figure 6.9E), the trunk and vocal sac inflate and deflate, disrupting the boundary layer of air around the frog. This pumping action mixes the air that is in contact with the frog's skin (which is saturated with water vapor) with the ambient air (which is not saturated with water vapor). Thus, the combined effects of exposing the entire body surface to the atmosphere and of disrupting the boundary layer by calling produce the highest rate of evaporation.

Some days rain does not fall, even in the rainy season, and the forest is dry when coquís emerge in the evening. Or sometimes only a little rain falls and the leaf surfaces dry off before midnight. Under these conditions, male coquís do

Figure 6.9 Behavioral control of evaporative water loss by male coquí (*Eleutherodactylus coqui***).** Postures of a male frog in order of increasing exposure of the body surface to evaporation. (A) Water-conserving posture (seen in many anurans). The frog's trunk and chin are pressed against the substrate, its legs and feet are in contact with the body, and the eyes are closed. (B) In this less extreme water-conserving position, the chin is lifted and the eyes are open. (C) An active male on low alert. (D) High alert. Almost the entire body surface is exposed to the atmosphere. (E) Calling. This position and behavior involve the highest rate of evaporation from the skin surface. Thus, male coquís typically call only on wet nights. (Photographs by Harvey Pough.)



not call very often, and instead spend most of the evening in postures that reduce the rate of evaporative water loss by exposing only part of the body surface to air. The waterconserving posture (see Figure 6.9A) is the most extreme of these postures and is adopted by many anurans when they are in dry situations. In the water-conserving posture a frog presses its trunk and chin against the substrate, draws its legs and feet into contact with the body, and closes its eyes. A frog in water-conserving posture exposes only half as much of its surface area to the air as it does in high-alert posture, and its rate of evaporative water loss is correspondingly reduced.

A frog benefits from adopting the water-conserving posture by reducing its rate of evaporative water loss, but it pays a price. Male frogs in the water-conserving posture are not vocalizing, and as a result they have no chance of attracting a mate. That may not be a serious cost, however, because on dry nights female coquís are not moving through the forest understory seeking mates. Like male coquís, females are resting in the water-conserving posture. However, coquís also sacrifice the opportunity to capture prey when they are in the water-conserving position (Woolbright and Stewart 1985). Resting with their eyes closed, they do not respond when an insect passes close to them. Insects are at least as abundant in the forest understory on dry nights as they are on wet nights, but many coquís return to their daytime retreats with empty stomachs after a dry night, whereas at the end of a wet night nearly all frogs have prey in their stomachs.

Thus, behavioral control of the rate of evaporation via postural adjustments allows male coquís to remain at their calling stations on a dry night, but only at the cost of not vocalizing or feeding under those conditions. The waterconserving posture minimizes water loss but does not stop it entirely. On dry nights male coquís lose an average of 8% of their initial body mass between dusk and dawn. That change in weight represents water lost by evaporation, but the tissue water content of the frogs does not change. The frogs reabsorb water from urine in their bladder to maintain the normal water content of their body tissues. Thus, they combine a behavioral response that minimizes evaporative water loss with a physiological response that preserves the normal tissue water content to withstand the rigors of a dry night. The frogs return to moist retreat sites at dawn and rehydrate through their pelvic patches during the day. Thus, they are ready to resume activity with a fresh water reserve in the bladder the next evening. A daily cycle of water loss and rehydration of this sort is probably characteristic of many terrestrial anurans, and it may apply to some salamanders as well.

Long-term water balance

Some reptiles tolerate long periods of high salt concentrations in their extracellular body fluids (Bradshaw 1986). For example, the small Australian lizard *Ctenophorus ornatus* eats mainly ants, which have a high sodium content. These lizards do not have salt-secreting nasal glands, so the only way they can excrete sodium is in the urine, and that requires a substantial loss of water. Instead of excreting sodium and losing water during dry spells, the lizards allow sodium to accumulate to twice its normal concentration in their extracellular fluids. Only when it finally rains and the lizards are able to drink do they excrete the excess sodium and return their body fluid concentrations to normal levels.

The Mohave desert tortoise (Gopherus agassizii) is a large herbivore found in California and Nevada. The variability of rainfall in these deserts produces year-to-year changes in the availability of food and water, and the tortoises are frequently out of water and salt balance for months at a time (Nagy and Medica 1986). A study of the water budget of these tortoises revealed large and prolonged deviations from normal body fluid and solute concentrations (Peterson 1996). In May and June of 1989 about 65% of the tortoises' body mass was water, but a drought in the summer of 1989 greatly reduced the growth of the annual plants that are the mainstay of the animals' summer diet. During this time the tortoises lost as much as 40% of their initial body mass, and the average body water content dropped below 60%. Sodium, chloride, and urea concentrations in the blood plasma increased, and the average osmolality of the blood plasma rose from about 300 mmol/kg H₂O to 400 mmol/kg H₂O. Some tortoises had osmolalities above 500 mmol/kg H₂O-among the highest values ever recorded for a vertebrate.

Urine in the bladder is a key element of the salt and water balance of desert tortoises. When rain falls, tortoises drink and then defecate, emptying the cloaca and bladder. The bladder is refilled with dilute urine and serves as a repository for potassium and nitrogenous wastes and as a source of water for the tortoises. The osmolality of the plasma is initially maintained at about 300 mmol/kg H₂O by withdrawing water from the bladder. Once the urine in the bladder is as concentrated as the blood plasma, the osmolalities of the two body compartments increase in parallel (**Figure 6.10**).

The importance of summer showers in the water budget of Mohave desert tortoises is shown clearly by changes in plasma and urine osmotic activity before and after a rainstorm (Figure 6.11). The tortoise in this example drank once during a rainstorm in May 1989 and filled its bladder with dilute urine. During June, July, and August the tortoise was able to maintain its plasma osmolality at 300 mmol/kg H₂O by withdrawing water from the bladder. By September 1989 the osmolality of its urine had risen to 300 mmol/kg H₂O; after that, urine and plasma concentrations increased in parallel until the late summer of 1990. The tortoise obtained a single drink in September 1990, which allowed it to flush out the wastes it had accumulated, returning its plasma osmotic activity to 300 mmol/kg H₂O, and then refill its bladder with dilute urine. Thus, the tortoise went 16 months between drinks and tolerated an elevated osmolality for an entire year.

Rainfall is a critical factor in the water balance of another group of reptiles—the marine elapids known as sea snakes



Figure 6.10 Urine as a water reserve for the Mohave desert tortoise (Gopherus agassizii). Withdrawal of water from urine in the bladder to stabilize plasma osmolality is illustrated by these measurements for individual tortoises. The diagonal line shows equal osmolal concentrations of plasma and urine. Urine osmolalities are initially as low as 50 mmol/kg H₂O and rise to 300 mmol/kg H₂O as tortoises withdraw water from the bladder to maintain plasma osmolalities near 300 mmol/ kg H₂O. As additional water is withdrawn from the urine, the osmolalities of urine and plasma rise in parallel, ultimately reaching 550 mmol/kg H₂O. (After Peterson 1996.)

(**Figure 6.12**). Sea snakes display a range of marine specializations, from sea kraits (*Laticauda*) that capture prey at sea but return to land to rest, digest their food, and lay eggs, to hydrophiine sea snakes that are viviparous and spend their entire lives at sea. Some species of hydrophiines forage at depths of 100 meters or more and remain underwater for 2 hours. Sea snakes occur primarily along coasts and is-

> lands of the Indian and western Pacific oceans. A single species, the yellowbellied sea snake (*Hydrophis platurus*, formerly *Pelamis platurus*), is pelagic, ranging across the tropical Pacific from Central America to Asia. This species uses a float-and-wait hunting strategy to capture small fish (Brischoux and Lillywhite 2011).

> Sea snakes have salt glands (see Figure 6.8B) that excrete Na⁺ and Cl⁻ at concentrations from 400 to 800 mmol/kg H_2O (Minnich 1982), but nonetheless they dehydrate at sea and must drink fresh water to remain in water balance (Lillywhite 2013). Species of sea kraits that spend time on land drink from puddles during rainstorms, and species

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Figure 6.11 Rainstorms are critical components of the water balance of desert tortoises. Concentrations of

Gesert tortoises. Concentrations of blood plasma and urine of a male Mohave desert tortoise (*Gopherus agassizii*) were tracked for 18 months. Cloud icons mark rainfalls of 5 mm or more. (A) A body condition index (body mass divided by carapace length cubed) reflects the hydration state of the tortoise as well as its energy stores and muscle mass. (B) Osmolalities of plasma and urine. Plasma osmolality varies less than urine osmolality because water is withdrawn from the bladder to stabilize the osmolality of plasma and body tissues. (After Peterson 1996.)



that live in coastal areas obtain fresh water from springs and streams, but hydrophiines depend on rainfall (Bonnet and Brischoux 2008; Lillywhite et al. 2008; Brischoux et al. 2012a,b). Fresh water is less dense than seawater, and rainstorms can create a lens of fresh water that floats at the surface of the sea. Sea snakes, including the pelagic yellow-bellied sea snake, drink from this freshwater lens (Lillywhite et al. 2012, 2014).

Rainstorms that create a lens of fresh water are intermittent, and sea snakes become dehydrated during the intervals between storms. Yellow-bellied sea snakes collected after periods without rainfall were dehydrated by at least 18% body mass, and probably more (H. B. Lillywhite, pers. comm.), and

this species may spend more than half of its life in negative water balance (Lillywhite et al. 2014). Coastal species of sea snakes are also dependent on rain, and the species richness of sea snake communities is directly related to mean annual rainfall; an average of only 6 species of sea snakes occur in sites that receive less than 80 mm of rain per year compared with an average of 19 species in areas that receive more than 80 mm of rainfall (Lillywhite et al. 2008).

6.3 Heat Gain and Loss

The energy-balance equation summarizes the routes of energy exchange between an animal and its environment. In its simplest form, the energy-balance equation for a steadystate situation is:

Heat energy gained = Heat energy lost

The full energy-balance equation includes a term for each of the major routes of heat gain or loss for an organism:

Heat energy gained = $Q_{abs} + M \pm R \pm C \pm LE \pm G$

All these values are rates expressed in units of watts per square meter (W/m^2) of animal body surface. (A watt is 1



joule per second.) Temperatures are expressed as absolute temperature (Kelvin, K), which is equal to the temperature in degrees centigrade plus 273.16. The symbols have the following meanings:

- Q_{abs} = Radiation absorbed by the surface of an animal
- M = Metabolic heat production
- *R* = Infrared radiation received or emitted by the surface of an animal
- C = Heat gained or lost by convection to the fluid surrounding an animal (the fluid is air for a terrestrial animal and water for an aquatic animal)
- *LE* = Heat gained by condensation or lost by evaporation
- *G* = Heat gained or lost by conduction through direct physical contact of an animal with the substrate it is resting on (soil, rock, tree trunk, etc.)

A detailed treatment of biophysical models is beyond the scope of this book; you can find a readable account of the assumptions and approximations that underlie the models in O'Connor and Spotila (1992) and more detail in Tracy



Figure 6.13 Biophysical pathways of energy gain and loss. The lizard, with a body temperature of 37°C, is gaining heat from direct, scattered, and reflected solar radiation, and by conduction from the hot ground (45°C). It is losing heat to the air (35°C) by convection, and also by evaporation. The lizard is both

(1982), Spotila et al. (1992), and Fei et al. (2012). Here we will briefly explain each pathway of energy exchange and give examples of how amphibians and reptiles use them during temperature regulation. Many components of temperature regulation are easy to observe in the field and even with preserved specimens in a collection. Figure 6.13 summarizes the pathways of energy exchange.

Absorption of solar radiation, Q_{abs}

This term refers to the solar energy absorbed by the animal. The entire spectrum of solar radiation extends from very short wavelengths, such as X-rays, to very long wavelengths, such as radio waves. However, only a portion of the solar spectrum is relevant to the thermoregulatory mechanisms of amphibians and reptiles. The wavelengths we are concerned with extend from approximately 400 to 700 nm (visible light) and from 700 to 1,500 nm (nearinfrared light). The total amount of light energy reaching Earth's surface is divided almost equally between the visible and the infrared, and these are the wavelengths that amphibians and reptiles use for thermoregulation. Ultraviolet (UV) light—wavelengths from about 200 to 400 nm—does not play a significant role in thermoregulation. Quanta of UV light have high energy, which is why gaining and losing heat via infrared radiation: it gains heat from sunlit surfaces (such as the rock to the lizard's right) that have surface temperatures higher than 37°C, and loses heat to shaded surfaces (cooler than 37°C). The lizard is also losing heat by radiation to the clear sky, which has a radiant temperature of 23°C.

they can damage living tissue, but the amount of UV light (i.e., the number of quanta) reaching Earth's surface is too small to significantly affect the body temperature of an organism.

 $Q_{\rm abs\prime}$ the rate of solar-energy absorption by an animal, is given by the equation

$$Q_{abs} = S \bullet A \bullet v f_s \bullet a$$

where

- S = intensity of solar radiation (W/m²)
- A = surface area of the animal in m²
- vf_s = view factor for solar radiation (i.e., the proportion of the animal's surface that the sun shines on)
- a = absorptivity to solar radiation (i.e., the proportion of solar energy striking the surface that is absorbed rather than reflected)

These factors offer an animal substantial control over the amount of solar radiation it absorbs. The easiest component of Q_{abs} for an amphibian or reptile to control with behavioral adjustments is *S*, the intensity of solar radiation to which it is exposed, and the animal does it exactly as you would—by moving between sun and shade.
(A) Neutral orientation



Shadow area = 1.62

(C) Negative orientation



Reptiles and amphibians can also change surface area and the view factor. For example, a lizard can change its surface area by spreading or compressing its rib cage, and it can change its view factor by changing its orientation to the sun (**Figure 6.14**). When a lizard is cool and trying to warm up, it adopts a positive orientation to the sun, spreading its ribs widely and orienting itself so the long axis of its body is nearly perpendicular to the sun's rays. In this situation, the sun strikes the entire dorsal surface of the lizard's body and the lizard casts a large shadow. A lizard in this posture intercepts the maximum amount of solar radiation possible. At the opposite extreme, when a lizard is hot and trying to minimize the amount of solar radiation it receives, Figure 6.14 Changes in posture and orientation can have large consequences for thermoregulation. The area of shadow cast by a Texas horned lizard (Phrynosoma cornutum) in three postures. (A) Not oriented. The ribs are relaxed and the sun is overhead. (B) Positive (warming) orientation. The ribs are spread, making the body nearly circular, and the lizard faces away from the sun and extends the forelegs so that its body surface is nearly perpendicular to the sun's rays. (C) Negative (cooling) orientation. The ribs are compressed to make the body narrow, and the lizard faces into the sun and extends its forelegs so that its body is nearly parallel to the sun's rays. The size of the lizard's shadow is proportional to the amount of sun intercepted. If the area of the shadow when the lizard is not oriented is 1.00, then the area of the shadow when the lizard is in positive orientation is 1.62. When it is in negative orientation the shadow area is 0.28. In other words, the lizard can change the amount of solar radiation it intercepts by a factor of 5.8 (1.62/0.28) simply by changing its posture and orientation. In addition to adopting a negative orientation, the lizard in (C) is resting on its heels and toe tips to minimize contact with the hot sand, and the smooth, shiny surfaces of its ventral scales reflect much of the infrared energy radiated by the sand. It is also cooling its head by panting.

it adopts a negative orientation, compressing its ribs and facing directly into the sun. In this position the sun strikes perpendicularly only on the lizard's head and shoulders and the lizard casts a much smaller shadow.

Many amphibians and reptiles can change color, and what you are seeing when you perceive a change in color is a change in absorptivity. A light-colored object appears light because it is reflecting light energy; a dark object looks dark because it is absorbing light instead of reflecting it. Lightening and darkening are accomplished by movements of granules of the dark pigment melanin in cells called melanophores found in the dermal layer of the skin. When melanin granules are concentrated in the body of the melanophore, the reflective pigments in other cells are exposed. A lizard in this condition appears light-colored. When the melanin is dispersed toward the surface of the skin, the granules cover the other pigments and absorb some of the light that strikes the lizard, making the animal appear darker. Light absorbed by melanin is converted into heat, thus warming the lizard.

Desert iguanas (*Dipsosaurus dorsalis*) can change color substantially (**Figure 6.15A**). In their darkest phase they absorb 73.7% of the visible light that strikes them, compared with 57.5% when they are in their lightest phase. That difference in absorptivity changes the rate at which a desert iguana heats by 0.42°C/min (Norris 1967). By midday, desert iguanas are so reflective that they are conspicuous—but by that time potential predators have retreated to the shade. Some frogs use color change to reduce absorptivity; for example, the African hyperoliid frog *Hyperolius viridiflavus* can increase its reflectivity by 22% by changing the orientation of guanine crystals in iridophore cells in the skin (Kobelt



Figure 6.15 Thermoregulatory changes in color. (A) The body temperature of a desert iguana (*Dipsosaurus dorsalis*) is near 35°C when it emerges from its burrow in the morning (left), and its dark color at this time speeds warming as it basks in the sun. By midday (right), the lizard's body temperature exceeds 40°C and it has turned light and climbed to the top

and Linsenmair 1992). The skin of some hylid frogs also lightens as it warms (**Figure 6.15B**) (Tattersall et al. 2006).

Metabolic heat production, M

Metabolic pathways are not 100% efficient. Some chemical energy is lost as heat when ATP is synthesized and again when it is hydrolyzed. A few large reptiles use metabolic heat production to accelerate heating and retard cooling, or even to maintain their body temperatures above ambient levels. Pure ectothermy and pure endothermy are the ends of a continuum of thermoregulatory patterns, and many species occupy intermediate positions. (The use of metabolic heat for thermoregulation is described in Section 6.5.)

Infrared (thermal) radiative exchange, R

Heat exchange takes place continuously between an animal and its environment in the near infrared (thermal) part of branches of a bush, where the wind speed is higher. (B) The South American hylid frog *Bokermannohyla alvarengai* lightens as it warms from 18°C to 28°C. (Photographs: A, left, © B. Christopher/Alamy; A, right, © Melody Marks; B from Tattersall et al. 2006, photographs by Glenn Tattersall and Denis Andrade.)

the electromagnetic spectrum (700–1,500 nm). Any object with a surface temperature above absolute zero (0 K, or –273.16°C) radiates energy in the infrared. Thus, during every moment of its life an organism radiates infrared energy from its surface to its surroundings and receives infrared radiation from its surroundings. The net heat transfer is from the hotter surface to the colder surface. You can easily perceive this phenomenon when you stand beside a wall that has been heated by the sun. The warmth you feel is infrared radiation from the wall.

The magnitude of heat flow depends on three variables:

1. The difference between the fourth powers of the absolute temperatures of the two surfaces—that is, $T_s^4 - T_e^4$, where T_s is the surface temperature of the animal and T_e is the surface temperature of the object in the environment with which it is exchanging radiation, both measured in Kelvin units.

- 2. The area of the animal exposed to thermal radiation—that is, $A \bullet vf_{t'}$ where A is the surface area and vf_t is the the view factor for thermal radiation (i.e., the proportion of the animal's surface that is receiving thermal radiation)
- 3. The infrared **emissivity** of the skin (represented by ε, the Greek letter epsilon), which provides information about how readily a surface radiates and absorbs infrared radiation

It is difficult to have an intuitive understanding of the thermal emissivity of the skin because few of the structural characteristics that determine emissivity are visible. Color does not provide a clue to how a surface behaves in the infrared, because color is the result of a surface's response to visible wavelengths. Thus, the statement that a black surface absorbs infrared radiation and a white surface reflects it is simply wrong, despite its appearance in some biology textbooks. The best visible cue to the infrared absorptivity and emissivity of a surface is its texture. Matte surfaces generally absorb and emit infrared radiation well, whereas smooth, shiny surfaces are poor absorbers and emitters of infrared.

Many lizards, especially species that live in open desert habitats, have scales with different infrared absorptivity on their dorsal and ventral surfaces. For several hours during the day the surface temperature of the sand is 60°C or even higher. The scales on the ventral surface of the lizards are smooth and shiny, and they reflect the infrared radiation that streams up from the sand, reducing the heat absorbed by the lizard. The scales on the dorsal surface of the lizards' bodies have a matte surface that is a good absorber and emitter of infrared radiation. When the lizards are basking in the sun in the morning, the high infrared absorptivity of these scales increases the rate of heating. Later in the day, when avoiding overheating is the problem, a lizard perched on the shady side of a rock can use the high emissivity of its dorsal scales to exchange thermal radiation with the sky. A clear sky behaves like an object with a surface temperature about 23°C, so the net movement of heat is from the lizard, which has a surface temperature about 37°C, to the sky.

Convective exchange of heat, C

Convective exchange occurs between an animal and the fluid medium surrounding it. For terrestrial animals the fluid is air, whereas for aquatic animals it is water. The principles of convective exchange are the same for either fluid, and for the sake of simplicity our discussion will consider a terrestrial animal in air.

Three variables are important in determining the magnitude of convective heat exchange between an animal and its environment:

1. The temperature difference between the animal and the air, that is, $T_s - T_{a'}$ where T_s is the animal's surface temperature and T_a is the air temperature

- The surface area of the animal exposed to convection, which can be changed by altering posture, or body shape
- 3. The convective coefficient of the animal, which depends on (a) the velocity of air movement and (b) the size of the animal, expressed as a measurement known as the characteristic dimension, which is roughly equivalent to the diameter of the animal in the direction parallel to airflow and can be modified by changing orientation.

Animals can adjust convective heat exchange by shuttling back and forth between still and moving air. One way to do this is to climb into a bush. Wind speed increases and air temperature decreases with height above the ground surface, and many lizards take advantage of that thermal profile by climbing into bushes during the hot part of the day. Air temperatures and wind speed change rapidly in the first 0.5 m above the ground, so a lizard does not have to climb very far to be in cooler air and a stronger breeze.

Evaporative cooling, LE

In addition to being an important part of water balance, evaporation plays a role in the energy balance of an organism because a substantial quantity of heat is needed to change water from a liquid to a vapor. The amount of energy required varies with temperature, and 128 J/g H₂O is an approximate value for biologically relevant temperatures.

The evaporation of water occurs in two stages. Initially water or water vapor must cross the barrier imposed by the skin; then water vapor must be moved away from the outer surface of the skin by convection. Either process can be the one that limits the rate of evaporation, depending on the permeability of the skin, the humidity of the air, and the rate of air movement.

Movement of water through the skin is the step that limits the rate of evaporation for reptiles. As we've noted, these animals have lipids in their skin that reduce permeability to water. As a result, evaporative water loss normally plays a small role in the energy balance of most reptiles. In many cases the heat lost by evaporation is approximately equal to the heat produced by metabolism.

Some reptiles increase respiratory water loss as a thermoregulatory device by accelerating evaporation from the oropharynx and cooling blood passing through these tissues (Tattersall et al. 2006). Many lizards breathe rapidly and shallowly (i.e., they pant) when overheated. Crocodylians and some lizards gape their mouths, exposing the moist tissues of the mouth and pharynx. These mechanisms maintain brain temperatures as much as 6°C below air temperatures. Gila monsters (*Heloderma suspectum*) expose cloacal mucosa at air temperatures above 35°C, increasing evaporative water loss and maintaining body temperatures as much as 3°C below air temperature (**Figure 6.16**) (De-Nardo et al. 2004).



Figure 6.16 Cloacal cooling by a Gila monster (Heloderma suspectum). (A) Evaporative water loss was measured by placing lizards in a chamber with compartments for the head and body. Each compartment had a separate flow of air to allow cutaneous and respiratory water loss to be distinguished. Cloacal water loss was calculated as the difference in evaporative water loss in the body compartment for animals with and without a diaper, which prevented evaporation of water from the cloaca. (B) Cloacal water loss increased abruptly at air temperatures above 35°C, whereas respiratory and cutaneous water loss showed only small increases across the entire temperature range. (C) Cloacal water loss reduced body temperature; at an air temperature of 40°C. Gila monsters without diapers had body temperatures more than 3°C below air temperature, whereas animals wearing diapers had body temperatures only 1.5°C below air temperature. (After DeNardo et al. 2004; photograph courtesy of Dale DeNardo.)

Evaporative cooling is a major element of the energy balance of most amphibians because their rates of cutaneous evaporation are high (Tracy et al. 2010). The body temperatures of amphibians are usually slightly lower than air temperature at night and when they are in shade during the day. Even when amphibians are in direct sunlight, evaporative cooling prevents most species from reaching the high body temperatures that are characteristic of lizards. Waterproof frogs, especially species of *Chiromantis* and *Phyllomedusa*, are exceptions to that generalization.

Conduction, G

Conduction refers to the transfer of heat to or from the surface on which an animal is resting or the fluid medium it is in. For some reptiles and amphibians, especially nocturnal species, surfaces that were heated by the sun during the day are a source of heat—snakes resting on asphalt roads at night are conspicuous examples of this mode of thermoregulation.

The surface area of the animal that is in contact with the substrate is an important factor that determines the magnitude of conductive heat exchange. In forest habitats you can watch foraging lizards move into a patch of sunlight and flop down on their bellies, maximizing conduction of heat from the warm ground by increasing the area of contact. In hot deserts you may see lizards standing with their legs



extended and their toes in the air. When a lizard stands this way, only a small part of its foot is actually in contact with the hot soil and conduction of heat is minimized.

Animals exchange heat with the fluid that surrounds them as well as with the substrate. For animals that live on land, this route of exchange is relatively unimportant, because air has a low heat capacity and low heat conductivity. For aquatic animals, however, conduction is a major source of heat exchange. Large animals can maintain body temperatures above water temperature, but small aquatic animals can only take advantage of temperature gradients in the water. For example, tadpoles of several different anuran species spent nights in deep water when that was the warmest part of the pool, moved into the shallows in the morning when the water was warmed by the sun, and then moved back into deeper water later in the day when the shallows became too warm (Brattstrom 1962).

6.4 ■ Mechanisms of Thermoregulation

Amphibians and reptiles use morphological, behavioral and physiological mechanisms to control body temperature. Several terms are used to describe thermoregulation: **heliotherms** (from the Greek *helios*, "sun," and *therm*, "heat") are animals that rely primarily on solar radiation to raise their body temperature, whereas **thigmotherms** (from the Greek *thigm*, "touch") rely on conduction of heat from the substrate. Most species of amphibians and reptiles employ both heliothermy and thigmothermy, shifting from one to the other according to the current environmental conditions. Some species, called **thermoconformers**, do not maintain body temperatures different from environmental temperatures.

Heliothermy

Heliothermic temperature regulation can be relatively easy for a reptile in an open, sunny habitat. A small lizard, for example, can position itself on the line between the sunny and shaded side of a tree trunk and adjust its balance of heat gain and loss by shifting just a few millimeters toward the sun or shade.

Relatively easy does not necessarily mean simple, however. **Figure 6.17** illustrates the interplay of behavioral and physiological mechanisms of thermoregulation for a Texas horned lizard (*Phrynosoma cornutum*). Like many lizards, the Texas horned lizard begins activity after sunrise, when it emerges from its nighttime shelter. The lizard has spent the night buried in loose soil, and at first it pokes only its head out of the soil. Blood is pooled in the head by constricting the internal jugular veins, and this mechanism accelerates warming of the brain.

After an initial period of basking with only its head exposed, the lizard emerges fully from the soil. At this stage the lizard's body temperature is still low, and it maximizes its rate of heating by darkening, spreading its ribs to increase its surface area, and adopting a positive orientation to intercept as much solar radiation as possible (see Figure 6.14B).

The activities of a horned lizard are limited in space and time by its thermoregulatory requirements. For example, during the early morning and late afternoon a lizard must be in the sun, whereas during the middle of the day the environment is so hot that it must remain in the shade. On particularly hot days a lizard might have to climb into a bush to take advantage of lower air temperature and greater convection at that height. Finally, on extremely hot days a lizard may cease activity entirely and burrow into cool soil. This behavior protects it from high temperature but precludes feeding and the other activities the lizard would normally engage in.

Most amphibians have only a limited capacity for behavioral regulation of body temperature because the cooling effect of evaporation of water from the skin counteracts the



Figure 6.17 Thermoregulatory activities of a Texas horned lizard (*Phrynosoma cornu*-

tum). Thermoregulation is a constant part of the behavior of P. cornutum. When its body temperature is in the basking range, the lizard engages in activities that accelerate heating. It begins to forage for food when its temperature reaches the activity range. At the upper end of the activity range, it changes to behaviors that minimize heating. When it is not possible to maintain body temperature within the basking or activity ranges, the lizard burrows into the soil. Evaporative cooling (i.e., panting and cloacal discharge) are emergency cooling measures that increase water loss and thus are used only if the animal's body temperature approaches lethally high levels. (After Heath 1965.)



Figure 6.18 Temperature regulation by an adult Andean toad (Rhinella spinulosa). At an elevation of 3,200 m, adult toads combine heliothermy and thigmothermy. On sunny days the toads moved into the sun between 7:30 and 8:30 AM and basked for several hours. They reached maximum body temperatures before noon and then retreated to shade. On cloudy and rainy days, the toads were primarily thigmothermal. Even under complete cloud cover, their body temperature equaled or slightly exceeded the air temperature. (After Sinsch 1989; photograph courtesy of Robert E. Espinoza.)

heat gained by basking while an animal is active, and water loss can force an amphibian to cease activity and move to a retreat site (Tracy et al. 2010).

Salamanders and caecilians appear to regulate their body temperatures primarily by selecting suitable microenvironments, but some frogs are heliotherms. On sunny days, Andean toads (*Rhinella spinosa*) reach body temperatures up to 23°C before moving to shade (**Figure 6.18**) (Sinsch 1989). Adult toads are solitary, but newly metamorphosed Andean toads gather in groups to bask. Because these toads are so small (average of 0.4 g and 15 mm snout-vent length), the body temperature of an individual toad is strongly affected by air temperature. An aggregation of toads acts as a larger object in terms of routes of energy exchange, however, and toads in groups have higher temperatures than individual toads (**Figure 6.19**). This higher body temperature can increase a toad's growth by 13.6% during its first activity season (Espinoza and Quinteros 2008).



Figure 6.19 A basking aggregation of recently metamorphosed Andean toads. The baby toads were on a sunward-facing bank in a wet meadow at an altitude of 4,323 m in the Andes Mountains. Representative body temperatures of individuals are shown. Toads in groups (red labels) were warmer than solitary toads (blue labels). In the morning, when air temperatures were low, the mean body temperature of toads in groups was 3.2°C higher than the mean body temperature of solitary toads. The difference decreased as air temperature warmed; it was 2.5°C at midday, and by afternoon aggregated toads were only 0.9°C warmer than solitary toads. (After Espinoza and Quinteros 2008; photograph by Robert E. Espinoza.)



Figure 6.20 Some frogs balance solar heating with evaporative cooling. High rates of evaporation combined with acceasing reflectivity when their body temperatures are high allow these frogs to remain in the sun without overheating. The Arizona canyon treefrog (*Hyla arenicolor*) (A) and the Brazilian

hylid frog *Bokermannohyla alvarengai* (B) spend most of the day motionless in a water-conserving posture. In contrast, the Australian hylid *Litoria meiriana* (C) forages actively on rocks during the day. (Photographs: A, R. D. Bartlett; B, Glenn J. Tattersall and Denis V. Andrade: C, Christopher R. Tracy.)

Waterproof frogs such as Phyllomedusa and Chiromantis spend prolonged periods-up to months-perched on exposed branches without rehydrating. Their waterproof coating can be so effective that a frog may overheat on a sunny day-a body temperature of 41°C has been recorded for the waxy leaf frog (Phyllomedusa sauvagii) (McClanahan and Shoemaker 1987). Both species secrete watery mucus onto the skin surface if their body temperature rises too high. Two additional methods of increasing evaporative cooling have been demonstrated for Phyllomedusa: (1) The epidermal layer of wax that waterproofs a resting frog melts at high temperatures, making the body surface permeable to water and allowing evaporative cooling to take place. (2) A frog opens its eyes as its brain temperature approaches a stressfully high level, and evaporation from the moist surface of the cornea cools the brain (Shoemaker and Sigurdson 1989).

Some anurans with permeable skins use evaporative cooling to engage in activities that would not otherwise be possible (Figure 6.20). Arizona canyon treefrogs (Hyla arenicolor) live near streams in small canyons in desert foothills. They spend the day resting on boulders several meters away from the stream, and a frog may be in full sun for several hours. The rocks themselves become nearly too hot to touch, but the frogs remain cool because they are losing water by evaporation. A plausible explanation of this seemingly unfroglike behavior is based on the risk of predation during the day. Black-headed garter snakes (Thamnophis cyrtopsis) are predators of the frogs, and the snakes forage in the water and along the banks of the stream. The rocks beside the stream are too hot for the snakes to cross during the heat of the day, however, and a frog on a boulder is safe (Wylie 1981). Because of the cooling effect of evaporative water loss through their permeable skin, the frogs can remain on the boulder even when the sun is shining directly on them (Preest et al. 1992). When the frogs must rehydrate, they cross the baking rocks to reach a stream or pool in a series of leaps and return to their resting sites in the same manner.

Another small hylid frog, *Bokermannohyla alvarengai* from Brazil (see Figure 6.15B), also rests on sunny rocks during the day (Tattersall et al. 2006; Denis Andrade and Glenn Tattersall pers. comm.). Both *Hyla arenicolor* and *B. alvarengai* are motionless, but an Australian hylid, *Litoria meiriana*, forages on sunny rock surfaces during the day (Tracy et al. 2013). This frog is tiny, about 0.75 g, and Christopher Tracy (pers. comm.) speculates that relying on evaporative cooling allows it to feed during the day when it is too hot for predators to be active. The large surface-to-volume ratio of *L. meiriana* both promotes evaporative cooling and allows it to rehydrate rapidly.

Thigmothermy and kleptothermy

When conditions are favorable, thigmothermy is an effective mechanism of thermoregulation. For example, granite night lizards (*Xantusia henshawii*) live in crevices beneath exfoliating flakes of granite on boulders. Despite their common name, these lizards are active during the day, moving between outer regions of the crevices and deeper recesses as the temperature changes (Mautz and Case 1970).

Kleptothermy (from the Greek *klept*, "thief") is closely related to thigmothermy. Kleptotherms are ectotherms that gain heat from the metabolic heat production of endotherms. For example, sea snakes and tuatara that shelter in burrows occupied by seabirds have higher body temperatures than those in burrows without birds (**Figure 6.21**) (Brischoux et al. 2009; Lane and Shine 2011; Corkery et al. 2014).

Reptilian embryos provide an unexpected example of thigmothermy. Embryos of the Chinese soft-shelled turtle (*Pelodiscus sinensis*) and of Reeve's turtle (*Mauremys* [Chine-



Figure 6.21 Kleptothermy by a sea kraits. The body temperature of a bluebanded sea krait (*Laticauda laticauda*) shows the effectiveness of kleptothermy. The snake was in a burrow occupied by a pair of seabirds (shearwaters) from January 5 to 8. During this period the snake's body temperature varied only slightly, between 37.1°C and 37.9°C (dashed line). The temperature of an unoccupied burrow was also stable, but cooler, whereas the temperature of the open beach fluctuated drastically, falling to 21.5°C and rising as high as 61.5°C. (After Brischoux et al. 2009 and F. Brischoux, pers. comm.)

is a dangerously high temperature for them. The movement required for embryonic thermoregulation uses energy, and hatchling Chinese soft-shelled turtles from embryos that were forced to reorient every 3 days were smaller than hatchlings from control eggs (Zhao et al. 2014). Embryonic thermoregulation is not limited to turtles; it has also been observed in snakes, alligators, and birds (Li et al. 2014).

Set-point temperatures

Heliothermic and thigmothermic reptiles regulate their body temperature between upper and lower set points. The

> preoptic nucleus of the hypothalamus is the temperature-sensitive region of the brain, and experiments have shown that the temperature of this region controls thermoregulatory behavior (Morrison and Nakamura 2011). The preoptic nucleus itself is temperature-sensitive, and it also receives input from peripheral temperature sensors and integrates information about the temperature of the body and the brain. When the hypothalamic temperature is below the low-temperature set point, cold-sensitive neurons fire and stimulate behavioral and physiological adjustments that result in raising the body temperature-for example, increasing exposure to sunlight, darkening the skin, and adopting a positive orientation. When the hypothalamic temper-

Figure 6.22 Turtle embryos thermoregulate in their eggshells. The position of the embryo of a Chinese soft-shelled turtle (*Pelodiscus sinensis*) changes in response to the location of a heat source. (A) When heat comes from above the egg, the embryo rotates so that it faces upward. (B) When heat comes from the left side, the embryo rotates so that it faces the heat source. (C) When the heat source is moved, embryos rotate to match the new orientation. (After Du et al. 2011; photographs courtesy of Wei-Guo Du.)

mys] *reevseii*) rotate within their eggshells to orient to a source of heat (Du et al. 2011; Zhao et al. 2013). Chinese soft-shelled turtle embryos rotated when the source of heat was moved from the left side of the egg to the right (**Figure 6.22**), and Reeve's turtle embryos moved toward temperatures of 29°C and 30°C, but moved away from 33°C, which





Figure 6.23 Set-point temperature range of the desert iguana (*Dipsosaurus dorsalis*). The orange bars

dorsalis). The orange bars show the temperatures at which iguanas in a laboratory temperature gradient shuttled from one end of the gradient to the other to warm up (at the low body-temperature set points, mean value 34.6°C) or cool off (at the high bodytemperature set points, mean value 44.6°C). The dashed line shows the distribution of body temperatures of lizards in the gradient. Approximately 50% of measurements of body temperature fall between 37°C and 41°C, with a modal value of 39°C. (After Withers 1992.)

ature exceeds the upper set point, heat-sensitive neurons fire and stimulate a set of behaviors that will reduce body temperature. In general, these responses are the opposite of the previous ones—for example, moving into shade, lightening the skin, and adopting a negative orientation.

Set-point temperatures are most often measured in laboratory temperature gradients, which provide an environment in which thermoregulation can be separated from other activities, such as social behavior, avoiding predators, and searching for prey. The central 50–80% of body temperatures measured in a gradient is considered to be the set-point temperature range (Angilletta 2009), and it can be as narrow as 2–5°C for heliothermic lizards. The most informative way to describe the thermoregulatory characteristics of a species is to say that it has a set-point temperature range of, for example, 37°C to 41°C (**Figure 6.23**).

Species of reptiles have characteristic set-point temperature ranges, and these tend to be conservative within evolutionary lineages (Avery 1982). Amphibians also can be characterized by temperature selection, but amphibians generally thermoregulate less precisely than reptiles do (Brattstrom 1979; Hillman et al. 2009).

Digestion, pregnancy, and infection can produce transient shifts in the set-point temperature ranges of reptiles, and probably of amphibians as well. In general, starvation lowers the set-point temperature range of amphibians and reptiles, and feeding sometimes leads to selection of higher temperatures (reviewed by Gvoždík 2003; Andrade et al. 2005; Wall and Shine 2008; Angilletta 2009). Many laboratory studies have shown an increase in set-point temperature after a meal. For example, in a thermal gradient the snake *Elaphe obsoleta* increased its average body temperature by nearly 2°C after feeding. The role of postprandial (after a meal) thermophily in the field is less clear. Free-ranging *E. obsoleta* showed no change in temperature after a meal, but they did regulate their body temperatures more precisely after eating (Blouin-Demers and Weatherhead 2001). The chemical processes of digestion themselves generate heat, and the surface temperatures of rattlesnakes increased by 0.9–1.2°C after they had been fed, even in the absence of an external heat source (Tattersall et al. 2004) (**Figure 6.24**).

Females of most viviparous reptiles increase the setpoint temperature range when they are pregnant, but a few species reduce the set-point temperature range (summarized by Shine 1980; Angilletta 2009). A life-history model that includes the effects of body temperature on the viability of the current litter and its effects on the future fecundity of the female provides a close match to the body temperatures of female lizards measured in the field (Beuchat and Ellner 1987).

Behavioral fevers occur widely among ectothermal vertebrates in response to viral, bacterial, and parasitic infections (Zimmerman et al. 2010). Higher body temperatures enhance the immune response of infected animals, increasing survival (reviewed by Kluger et al. 1998). Infected animals raise their set-point ranges in thermal gradients. For ex-



Figure 6.24 Digestive thermogenesis of a rattlesnake. Infrared thermal image of a rattlesnake before feeding (A) and 48 h following a meal (B). The scale bar shows a total range of 2°C, where black is the coldest temperature and white is the warmest. The uniform color of the body surface temperature following feeding shows that warming is not confined to the stomach. The darkest spot in each image is the nose, where evaporative cooling leads to a significantly reduced temperature. (Photographs courtesy of Glenn J. Tattersall.)

ample, desert iguanas (*Dipsosaurus dorsalis*) increased both upper and lower set-point temperatures by about 2°C after receiving an injection of killed bacteria (**Figure 6.25**). In a separate study, lizards were infected with living *Aeromonas hydrophila* bacteria and held at temperatures between 34°C and 42°C for a week. Survival increased with temperature (Vaughn et al. 1974; Kluger et al. 1975)

6.5 ■ Physiological Mechanisms of Thermoregulation

Although reptiles and amphibians are ectotherms and their metabolic rates are low compared with those of endotherms, physiological mechanisms contribute to thermoregulation (reviewed by Bartholomew 1982; Seebacher and Franklin 2004).

Moving heat within the body

The circulatory system transports heat as well as oxygen, and a basking lizard can speed warming by increasing transfer of heat from the skin to the body core. Three mechanism are involved in this adjustment:

- 1. Blood vessels in the skin dilate.
- 2. Heart rate increases.
- An intracardiac right-to-left (pulmonary-to-systemic) shunt increases the blood flow in the systemic (i.e., body) circulation.

A lizard can retard cooling by making the reverse adjustments: constricting cutaneous circulation, slowing the heart rate, and shutting down the intracardiac shunt. These phys-



Holding temperature (°C)

lesert igua-
ter injectionnas infected with live cultures of A. hydrophila as a function of
temperature. After one day, 75% of the lizards held at 34°C had
died, while all of the lizards held at 42°C were alive. After 7 days,
all of the lizards held at 34°C were dead, but mortality at 42°C
was only 25%. (After Vaughn et al. 1974; Kluger et al. 1975.)



iological adjustments allow an Australian bearded dragon (*Pogona barbata*) to heat twice as fast as it cools, and thus spend more time in its set-point temperature range (Bartholomew and Tucker 1963).

All reptiles can probably control their rates of heating and cooling to some extent. Large animals have more capacity for these adjustments than do small animals, but some very small lizards, such as the green anole (*Anolis carolinensis*; 2–7 g) and the six-lined racerunner (*Aspidoscelis sexlineatus*; 4–7 g), can exert some control over their rates of heating and cooling. Even snake embryos are able to heat faster than they cool (Du et al. 2013).

Circulatory and behavioral thermoregulatory mechanisms work together, and the Galápagos marine iguana (*Amblyrhynchus cristatus*) provides an elegant example of this interaction (White 1973). Marine iguanas live at the edge of the sea on barren lava flows where there is no shade at midday. The Galápagos Islands lie on the Equator, and by midday the black lava rock becomes very hot. Many of the iguanas move into shaded cracks and crevices, but others use circulatory adjustments and the cool trade winds to create a heat shunt that absorbs solar radiation from the dorsal surface of the body and dumps it through the ventral surface.

The iguana faces into the sun, with the forepart of the body held off the ground (**Figure 6.26**). The iguana's ventral surface is exposed to the cool wind blowing off the ocean, and a patch of lava under its body is shaded. The warmth of the sun shining on the dorsal skin causes blood vessels in the skin to dilate, increasing blood flow to the dorsal surface and carrying heat away from the back. As that warm blood flows through vessels on the ventral surface, it causes

them to dilate. Warm ventral skin loses heat by convection to the cool breeze and by infrared radiation to the cool lava. By combining these physiological adjustments with appropriate behaviors, such as selecting a site where the breeze is strong and minimizing the amount of direct sunlight it receives by facing into the sun, a male iguana can remain in its territory all day.

Metabolic heat production

All of the reptiles that have a substantial endothermal component to their thermoregulation are large species, which means that their surface area-to-volume ratios are relatively low. A small surface area for heat loss in relation to the volume of tissue that is producing heat is a first step toward retaining enough metabolic heat to raise the body temperature.

The leatherback sea turtle (Dermochelys coriacea) is the largest extant turtle. Adults of this pelagic species can weigh more than 850 kg. Leatherbacks range north and south into water as cold as 8-15°C, and dive to depths of 1,200 m or more where the water can be as cold as 0.4°C. Metabolic heat is produced by muscular activity as the turtles swim, and by digestion of the jellyfish they eat. Arteries and veins in the limbs lie close to each other, creating a countercurrent heat exchange system that use heat from arterial blood to rewarm cold venous blood as it returns from the flippers. In addition, adipose tissue insulates the head and neck, and a vascular plexus in the trachea minimizes respiratory heat loss. The mean body temperatures of leatherback sea turtles in the North Atlantic range from 25°C to 27°C, which is 11-12°C above water temperature (Casey et al. 2014).



Figure 6.26 A Galápagos marine iguana (Amblyrhynchus cristatus) acting as a regulated heat shunt.

By facing into the sun, the iguana minimizes the amount of solar radiation it absorbs and creates a shaded area beneath its body. Dilation of cutaneous capillaries in the skin allows blood to transport heat from the dorsal side of the body to the ventral side. Heat is lost via infrared radiation from the ventral skin to the shaded rock beneath the lizard. Trade winds blowing across the cool ocean facilitate convective cooling of the lizard's body and of the shaded area beneath it. (After White 1973; photograph courtesy of Robert Rothman.)

Several species of pythons use metabolic heat production to maintain body temperatures of about 30°C while they are incubating eggs. This use of endothermy is seen only in female pythons when they are preparing to lay eggs and brooding their eggs. A gravid female deposits her eggs in a cavity in an earthen bank or beneath a log, then gathers the eggs into a heap and curls around them, enclosing them with her body (Figure 6.27A). Heat is produced by muscular thermogenesis-spasmodic contractions of the muscles. The snake twitches visibly with each contraction. These twitches are produced by coordinated contraction of muscle fibers, and they are different from the uncoordinated muscle contractions that are responsible for mammalian shivering. The frequency of contractions by a snake are at a minimum at approximately 31°C and increase as temperature falls (Figure 6.27B). While a snake is brooding eggs, her metabolic rate at an air temperature of 25.5°C is about 20 times the rate of a nonbrooding snake at the same temperature (Figure 6.27C). A brooding female python adjusts her metabolic rate to maintain a stable core body temperature, keeping the temperature of her body near 32°C at air temperatures from 25.5°C to 31.5°C (Figure 6.27D) (Brashears and DeNardo 2013).



Figure 6.27 A Burmese python (*Python bivatattus***) brooding her eggs.** (A) This captive-bred albino python was 3.2 m long and weighed 16.3 kg. Her clutch, enclosed within the coils of her body, consisted of 42 eggs with a total weight of 6.1 kg. For this study, gravid female pythons were placed in an enclosed chamber the size of a natural nest cavity. Measurements were made at chamber temperatures of 25.5°C, 28.5°C, and 31.5°C. Instruments measured the snakes' body temperature and temperature of their clutch, muscular contractions (twitches), and metabolic rate (CO₂ production); some of the electrical leads of these instruments are visible. (B) The average rate of twitching at 25.5°C was nearly twice the rate at 31.5°C. (C) Metabolic rate increased at low temperatures when snakes were brooding clutches, whereas the metabolic rates of the same two individuals decreased at lower temperatures when they were not brooding. (D) The snakes' body temperatures did not change significantly as the chamber temperature expected without thermogenesis by a brooding female; both body and clutch were always warmer than the expected temperature. (After Brashears and DeNardo 2013; photograph courtesy of Jake A. Brashears.)

6.6 ■ Effectiveness of Thermoregulation

The thermoregulatory activities of amphibians and reptiles are often conspicuous, but defining the effectiveness of thermoregulation has been difficult because several related but distinct questions are involved (Hertz et al. 1993).

We need to know three things to evaluate the effectiveness of thermoregulation:

- What are the body temperatures (T_b) of the animals while they are thermoregulating?
- 2. What would their body temperatures be if they were not thermoregulating but were merely scattered randomly through the habitat? That is, what are the operative (environmental) temperatures (T_e) in that habitat?
- 3. How well do *T_b* and *T_e* match the set-point temperature (*T_{set}*) of that species?

Figure 6.28 Thermoregulation by Puerto Rican Anolis. (A) Anolis cristatellus lives in open habitats and is a heliotherm. (B) A. gundlachi lives beneath the forest canopy and is a thermoconformer. In each of the paired graphs, the upper graph shows the distribution of body temperatures (T_{b}) for active lizards in August, while the lower graph shows the distribution of operative temperatures (T_{a}) in the lizards' environments. The vertical bars (tan) show the set-point temperature range for lizards from the studied population as measured in the laboratory; in each case the lower set-point temperature is about 2°C below the upper set point. (After Hertz et al. 1993. Photographs: A, Kentwood D. Wells; B, courtesy of Manuel Leal.)

Figure 6.28 shows the effectiveness of thermoregulation of two species of Anolis from Puerto Rico. We are interested in how closely the lizards' body temperatures match the set-point ranges compared with how closely the operative temperatures are to those ranges. If the lizards are thermoregulating effectively, their body temperatures will be closer to the set-point temperatures than the operative temperatures will be.

Comparing the data for Anolis gundlachi and A. cristatellus reveals three differences:

- 1. A. gundlachi has a lower set-point temperature range-about 24-26°C compared with about 28-30°C for A. cristatellus.
- 2. The mean Tb of A. cristatellus was 27.2°C, which is below its set-point range.
- 3. The mean Tb of A. gundlachi was 25.7°C, which is within its set-point range.

Does the fact that the mean T_b of A. gundlachi is within its set-point range but that of A. cristatellus is below its set-point mean that A. gundlachi is a more effective thermoregulator than A. cristatellus? Calling gundlachi's thermoregulation effective hardly seems fair, because it isn't actively regulating anything. Its body temperature is no different from the operative temperature of the habitat, and the temperatures of twigs and pebbles are as close to the set-point temperature range as the lizards are.

In August, Anolis cristatellus had a mean body temperature of 27.2°C, which is 2.5°C below the lower boundary of its set-point temperature. The mean operative temperature of the environment was 23.4°C, however, which is 5.0°C below the lower set-point temperature. In other words, the thermoregulatory behavior of A. cristatellus brought its body temperature closer to its set-point temperature range than it would have been without thermoregulation.

Paul Hertz and his colleagues (1993) formulated a mathematical method of distinguishing species that are thermoconformers from species that are thermoregulators by





comparing the difference between average body temperature of the lizards and the set-point temperature (d_p) and the difference between the average operative temperature and the set-point temperature (d_s) :

E (effectiveness of thermoregulation) = $1 - (d_p/d_p)$

Anolis cristatellus has an effectiveness value of 0.50, whereas the effectiveness for A. gundlachi is only 0.14 (Table 6.2). Thus, the value of E distinguishes between thermoconformers like A. gundlachi that can be in their set-point temperature ranges without thermoregulating, and spe-

TABLE 6.2 Thermoregulation by Puerto Rican Anolis in August ^a								
Species	T _{set}	Mean T _b	Mean T	Mean d _b	Mean d _e	$E = 1 - \left(\frac{\text{mean } d_b}{\text{mean } d_e}\right)$		
A. cristatellus	28.1-29.7°C	27.2 ± 0.3°C	23.4 ± 0.1°C	2.5 ± 0.2°C	5.0 ± 0.1°C	0.50		
A. gundlachi	24.3-26.1°C	25.7 ± 0.1°C	25.1 ± 0.1°C	0.6 ± 0.1°C	0.7 ± 0.1°C	0.14		

TABLE 6.2	Thermoregulation by	y Puerto Rican Anolis in August ^a	
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Based on data from Hertz et al. 1993.

^aMean values are + standard error.

cies like A. cristatellus that can get closer to their set-point temperature ranges by thermoregulating, even though they cannot quite reach their set-point temperature. In January, A. cristatellus has a mean $T_{\rm h}$ of 23.5°C, which is 4.6°C below the low end of the set-point range. The mean T_e in January is only 19.0°C, however, which is 9.1°C below that low end. Thus, A. cristatellus thermoregulates effectively even in winter (E = 0.46).

The spatial distribution of suitable microclimates affects the cost of thermoregulation, and lizards thermoregulate in extreme environments when the benefits outweigh the costs (Blouin-Demers and Nadeau 2005; Sears and Angilletta 2015). For example, even north of the Arctic Circle the lacertid lizard Zootoca vivipara reaches its set-point temperature by careful thermoregulation. For these warm lizards, increased foraging effectiveness, faster prey handling, faster locomotion, and a greater capacity to escape from predators apparently more than balance the costs of thermoregulation in this particular habitat (Herczeg et al. 2003).

6.7 ■ The Coevolution of Energy and Water Exchange

The body temperature and evaporative water loss of an organism are linked in ecological time by the biophysical processes of energy and water exchange, and that linkage extends to evolutionary time as well. The coevolution of



temperature and water relations is illustrated by an analysis of the New World eublepharid geckos in the genus *Coleonyx* (Dial and Grismer 1992). **Figure 6.29** shows the most plausible phylogenetic relationship of the seven species of *Coleonyx*. The outgroup includes several Asian species of geckos, among them *Goniurosaurus kuroiwae*, which lives in the leaf litter on the floor of subtropical forests.

Goniurosaurus and six of the seven species of *Coleonyx* (no data are available for *C. fasciatus*) can be separated into two groups in terms of their rates of evaporative water loss (more or less than 1 g of water per h per g of body mass and two categories of activity temperature (above or below 30°C).

High rates of evaporative water loss and low activity temperatures are characteristic of *Goniurosaurus kuroiwae*, and the two most primitive species of *Coleonyx* (*C. mitratus* and *C. elegans*) retain those ancestral characters. Like *G. kuroiwae*, *C. mitratus* and *C. elegans* inhabit leaf litter on the cool floors of wet forests. Evaporative stress is low in this humid environment, and the forest canopy intercepts sunlight before it reaches the ground.

The remaining four species of *Coleonyx* in this study inhabit deserts in Mexico and the United States. These habitats are hotter and drier than the forest floor, and they expose the lizards to greater evaporative stress and higher environmental temperatures. Three of these species (*C. switaki*, *C. variegatus*, and *C. brevis*) have low rates of evaporative water loss and high activity temperatures. The exception to that generalization is *C. reticulatus*, which retains the high skin permeability and low activity temperature of the ancestral species.

Dial and Grismer (1992) have proposed that the derived characters in *Coleonyx* evolved at least twice, and that these evolutionary steps can be placed in the context of environmental changes in North American deserts. The ancestral *Coleonyx* is believed to have entered North America from Asia via the Bering land bridge late in the Late Cretaceous or Early Cenozoic. During this period almost all of North America had a moist, subtropical climate. This ancestral *Coleonyx* probably lived in leaf litter on the forest floor and retained the ancestral characters of high evaporative water loss and low activity temperature.

North America became drier during the Eocene, and the ancestral *Coleonyx* may have moved with the forests as they retreated southward, ultimately reaching southern Mexico and northern Central America. During the early Pliocene, part of southern Mexico was covered by the Pacific Ocean, and this inland sea is believed to have divided the range of *Coleonyx* into northern and southern populations. Tropical forests persisted in the south, and the species living there retained the ancestral physiological characteristics. In the north, however, the habitat became drier and *Coleonyx* living there adjusted to the new conditions.

Three species (*C. switaki*, and independently, *C. variegatus* and *C. brevis*) apparently responded by evolving lower rates of evaporative water loss and higher activity temperatures,

but *C. reticulatus* retained the ancestral physiological conditions despite the environmental changes that were occurring around it (Dial and Grismer 1992). An organism is more than its physiological characteristics, however, and behavior is apparently an important part of a gecko's response to aridity. *C. variegatus* form groups in retreat sites during the day (Burke 1994). In an elegant experimental study, Jennifer Lancaster and her colleagues (2006) found no evidence that banded geckos achieved social benefits from these aggregations, but they showed that when geckos gathered in groups of three, their evaporative water loss was reduced by nearly 50% (**Figure 6.30**).

How does C. *reticulatus* survive in its new environment without a low evaporative water loss and high setpoint temperature? Dial and Grismer (1992) suggested that because C. *reticulatus* lives in rock crevices, which are relatively cool and wet, it is not exposed to conditions as harsh as those that confront the other three species. Furthermore, aggregation behavior might reduce evaporative water loss for C. *reticulatus* and the other desert-dwelling species of *Coleonyx*, but the behavior of those species has not been studied.

(A)



Figure 6.30 Rates of evaporative water loss are lower for banded geckos (*Coleonyx variegatus*) in groups than for individuals. (A) Two banded geckos in a diurnal retreat site. (B) The presence of two or three lizards in the same site reduces evaporative water loss by increasing relative humidity. (After Lancaster et al. 2006; photograph courtesy of Robert E. Espinoza.)

SUMMARY

■ All animals are mostly water. Water makes up 65–75% of the body mass of reptiles and 75–85% of the body mass of amphibians.

Water can be gained in three forms: as liquid water (e.g., a stream, pond, puddle, raindrop, or dew), preformed water (water molecules in the food an animal eats), and metabolic water (water produced when carbohydrates, lipids, and proteins are metabolized).

Amphibians do not drink; they absorb water across the skin (especially via the pelvic patch) and from their food.

Reptilian skin is nearly impermeable to water, and even aquatic reptiles gain water by drinking and from their food.

Regulating the water versus solute content of cells is an important part of controlling the rates of biological processes.

Metabolism of proteins yields nitrogenous waste products that must be excreted. Ammonia is lost primarily across the gills and skin and also in urine. Urea also leaves the body by those routes. Reptiles and a few frogs excrete uric acid, which precipitates to form a gray or white slurry that can be excreted with little loss of water.

Cutaneous evaporation is the primary route of water loss for most amphibians, although the waterproof frogs and amphibians that form cocoons are exceptions. Respiratory, urinary, and fecal water loss are relatively more important for reptiles, but generalization is difficult for both groups because behavioral and physiological adjustments have large effects on water flux.

Salt-secreting glands have evolved independently in several lineages of reptiles. These glands secrete Na⁺ and Cl⁻, and in the case of lizards K⁺ and HCO₃⁻, ions at high concentrations, allowing reabsorption of water from the bladder or cloaca, and complementing excretion of uric acid.

Adaptations to the moisture in their external environments extend the range of ecological conditions amphibians and reptiles can tolerate.

Most amphibians and some reptiles reduce activity or move to retreat sites and cease activity during dry periods and resume activity following rain.

Many amphibians and reptiles extend activity by tolerating substantial dehydration—some on a daily basis, others over periods of several days, and some over periods of months and perhaps years. The effect of body temperature on an animal's physiology and biochemistry is profound. Biophysical models quantify energy exchange and identify morphological, physiological, and behavioral mechanisms used for thermoregulation.

The rates of many biochemical reactions approximately double when the temperature increases by 10°C and fall to half the original rate when the temperature decreases by 10°C. This phenomenon is known as the Q_{10} effect.

Six pathways of energy exchange can be described:

- *Q*_{*abs*} Solar radiation. Organisms receive solar radiation directly and by reflection.
- M Metabolic heat production. This pathway plays a minor role in thermoregulation, except in a few very large reptiles such as the leatherback sea turtle.
- *R* Infrared radiation. All organisms exchange infrared radiation with their surroundings. The net gain or loss of energy depends on the surface temperatures of an organism and its surroundings.
- *C* Convection. Heat is gained from or lost to the fluid medium that surrounds an organism. The value of *C* depends on the temperatures of the fluid and the organism.
- LE Evaporation. Evaporation of water cools an organism.
- *G* Conduction. Heat is gained or lost by conduction from surfaces that an organism is in direct contact with.

The thermoregulatory mechanisms of amphibians and reptiles are more closely linked to their environment than are those of endotherms.

Thermoregulatory mechanisms can be characterized as heliothermy (relying on solar radiation), thigmothermy (absorbing heat from warm surfaces), and kleptothermy (taking advantage of metabolic heat production by an endotherm). These mechanisms are not mutually exclusive, and most species use more than one of them. Amphibians and reptiles that do not thermoregulate are called thermoconformers.

Heliotherms and thigmotherms regulate their body temperatures between upper and lower set points that are characteristic of their species.

Most amphibians have only a limited capacity for thermoregulation because the cooling effect of evaporation from the skin counteracts the heat gained by basking in the sun. Patterns of blood circulation can be modified to speed heating, slow cooling, and shunt excess heat out of the body.

A few large species of reptiles generate enough metabolic heat to remain warmer than their environments.

■ The time and energy an animal devotes to regulating its body temperature reduce the time and energy it can devote to other important activities.

For most reptiles and amphibians, the cost of thermoregulation is low in open, sunny habitats and higher in habitats where sources of energy are limited. For some species, however, the benefits of thermoregulation outweigh the costs even in high-cost habitats. The effectiveness of thermoregulation can be evaluated by comparing the body temperature of an organism to the distribution of operative temperatures in that habitat. Effective thermoregulation is denoted by body temperatures that differ from operative temperatures.

The body temperature and evaporative water loss of an organism are linked by the biophysical processes of energy and water exchange and are responsive to behavior.

The multimodal evolutionary transition of North American eublepharid geckos from the ancestral habitat of moist forests to arid deserts included changes in set-point temperatures, evaporative water loss, and probably behavior.

Go to the *Herpetology* Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

Energetics and Performance

s we saw in Chapter 6, regulation of body temperature and body water content is often critical in determining when and where amphibians and reptiles can be active. Metabolic characteristics have equally profound effects on the day-to-day activities of amphibians and reptiles. Because the physiological characteristics of amphibians and reptiles are so clearly reflected in their behavior and ecology, these animals have played an important role in studies of ecological and evolutionary physiology. This chapter traces some of those relationships, emphasizing the close connections between physiology and the behavior and ecology of amphibians and reptiles.

We will start with the structures used for gas exchange and then consider the cardiovascular system, which transports oxygen and other substances throughout the body. Next we will consider how the production of ATP meets the needs of different ways of life and the energy costs of natural activities.

7.1 Sites of Gas Exchange

Water and air are the respiratory media for aquatic and terrestrial animals, respectively, but all amphibians and some reptiles can use both media, often simultaneously. The sites at which gas exchange takes place include the lungs (pulmonary gas exchange), the skin surface (cutaneous gas exchange), and the gills, pharynx, and cloaca.

Nonpulmonary gas exchange

We mentioned the role of amphibian skin in gas exchange when we discussed evaporative water loss in Chapter 6. Permeability to oxygen and carbon dioxide is inseparable from permeability to water in biological systems, and the skin of amphibians plays a major role in gas exchange as well as in water balance (Feder and Burggren 1985). The buccopharyngeal region (the oropharynx) of the throat can be a site of gas exchange, and salamanders in the family Plethodontidae (which is characterized by the absence of lungs) carry out all of their gas exchange via the skin and buccopharyngeal region.

Most other amphibians have lungs as adults, although the lungs of some aquatic species of salamanders and frogs appear to be more important for adjusting buoyancy than for respiration. Some aquatic amphibians have folds of skin that increase the surface area (Figure 7.1). These folds are highly vascularized, and the capillaries run close to the surface of the skin. In a stream of moving water the current carries away carbon dioxide and brings water containing oxygen into contact with these folds, but in still water the animals must renew the layer of water in contact with the skin by moving. Aquatic amphibians such as the hellbender (Cryptobranchus alleganiensis) and the Lake Titicaca frog (Telmatobius culeus) do this by swaying from side to side and up and down with a rippling of their skin folds that mixes the water around their bodies; larval salamanders and paedomorphic adults wave their gills.

Amphibians that are primarily lung-breathers may have specialized sites for aquatic gas exchange that are important for particular activities. During the breeding season, adult males of the African hairy frog (Trichobatrachus robustus) grow filaments of skin from the posterior part of the trunk that, like gills, have an extensive blood supply and a large surface area (Figure 7.2A). These filaments increase the surface area available for gas exchange with water. Several functions have been suggested for these structures, which are seen only in males and only during the breeding season. Initially, G. Kingsley Noble (1925) proposed that the extra surface area for gas exchange provided by the filaments helped male frogs sustain high levels of activity associated with breeding. Subsequently it was proposed that the hairs increase oxygen uptake from water and allow males to remain with their eggs in underwater nests. Yet another possibility is that the hairs may actually release oxygen absorbed through the lungs into the water in the nest, thereby

(A)

(B)



Figure 7.1 Skin folds as gas-exchange structures. Some aquatic amphibians, such as (A) the hellbender salamander (Cryptobranchus alleganiensis) and (B) the Lake Titicaca frog (Telmatobius culeus), have folds of skin that increase the area available for cutaneous gas exchange. Both of these species rock their bodies from side to side and up and down to disrupt the boundary layer of water and increase oxygen diffusion. (A C Alvon E. Staffan/Science Source; B C Pete Oxford/ Nature Picture Library/Corbis)

aerating the egg mass and promoting embryonic development (Zippel 1997).

The dramatic crests and tail fins developed by male newts during the breeding season probably increase aquatic gas exchange as well as play a role in courtship display (Figure 7.2B). Male newts court females underwater, leading them through an extended series of activities (see Chapter







14), and the longer a male can continue courtship without surfacing to breathe, the better are his chances of mating (Halliday and Sweatman 1976).

All aquatic larval amphibians have gills, and adults of some paedomorphic salamanders, such as *Pseudobranchus*, Necturus, Proteus, and some Ambystoma, retain gills as adults. Gills are effective for gas exchange in water because water is dense and supports the individual gill filaments. The embryos of direct-developing and viviparous species of amphibians respire with modified gills or with vascularized tails that are pressed against the egg capsule or the wall of the oviduct (Figure 7.3) (M. H. Wake 1993).

Figure 7.2 Some supplementary gas-exchange structures of amphibians are associated with reproduction.

(A) Males of the African hairy frog (Trichobatrachus robustus) develop highly vascularized skin filaments while they are attending their eggs. (B) Males of many species of newts, such as the smooth newt (Lissotriton vulgaris), develop an elaborate crest that increases surface area while also providing a visual signal used in courtship (see Chapter 13). (A © Paul Starosta/ Corbis; B © Miroslav Hlavko/Shutterstock.)



(B)



Modified tail

(B)

Figure 7.3 Gas-exchange structures of embryos of direct-developing and viviparous amphibians. (A) The modified gills of direct-developing plethodontid salamanders like the Mexican salamander (*Pseudoeurycea nigromaculata*) have short branches. (B) The gills of the viviparous caecilian *Typhlonectes compressicauda* are membranous. Larvae retain the gills for a day or two after birth. (C) Some directdeveloping amphibians have modified other structures for gas exchange, such as the tail of the Mexican frog *Eleutherodactylus nitidus*. (A after Kerney 2011; B after Taylor 1968; C after Duellman and Trueb 1986.)

The skin of reptiles is less permeable to water and gases than is the skin of amphibians, and cutaneous gas exchange is less important for most reptiles than it is for amphibtans. Nonetheless, cutaneous gas exchange is significant for some aquatic reptiles, and appears to be correlated with the extent of aquatic specialization. Sea snakes in the genus *Hydrophis* can probably obtain all of the oxygen they require at rest via diffusion across the skin, whereas sea kraits (*Laticauda*), which spend part of their time on land, have much lower rates of cutaneous respiration (Heatwole and Seymour 1975; R. S. Seymour pers. com.).

Cutaneous gas exchange plays a role in respiration by aquatic turtles, but two other structures—the buccopharyngeal region and the cloaca—are more important sites of gas exchange than the skin (Peterson and Greenshields 2001). In 1857, Louis Agassiz reported the presence of short, filamentous projections (papillae) in the pharynx of the soft-shelled turtle Apalone (then Trionyx) and suggested by analogy to the structure of the gills of tadpoles-that these papillae were sites of gas exchange. A century later, William Dunson (1960) determined that buccopharyngeal respiration is indeed the predominant form of aquatic oxygen uptake by spiny soft-shelled turtles (Apalone spinifer), and Wang and colleagues (1989) reported that buccopharyngeal respiration accounts for two-thirds of the aquatic oxygen uptake by the Chinese soft-shelled turtle Pelodiscus (formerly Trionyx) sinensis. Similar papillae have been observed in the buccopharyngeal regions of other cryptodire turtles, and buccopharyngeal respiration appears to be a major route of aquatic gas exchange for this lineage (Heiss et al. 2010).

For pleurodires, however, a pair of evaginations (bursae) from the cloaca that are lined with highly vascularized papillae are the primary sites of aquatic gas exchange (Fielder 2012). The Fitzrov River turtle (Rheodytes leukops) in Australia has the best-developed cloacal bursae vet studied, and this species rarely comes to the surface to breathe air (Clarke et al. 2008). Rheodytes swims with its cloaca open and pumps water in and out of the bursae at rates of 10-20 cycles per minute (Gordos et al. 2006). Although other Australian pleurodires use cloacal bursae for aquatic respiration, Rheodytes has the most impressive diving performance. Spontaneous dives have lasted up to 2.5 hours, and dives lasting more than 2 days have been recorded (Figure 7.4) (Gordos et al. 2006).

Although cryptodires use their cloacal bursae to adjust buoyancy, the bursae play no role in respiration (Peterson and Greenshields 2001; Peterson and Gomez 2008). Thus the phylogenetic origin of the distinction between cloacal and buccopharyngeal respiration probably dates from the separation of the cryptodire and pleurodire lineages, which had occurred by the Jurassic (see Chapter 4).

Pulmonary gas exchange

Excellent as gills are in water, they are useless in air. Without water to support them, gill filaments collapse on each other and the surface area available for gas exchange is drastically reduced. Most air-breathing animals rely on lungs, which are sacs of air inside the body that are ventilated by respiratory movements of the buccopharyngeal region and trunk.

POSITIVE-PRESSURE VENTILATION: BUCCOPHARYNGEAL

PUMPING Pumping movements of the buccopharyngeal region of the mouth and throat are an ancestral character of tetrapods, and amphibians and reptiles use buccopharyngeal movements to move both water and air (Brainerd 1994). Amphibians use buccopharyngeal pumping to force air into the lungs. This method of breathing is called positive-pressure ventilation, because air is forced into the lungs by raising the pressure in the buccopharyngeal region above the pressure in the lungs. In contrast, reptiles and other amniotes use a negative-pressure system that sucks air into the lungs by reducing intrapulmonary pressure.

Terrestrial salamanders and most frogs use a two-stroke breathing pattern (Brainerd 1999). A respiratory cycle starts by expanding the buccopharyngeal region, drawing in fresh air through the nostrils. Expiration of air from the (A)







Figure 7.4 Cloacal respiration and diving by pleurodire turtles.

Both (A) the Murray River turtle (*Emydura macquarii*) and (B) the Fitzroy River turtle (*Rheodytes leukops*) are aquatic. *Rheodytes* keeps its cloaca open while diving and respires by pumping water in and out of its cloacal bursae (inset). (C) *Rheodytes* makes longer dives, averaging 37 minutes underwater compared with 5 minutes for *Emydura*. The maximum length of a spontaneous dive by *Rheodytes* (155 min) is nearly 8 times that of *Emydura* (20 min). Despite remaining underwater longer, *Rheodytes* spends an average of only 52 seconds at the water surface between dives, compared with 80 seconds for *Emydura*. (After Priest and Franklin 2002; photographs: A, © Kitch Bain/Alamy; B and inset, Craig E. Franklin.)

> lungs occurs at the same time, and the two air streams enter the buccal cavity (Figure 7.5). Elastic recoil forces air out of the lungs of most frogs and caecilians, but salamanders use contraction of axial muscles to drive air out (Brainerd and Owerkowicz 2006). In the second stroke, contraction of the buccopharyngeal region forces fresh air into the lungs and used air out of the nostrils. The volume of air that is drawn into the buccal cavity during the first stroke is much greater than the volume of air drawn from the lungs, and much of that fresh air is exhaled along with the used air on the second stroke. As a result, 80% of the air that enters the lungs is fresh and only 20% is rebreathed.

Figure 7.5 Two-stroke buccal pumping by a frog. Most amphibians use a two-cycle buccal pump to fill their lungs. (A) Expanding the buccal region draws fresh air through the nostrils and oxygen-depleted air from the lungs into the buccal cavity. Only a small amount of mixing occurs. (B) Contraction of the buccal region forces fresh air into the lungs and oxygen-depleted air out through the nostrils. (After Brainerd et al. 2006.)



NEGATIVE-PRESSURE VENTILATION A negative-pressure pumping system is the primary respiratory mechanism of reptiles, but some reptiles use pumping movements of the throat (gular) region to supplement inspiration (Brainerd and Owerkowicz 2006). Inflating the lungs by gular pumping is also used for defense. For example, chuckwallas (*Sauromalus*) and other rock-dwelling lizard species can wedge themselves so tightly into a crevice that a predator cannot pull them out.

Respiration by lizards, snakes, and the tuatara (*Sphenodon punctatus*) includes three components: expiration, inspiration, and relaxation. During expiration the glottis is open and active contraction of specific regions of two hypaxial trunk muscles—the transversalis and retrahentes costarum—compresses the rib cage, raising the pressure in the lungs and forcing air out through the nostrils. Air is inhaled by contracting a different set of trunk muscles, the external and internal intercostals, to expand the rib cage. This expansion drops the pressure in the lungs via the nostrils and through the open glottis. When these muscles relax, the elasticity of the rib cage causes it to contract slightly. The glottis is closed, sealing off the respiratory tract and maintaining the lungs in a partly inflated state.

Reptiles usually pause after the relaxation phase of ventilation before they initiate the next respiratory cycle by exhaling. Two ventilatory patterns can be identified: terrestrial reptiles generally take single breaths separated by periods without breathing (apneic periods), which last from seconds to a minute or so, whereas aquatic species alternate periods of continuous ventilation with apneic periods, which last from minutes to an hour or more (Wang et al. 1998). Pulmonary oxygen concentration is highest immediately after fresh air has been drawn into the lungs and decreases during periods of apnea.

Using trunk muscles to ventilate the lungs creates problems for lizards during locomotion because the muscles that change the volume of a lizard's thoracic cavity during breathing are the same muscles that produce lateral bending and stabilize the trunk during locomotion (**Figure 7.6A**). As a result, locomotion and lung ventilation are incompatible—a lizard cannot breathe and run simultaneously (Carrier 1986). When a green iguana (*Iguana iguana*) walks or runs, airflow through the nostrils is greatly reduced. Both airflow and oxygen and carbon dioxide exchange are highest immediately following a period of locomotion (Wang et al. 1997). The stop-and-go locomotor pattern that is typical of many lizards may be related to this conflict between locomotion and respiration, with lizards stopping to breathe between bouts of movement.

Varanid lizards have found a solution to the conflict between locomotion and lung ventilation—they inflate the gular cavity of the throat and use contractions of the gular muscles to force that air into the lungs (**Figure 7.6B**) (Owerkowicz et al. 1999). As a result, varanid lizards maintain lung ventilation and gas exchange at high levels during locomotion (Wang et al. 1998).

Pregnancy interferes with lung ventilation by viviparous Australian skinks that give birth to babies that are large relative to the size of the mother (Munns and Daniels 2007; Munns et al. 2015). The shingle-backed skink (*Tiliqua rugosa*) has litters of one or two offspring, and the embryos



Figure 7.6 The activity of a lizard's trunk muscles during locomotion interferes with lung ventilation. (A) The axis of bending of a green iguana (*Iguana iguana*) lies between the left and right lungs. As the lizard bends, the lung on the concave side is compressed and the lung on the convex side is expanded. Air pressure in the lung on the concave side increases (+), whereas pressure on the convex side decreases (-). These pressure changes move air between the left and right lungs while little or no ventilation occurs via the trachea. (B) X-ray negative image of a savannah monitor lizard (*Varanus exanthematicus*) using a gular pump to supplement lung ventilation during locomotion on a treadmill. The images show three stages of a single breath cycle: the end of exhalation (left), the end of expansion of the thorax and gular cavity (center), and after the gular pump has forced air from the gular cavity into the lungs (right). (A after Carrier 1987; B from Owerkowicz et al. 1999.)

comprise about 22% of the body mass of the mother (Figure 7.7). Female blue-tongued skinks (*T. nigrolutea*) carry an even larger burden—an average of eight babies with a combined mass of 39% of the mother. The embryos take up so much space in the body of the mother that they compress or even collapse some regions of the lungs.

Munns and colleagues found that early in pregnancy, while the embryos were small, female *T. ni*grolutea that were exercising vigorously were able to increase their rates of oxygen consumption to 6 times the resting rate, but during the final 5 weeks of pregnancy exercising lizards could only double oxygen consumption. A week after the young were born, the lizards' oxygen consumption during exercise returned to its original high level (Munns et





al. 2015). The limitation of oxygen consumption imposed by embryos may be one of the factors responsible for the reduced locomotor capacity of pregnant lizards.

The exchange of oxygen and carbon dioxide between air and blood takes place across the lung surface, and lungs of amphibians and reptiles range from simple sacs, with few if any internal divisions, to complex structures with interior walls and passages that direct airflow and increase the surface area (Perry 1998). This morphological variation is related to physiological differences in the importance of lungs for gas exchange and in the metabolic requirements of different species. Amphibian lungs are generally simple, reflecting the large role the skin plays in gas exchange for these animals. In general, the lungs of frogs are more complex than those of salamanders and have a larger surface area for gas exchange.

Having paired lungs is the ancestral condition for reptiles, but reduction or loss of one lung is characteristic of Figure 7.7 The large embryos of the Australian shingle-backed skink (*Tiliqua rugosa*) interfere with maternal breathing. (A) A computed tomography (CT) scan shows that even a single embryo occupies a large portion of the mother's body cavity. In a non-pregnant lizard, the lungs extend back to the point indicated by the arrow, but the posterior portions of the lung are compressed in a pregnant lizard. (B–E) Comparison of CT scans of a non-pregnant lizard (B) and a lizard with one embryo reveals regions where the fetus compresses (C,D) or entirely collapses (E) portions of the lungs. (From Munns and Daniels 2007; Munns 2013).

elongate forms such as snakes and amphisbaenians, most of which have only one functional lung. In amphisbaenians the right lung has been lost, whereas in snakes it is the left lung that has been reduced. In most snakes the left lung is only 1–2% of the length of the right lung, but boids are an exception—the left lung is 30–65% of the length of the right lung.

About half of the extant snake families have evolved a vascular lung that lies anterior to the heart (**Figure 7.8**). The vascular lung is well supplied with blood vessels, and its walls are elaborated into chambers that provide a large surface area for gas exchange. In contrast, the saccular lung lacks partitions or other structures to increase the surface area, and it has a limited blood supply. Gas exchange takes place in the vascular lung, whereas the saccular lung appears to regulate airflow. Oxygen and carbon dioxide pressures in the vascular lung rise and fall with each breath, but they show little change in the saccular lung. Both the saccular

lung and the vascular lung are especially long in specialized aquatic snakes—hydrophiines and acrochordids—where the saccular lung extends almost to the cloaca and is used to adjust buoyancy.

Crocodylians have a well-developed rib cage, and the trunk muscles appear to play a major role in lung ventilation when these animals are at rest. During exercise, however, the liver (which lies posterior to the lungs) acts as a piston, compressing and expanding the lungs (Munns et al. 2012). During expiration, several abdominal muscles pull the liver forward, compressing the lungs and forcing air out. Inspiration is accomplished by a posterior movement of the liver that is produced by contraction of the diaphragmaticus muscles, which originate on the pelvis. Connective tissues attach the liver to the lungs, so that the lungs are expanded when the liver is pulled backward. Airflow is unidirectional in crocodylian lungs, as it is in the lungs of birds (Farmer and Sanders 2010). Unidirectional airflow has





also been identified in two lizards—the savannah monitor lizard (*Varanus exanthematicus*) and the green iguana (*Iguana iguana*)—and the capacity for unidirectional pulmonary flow may be ancestral for diapsids (Cieri et al. 2014; Schachner et al. 2014).

Turtles face a unique problem in breathing: how to change the volume of a thoracic cavity that is enclosed in a rigid shell. The ribs of turtles are fused to the dermal bone forming the carapace, and no movement of the ribs is possible. Only the skin and muscle at the anterior and posterior openings of the shell provide the flexibility needed to change the volume of the lungs.

The dorsal surfaces of turtle lungs are attached to the carapace, and the ventral surfaces are attached to a sheet of connective tissue that in turn is attached to the viscera. Turtles exhale by forcing the viscera upward against the lungs, driving air out (**Figure 7.9**). Enlarging the visceral cavity allows the viscera to slump downward, and the tissue connecting the viscera to the lungs pulls the ventral surface of the lungs down, increasing the volume and drawing air inward.

Gas exchange by eggs

The gelatinous material that surrounds the eggs of many amphibians is a potential barrier to diffusion of oxygen, from the water (Mueller and Seymour 2011). Many frogs



(B) Viscera Lungs Pectoral girdle



Figure 7.9 Lungs and respiratory movements of turtles. A turtle's viscera act as a piston that contracts and expands the lungs. The in-and-out movement of the pectoral girdle as the animal breathes can be duplicated in an anesthetized turtle by moving the forelimbs. (A) X-ray photographs show that extending the forelimbs (arrow) mimics inhalation, decreasing the volume of the visceral cavity and allowing the lungs to expand and draw air through the trachea into the lungs. (B) Moving the forelimbs posteriorly (arrow) forces the viscera upward, mimicking exhalation as air is driven out from the lungs via the trachea. (From Wang 2011, courtesy of Tobias Wang.)

deposit their eggs in relatively loose masses, and channels running among the eggs allow a convective flow of oxygen-rich water that replaces water from which oxygen has been removed by respiration of the embryos. Water flow increases as the eggs develop, because the gelatinous material becomes more fluid and channels for water flow increase as the egg mass expands (Seymour 1995). Solar heating during the day raises the temperature in the egg mass as much as 2°C above the external water temperature, creating convention currents that draw fresh water in through the bottom of the egg mass (**Figure 7.10**). The aerial egg masses of red-eyed treefrogs (*Agalychnis callidryas*) hang from leaves over water, and embryos orient themselves to place their gills in the area of highest oxygen concentration (Rogge and Warkentin 2008).

Amphibian eggs must resolve the conflicting demands of maximizing gas exchange by having a thin capsule and maximizing structural support by having a thick capsule.





As a result, the largest amphibian eggs have volumes of less than 1 ml (Seymour and Bradford 1995). The evolution of reptile eggs solved that constraint on egg size by replacing the membranous amphibian egg capsule with a shell that contains channels for diffusion of respiratory gases (Packard and Seymour 1997). Eggs of crocodylians, birds, many turtles, and some squamates have rigid shells formed by crystals of calcium minerals. Pores extend through the crystalline layer of the eggshell, allowing oxygen to diffuse in and carbon dioxide to diffuse out. Other turtles and many squamates have eggs with flexible, fibrous shells that lack discrete pores. Oxygen and carbon dioxide diffuse through gaps between fibers of these shells. Two extraembryonic membranes-the allantois and chorion—rest against the inside of the shell. Blood vessels in these membranes transport gases to and from the embryo (see Chapter 9).

7.2 Patterns of Blood Flow

The circulatory system (which includes the heart, blood vessels, and the blood itself) carries oxygen from the sites of gas exchange to metabolically active tissues and brings carbon dioxide produced by metabolism to sites where it is released. The circulatory system of a lung-breathing animal can be pictured as a figure eight with the heart at the intersection of two loops, which represent the pulmonary (lungs) and systemic (head and body) circuits. In the pulmonary loop, oxygen-poor blood flows from the right side of the heart via the pulmonary artery to the lungs, where it is oxygenated, and returns via the pulmonary vein to the left atrium. In the systemic loop, oxygen-rich blood flows from the left side of the heart via the aortas to the body and returns via the vena cava to the right atrium.

Pulmonary and systemic blood flow

Anatomical separation of the pulmonary and systemic circuits (as in the mammalian heart, for example) allows the pressures in the two systems to be different. The systemic vessels ramify into tiny capillaries so narrow that red blood cells must squeeze through them. Forceful contraction by the heart is needed to drive blood through these capillaries, and the systemic system operates under high pressure.

Blood pressure in the pulmonary circuit is substantially lower than in the systemic circuit. The cells forming the walls of the pulmonary capillaries and the cells lining the gas-exchange sites of the lungs are thin, minimizing the distance between the blood in the capillaries and the air in the lung. Because these tissues are so thin, high blood pressure in the pulmonary capillaries would force fluid into the lungs, where it would interfere with gas exchange.

MULTIPLE SITES OF GAS EXCHANGE Amphibians are the only vertebrates in which the cardiovascular system carries oxygen-poor blood to the skin as well as to the lungs. Adult amphibians have paired pulmocutaneous arteries that divide into two branches. The pulmonary branch carries blood to the lungs, and the cutaneous branch carries blood to the skin, especially to the flanks and dorsal surface of the trunk. Cutaneous respiration accounts for 20–90% of the total oxygen uptake and 30–100% of the total carbon dioxide release for a variety of adult amphibians (reviewed by Hillman et al. 2009). Oxygen-rich blood returning from the cutaneous arteries enters the heart via the vena cava, where it mixes with oxygen-poor blood returning from the systemic circuit.

Blood flow in the heart

Separation of the pulmonary and systemic circuits requires a mechanism to keep oxygen-rich and oxygen-poor blood from mixing as they pass through the heart. The hearts of birds and mammals have a septum that divides the ventricle into systemic (left) and pulmonary (right) chambers and prevents blood from mixing. However, the hearts of amphibians, and of all reptiles except crocodylians, lack a ventricular septum. Nonetheless, these hearts can separate oxygen-rich and oxygen-poor blood and can even maintain different pressures in the systemic and pulmonary circuits.

AMPHIBIANS The functional aspects of blood flow through the amphibian heart are best understood for anurans, and we will focus on them and note some differences found in salamanders and caecilians. Figure 7.11 shows the major features of blood flow through the heart of the African clawed frog (Xenopus laevis). Blood from the left and right atria enters the single ventricle, where sheets of tissue (trabeculae) extend from the walls of the ventricle into the central space. The trabeculae form compartments that are believed to limit mixing by creating separate channels for oxygen-rich and oxygen-poor blood. As the ventricle contracts, the trabeculae on the left side of the heart trap oxygen-rich blood and direct it into a spiral valve that runs from the ventricle to the point at which the outflow divides into the carotid, systemic, and pulmocutaneous arteries. Oxygen-rich blood enters on one side of the spiral valve and flows into the carotid and systemic arteries. Oxygen-poor blood is directed by trabeculae into the other side of the spiral valve and flows into the pulmocutaneous artery.

The paths followed by arterial and venous bloodstreams in the single ventricle of amphibians range from complete mixing to nearly complete separation (Hedrick 1999; Hillman et al. 2014). Separation of oxygen-rich and oxygenpoor blood is most complete at intermediate heart rates and at rest or during moderate activity within a species' activity temperature range.

The hearts of salamanders and caecilians are structurally less complex than those of anurans. The atria of salamander and caecilian hearts are not always completely separated—the wall between the atria may be pierced by openings called fenestrae (Latin for "windows"). The pulmonary artery of salamanders lacks a cutaneous branch, and cutaneous gas exchange occurs via the systemic circulation. Plethodontid salamanders do not have lungs, and all gas exchange is carried out via the skin and buccopharyngeal region of the throat. The hearts of plethodontid salamanders have no structures for separating oxygen-rich and oxygen-poor blood (Burggren 1988). The septum dividing the left and right atria is greatly reduced, and oxygenrich blood returning from the skin mixes with oxygen-poor blood from the body.

TURTLES AND SQUAMATES The hearts of turtles and squamates consist of two atria and a single ventricle with three connected chambers: the cavum pulmonale, cavum arteriosum, and the cavum venosum. Thus, the heart is anatomically three-chambered but functionally five-chambered, because contraction of the ventricle turns its single chamber into three compartments (Hicks and Wang 2012).



Figure 7.11 Blood flow in an anuran heart. Oxygen-rich blood (red arrows) entering the ventricle from the left atrium* is largely separated from oxygen-poor blood (blue arrows) entering from the right atrium by the complex internal structure of the ventricle. When the ventricle contracts, the spiral valve directs oxygen-poor blood primarily to the pulmocutaneous artery and oxygen-rich blood primarily to the carotid and systemic arteries. (After Shelton and Boutilier 1982.)

Figure 7.12 shows a schematic view of the heart of a turtle or squamate. The left and right atria are completely separate, and three subcompartments can be distinguished in the ventricle. A muscular ridge in the core of the heart divides the ventricle into two spaces: the cavum pulmonale and the cavum venosum. The muscular ridge is not fused to the wall of the ventricle, and thus the cavum pulmonale and cavum venosum are only partially separated. A third subcompartment of the ventricle, the cavum arteriosum, is located dorsal to the cavum pulmonale and cavum venosum. The cavum arteriosum communicates with the cavum venosum through an intraventricular canal.

The heart has two inflow routes (the right and left atria) and three outflows (the pulmonary artery and the left and right aortas). The right atrium receives oxygen-poor blood from the body via the sinus venosus and empties into the cavum venosum, and the left atrium receives oxygen-rich blood from the lungs and empties into the cavum arteriosum. The pulmonary artery opens from the cavum pulmonale, and the left and right aortas open from the cavum venosum.

^{*}Figures 7.11 through 7.14 show the heart as if the animal were standing erect facing you. Thus, the left (systemic) side of the heart is on the right side of the drawing and the right (pulmonary) side of the heart is on the left side of the drawing.



Figure 7.12 Blood flow in the heart of a turtle or squa-

mate. Although the ventricle is anatomically a single chamber, contraction transiently creates three ventricular chambers and produces considerable separation of oxygen-rich and oxygen-poor blood. (A) As the atria contract, oxygen-rich blood (red) from the left atrium enters the cavum arteriosum while oxygen-poor blood (blue) from the right atrium first enters the cavum venosum, then crosses the muscular ridge and enters the cavum pulmonale. The atrioventricular valve blocks the intraventricular canal and prevents mixing of the oxygenrich and oxygen-poor blood. (B) As the ventricle contracts, the oxygen-poor blood in the cavum pulmonale is expelled through the pulmonary artery and travels to the lungs. The atrioventricular valve closes and no longer obstructs the intraventricular canal, and oxygen-rich blood in the cavum arteriosum is forced into the cavum venosum and expelled through the left and right aortas. Contact between the wall of the ventricle and the muscular ridge prevents mixing of oxygen-rich and oxygen-poor blood. (C) Summary of the pattern of blood flow through the heart. Oxygen-poor blood passes from the right atrium through the cavum venosum, across the muscular ridge, into the cavum pulmonale, and out the pulmonary artery into the pulmonary circuit. Oxygen-rich blood passes from the left atrium into the cavum arteriosum, through the intraventricular canal to the cavum venosum, and out the left and right aortas into the systemic circuit.

The mechanisms responsible for keeping oxygen-rich and oxygen-poor blood separate as they pass through the heart can be understood by tracing the movement of blood during a cardiac cycle.

- 1. When the atria contract, the atrioventricular valves open and allow blood to flow into the ventricle.
- 2. At this stage in the cardiac cycle the large median flaps of the atrioventricular valve between the right atrium and the cavum venosum are pressed against the opening of the intraventricular canal, blocking the path to the cavum venosum. As a result, the oxygen-rich blood from the left atrium is confined to the cavum arteriosum. Oxygen-poor blood from the right atrium fills the cavum venosum and then continues over the muscular ridge into the cavum pulmonale.
- 3. When the ventricle contracts, blood pressure inside the heart increases. Blood begins to flow into the pulmonary circuit before it flows into the systemic circuit because resistance is lower in the pulmonary circuit.
- 4. As oxygen-poor blood flows out of the cavum pulmonale into the pulmonary artery, the displacement of oxygen-poor blood from the cavum venosum across the muscular ridge into the cavum pulmonale continues. As the ventricle shortens during contraction, the muscular ridge comes into contact with the wall of the ventricle and closes off the passage

for blood between the cavum venosum and cavum pulmonale.

- 5. Simultaneously, blood pressure inside the ventricle increases, and the flaps of the right atrioventricular valve are forced into the closed position, preventing backflow of blood from the cavum arteriosum and cavum venosum into the atria.
- 6. When the atrioventricular valve closes, it no longer blocks the intraventricular canal. Oxygen-rich blood from the cavum arteriosum can now flow through the intraventricular canal and into the cavum venosum. At this stage in the heartbeat, the wall of the ventricle is pressed firmly against the muscular ridge, separating the oxygen-rich blood in the cavum venosum from the oxygen-poor blood in the cavum pulmonale.
- 7. As the pressure in the ventricle continues to rise, the oxygen-rich blood in the cavum venosum is ejected into the right and left aortas. At this time, blood pressure in the cavum venosum and the aortas is more than twice that in the cavum pulmonale and pulmonary artery.

Cardiac shunts

The shifting of blood between the left and right sides of the heart is called a **cardiac shunt**. A right-to-left shunt means that a portion of the oxygen-poor blood from the right atrium that would normally go to the pulmonary artery and lungs is redirected via the aortas into the systemic circulation. Thus, a right-to-left shunt increases the volume of blood going to the body and lowers its oxygen content. A left-to-right shunt means that blood is diverted from the systemic circulation into the pulmonary artery, increasing the volume and oxygen content of blood going to the lungs.

The direction and degree of shunting are controlled by differences in pressure, and pressure is controlled by resistance—high resistance to flow in a circuit means that high pressure is needed to move blood. In general, resistance in the pulmonary circuit increases when an animal is at rest, a right-to-left shunt develops, and oxygen saturation in the systemic blood decreases. In contrast, pulmonary resistance decreases during activity, a left-to-right shunt develops, and oxygen saturation in the systemic system increases (Hicks and Wang 2012).

TURTLES AND SQUAMATES: INTRACARDIAC SHUNTS The absence of a ventriocular septum in the hearts of turtles and squamates permits blood to be shunted between the pulmonary and systemic circuits within the heart (**Figure 7.13**). For example, when resistance in the systemic circuit decreases because capillary beds in the skin have been opened, blood pressure in the aortas drops. A right-to-left shunt develops and some oxygen-poor blood enters the systemic circulation. When capillary beds in the lungs open and resistance in the pulmonary circuit falls, a left-to-right shunt occurs.

CROCODYLIANS: EXTRACARDIAC SHUNTS The left and right ventricles of crocodylian hearts are anatomically separate. As in the hearts of birds and mammals, oxygen-poor





of oxygen-rich and oxygen-poor blood. (B) Dilating capillaries in the skin reduces resistance to flow in the systemic circuit. Blood flow to the skin increases because a right-to-left shunt redirects some oxygen-poor blood into the left and right aortas. (C) Increased resistance in cutaneous capillaries creates a leftto-right shunt, redirecting some oxygen-rich blood into the pulmonary artery. (After Hicks and Wang 2012.) blood enters the heart through the right atrium and exits through the pulmonary artery to the lungs, and oxygen-rich blood returning from the lungs enters the left atrium. At this point, however, crocodylian hearts differ from those of birds and mammals because the left aorta opens from the right atrium. Despite that anatomy, the left aorta receives oxygen-rich blood because an opening, called the foramen of Panizza, connects the left and right aortas. Blood pressure is normally higher in the left ventricle than in the right ventricle, and this pressure difference forces oxygen-rich blood from the left ventricle through the foramen of Panizza and into the left aorta (Figure 7.14A). Thus, the left aorta contains primarily oxygen-rich blood mixed with some oxygen-poor blood from the right ventricle.

The pattern of blood flow changes, however, when the dilation of blood vessels reduces resistance in the systemic circuit. With less resistance, pressure in the left ventricle falls and the left-to-right flow of blood through the foramen of Panizza slows or even reverses direction to become a right-toleft flow (**Figure 7.14B**).

FUNCTIONS OF CARDIAC SHUNTS

Does shifting blood between the pulmonary and systemic circuits have a function, or is this phenomenon merely

a hydrodynamic consequence of the plumbing of the hearts of reptiles? A variety of physiological functions have been proposed for intracardiac shunts, including the following:

- A right-to-left shunt could speed warming by increasing systemic blood flow to sun-warmed surface tissues, thereby increasing transport of heat to the core of the body (Baker and White 1970).
- 2. Both left-to-right and right-to-left shunts (i.e., variable mixing of oxygen-rich and oxygen-poor blood) might stabilize the oxygen content of blood during the pauses in lung ventilation that are a normal part of respiratory patterns of reptiles (Wood 1984).
- 3. A left-to-right shunt could provide oxygen to the heart muscle—a potentially important function because reptilian hearts lack cardiac vessels and receive oxygen only from blood in the chambers (Farmer and Hicks 2002).

A right-to-left shunt that speeds heating by increasing blood flow to the sun-warmed periphery of the body is the most robust example of a function for a reptilian intracardiac



Figure 7.14 Extracardiac shunts in the crocodylian heart. A septum completely divides the ventricle of the crocodylian heart into right (pulmonary) and left (systemic) chambers. The pulmonary artery exits from the right chamber. The left aorta exits from the right ventricle, and the right aorta exits from the left ventricle. The septum prevents shunts between the pulmonary and systemic circuits within the ventricle. Instead, crocodylians create blood shunts via the foramen of Panizza, a connection between the left and right aortas. As in turtles and squamates, the paths the blood follows are determined by changes in resistance. (A) Normally, pressure in the left ventricle is higher than in the right ventricle, and oxygen-rich blood flows from the right aorta into the left aorta through the foramen of Panizza, mixing with some oxygen-poor blood from the right ventricle. (B) When capillary beds in the skin are opened, resistance in the systemic circuit falls. Reduced blood pressure in the systemic circuit allows more oxygen-poor blood to enter the left aorta, while the right aorta continues to receive oxygen-rich blood from the left ventricle. The left aorta carries blood to the posterior part of the body, whereas the right aorta carries blood that travels to the brain. Thus, the brain receives oxygen-rich blood at all times.

> shunt, and even this example has been refined by studies of the physiological mechanism responsible for the shunt. The reduced resistance in the systemic circuit produced by vasodilation of warmed tissues appears to be the primary mechanism responsible for initiating the right-to-left shunt that increases blood flow to the body surface. The importance for an ectotherm of speeding warming via a right-to-left shunt may explain the presence of the foramen of Panizza in crocodylians. The complete ventricular septum of the crocodylian heart would prevent an intracardiac shunt were it not for that connection between the right and left sides of the heart.

7.3 ■ ATP Synthesis: Oxidative and Glycolytic Metabolism

The metabolic processes that support muscular activity take place in stages. The first seconds of muscle contraction are powered by energy stored in the cell as adenosine triphosphate (ATP) and phosphocreatine. The concentration of phosphocreatine in amphibian skeletal muscle is about six times that of ATP. Phosphocreatine is used to regenerate ATP as it is consumed by muscle contraction during the initial 20 to 30 seconds of exercise. The total energy stored in ATP and phosphocreatine in the limb muscles of anurans is sufficient for about 100 muscle contractions, allowing an African clawed frog (*Xenopus laevis*) to sprint about 1.4 meters to escape from a predator. When phosphocreatine is exhausted, new ATP can be synthesized by oxidative (aerobic) and glycolytic (anaerobic) metabolic pathways.

Oxidative metabolism uses energy in substrate molecules more efficiently than glycolysis, but glycolysis starts working faster. Oxidative metabolism of 1 mole of glycogen to carbon dioxide and water yields 35 moles of ATP, whereas glycolytic metabolism of the same quantity of glycogen to lactic acid produces only 3 moles of ATP. But accelerating oxidative metabolism in a muscle has a lag time of about 30 s while the circulatory system brings glucose from the liver and oxygen from the lungs. In contrast, glycolysis springs into action immediately because all of the components are present in muscle cells.

Thus, despite its inefficiency, glycolysis is the most effective metabolic pathway for situations that demand a quick response, such as escaping from a predator. Glycolysis is not good in situations that require sustained ATP synthesis, however, because the glycogen stored in a cell is quickly exhausted. Activities that continue for long periods are supported by oxidative metabolism because the circulatory system can replace glucose and oxygen as they are used. Some muscles are specialized for oxidative metabolism and others for glycolytic metabolism. The muscles that male frogs use for vocalization, for example, are capable of very high rates of oxidative metabolism, whereas the limb muscles of the same frogs are primarily glycolytic.

Red and white muscle

Muscle is composed of different types of fibers with different responses to stimulation (e.g., fast twitch, slow twitch, tonic) and different biochemical characteristics (e.g., oxidative, glycolytic, and oxidative–glycolytic). Oxidative fibers contain more myoglobin, a pigment that facilitates the uptake of oxygen from blood, than do glycolytic fibers. Red muscle contains primarily oxidative fibers, while white muscle contains primarily glycolytic fibers. (When you ask for dark meat or light meat from a chicken, you are choosing oxidative or glycolytic muscle, respectively.)

Individual muscles and even parts of muscles differ in the proportions of different fibers, and physical training can change some characteristics of the fibers (Bonine 2007; Husak et al. 2015). For example, in the desert iguana (*Dipsosaurus dorsalis*) the iliofibularis (a muscle in the thigh) is largely white but has a central region of red muscle running its entire length. Other limb muscles, such as the gastrocnemius, have red fibers near the joints. The white regions are composed primarily of fast-twitch glycolytic fibers, whereas the red regions are fast-twitch oxidative–glycolytic fibers with a substantial proportion of tonic fibers. Oxidative fibers are capable of more sustained contraction than are glycolytic or oxidative–glycolytic fibers. The discrete pockets of red muscle in muscles such as the gastrocnemius may strengthen and stabilize the joints. Red fibers that run parallel to the limb bones, as in the iliofibularis, may be directly involved in locomotion.

The total metabolic energy available to an animal is the sum of the ATP synthesized by both oxidative and glycolytic metabolic pathways. Oxidative metabolism is usually determined by measuring oxygen consumption, and glycolysis is measured as lactic acid production.

Comparisons of the total energy used by different species and of the relative importance of oxidative versus glycolytic metabolic pathways have revealed a variety of correlations that link phylogeny, ecology, and behavior. Certain evolutionary lineages of reptiles have high oxidative metabolic rates, for example, and other lineages have especially low rates. High versus low reliance on glycolytic metabolic pathways is associated with different methods of hunting for prey and is reflected in other aspects of an animal's life, including diet, social behavior, reproductive mode, and defenses against predators (Reilly et al. 2007; Wells 2007). Superior individual metabolic performance may be linked to high reproductive success. The following sections describe how metabolic rates are measured and some of the variables that affect metabolism.

Metabolic rates

Animals consume energy every moment of their lives. Even when a lizard is motionless on a rock, it is using muscular contractions to breathe and to pump blood, intracellular transport systems are consuming ATP as they move ions and molecules across membranes, and myriad biochemical processes are consuming energy. The lizard's rate of energy consumption increases if it moves its head to scan its surroundings, increases a bit more if it stands erect, still more if it runs a few centimeters, and so on. The metabolic rate of an animal is not a single value; rather, it is a continuum of values, and an animal's metabolic rate is affected by many variables simultaneously-what it is doing, its body temperature, whether it is digesting food, the time of day, and its state of alertness, to list only a few. In an attempt to define repeatable conditions, physiologists have focused on three situations for measurement of oxidative metabolism: resting metabolism, exercise metabolism, and field metabolism.

RESTING METABOLISM Resting metabolic rates $(V_{O_{2rest}})^*$ are measured from animals that have not eaten recently and

^{*} The symbol \dot{V}_{O_2} indicates volume of oxygen, and the dot over the V is a convention that indicates a rate. Thus, $\dot{V}_{O_{2'}}$ which is read "V dot O 2," refers to oxygen consumption per unit of time, most often expressed as ml/min or ml/h. A subscript is used to indicate the conditions under which the measurement was made. \dot{V}_{O_2} is sometimes converted to calories per unit of time (1 ml $O_2 = -5$ cal) or Joules per unit of time (1 ml $O_2 = -21$ J). These conversions are approximate because the energy equivalence of oxygen consumption is different for different metabolic substrates and with atmospheric pressure.

are inactive in the measurement chambers during the time of day they usually would be active (i.e., day or night). These animals are alert and may make small postural adjustments during the measurement period, but they are not engaged in locomotion.

Both phylogeny and ecology are reflected in resting metabolism. Among squamates, for example, varanid and lacertid lizards have high metabolic rates, whereas helodermatid lizards and boid snakes have low rates. Surface-dwelling squamates have higher metabolic rates than fossorial (burrowing) species, and species of lizards that eat insects or other vertebrates have higher rates than herbivorous species (Andrews and Pough 1985).

EXERCISE METABOLISM Measurements of exercise metabolism ($V_{O_{2ex}}$) are difficult to standardize. The goal is to induce an animal to reach a high level of activity in a way that allows comparison of different levels of an experimental variable, such as temperature. Natural forms of activity hopping, walking, or running—provide the most ecologically relevant measurements, and locomotion is the method most commonly used to elicit high levels of activity. The rate of oxygen consumption during exercise is called $V_{O_{2ex}}$.*

Figure 7.15 illustrates the general pattern of oxygen consumption in relation to speed of locomotion. V_{O_2} increases as the speed of locomotion increases, and the energy cost of locomotion can be expressed mathematically as the slope of the increase in V_{O_2} with speed. At some speed (which depends on the species of animal being tested, its size, body temperature, and many other variables), the rate of oxygen consumption no longer increases. This speed is referred to as the **maximum aerobic speed**. To go faster than the maximum aerobic speed, the animal must use glycolytic (anaerobic) energy production to supply part of the total ATP.

FIELD METABOLISM The metabolic rate of a free-ranging animal varies continuously as it engages in different activities—moving or resting, pursuing prey or escaping from a predator, experiencing hunger or digesting a meal, and so on. Metabolic rates fall during the portion of the day when an animal is inactive in its retreat site, and the decline can be substantial if body temperature is low at night. The **field metabolic rate** (**FMR**) integrates the rate of energy use over periods of days or longer and thus provides information about how much energy an animal uses when it is engaged in its usual behaviors in its natural environment.

Glycolytic metabolism

Glycolysis provides as much as 80% of the ATP used for sprint locomotion by amphibians and reptiles, and ATP production by glycolysis is most rapid in the initial 30 s or so of activity. Glycogen stored in the muscles is used dur-



Figure 7.15 Relation of metabolic rate to speed of locomotion. The metabolic rate $\dot{V}_{O_{2rest}}$ is the rate of oxygen consumption by an animal when it is standing motionless. \dot{V}_{O_2} rises when the animal starts to walk, and continues to rise as the speed of locomotion rises. At the maximum aerobic speed, the rate of oxygen consumption is $\dot{V}_{O_{2ex}}$. This is the highest speed that can be sustained by oxidative metabolism. To run faster, an animal must use glycolytic as well as oxidative metabolism. (After Gatten et al. 1992.)

ing exercise, and depletion of glycogen is one of the factors that produces exhaustion following high levels of activity. Lactate, the ionic form of lactic acid, is the metabolic product of glycolysis, and whole-body lactate concentrations can increase as much as 20-fold during intense activity.

Most studies of glycolytic metabolism have been carried out in laboratory settings in which animals are forced to engage in activity, but a few studies have shown that reptiles engaged in natural activities in the field use glycolysis as a source of ATP. Female green sea turtles (*Chelonia mydas*), for example, accumulate moderate levels of lactic acid when they come ashore to dig nests and deposit eggs, and hatchling sea turtles use glycolysis as they dig out of nests and scramble to the water (Dial 1987; Baldwin et al. 1989; Jessop and Hamann 2004).

Two studies have shown that free-ranging lizards use glycolysis when they defend territories and engage in other kinds of activity (Bennett et al. 1981; Pough and Andrews 1985b). Male Yarrow's spiny lizards (*Sceloporus jarrovii*) survey their territories from perches on large boulders and attack intruding males (**Figure 7.16**). Lactate concentrations of male *S. jarrovii* were low when they emerged in the morning, and remained low as the lizards moved to their perch sites and engaged in feeding and thermoregulatory activities. That situation changed, however, when another male lizard, tethered to a pole, was moved into a male's territory. The resident male approached the intruder, gave threat displays, and ultimately attacked. The high level of activity during territorial defense was fueled partly by glycolysis, and the lactic acid concentrations of the territorial defend-

^{*}Exercise metabolism is sometimes called maximum metabolism $(\dot{V}_{O_{2max}})$, but it is impossible to know if the experimental conditions truly produce the maximum possible rate of oxygen consumption, so $\dot{V}_{O_{2ex}}$ is a better description.





Figure 7.16 Measurement of glycolysis during territorial defense. Use of glycolysis by male Yarrow's spiny lizards (*Sceloporus jarrovii*) was assessed by measuring the whole-body lactate concentration of free-ranging lizards. (A) Males emerged in the morning with low levels of lactic acid that did not increase significantly as they engaged in routine activity. (B) Territorial defense requires glycolytic metabolism and, compared with routine activity, can produce a fourfold increase in lactic acid. The increase in lactic acid is proportional to the intensity of defense, measured as the average number of bites per minute by the territorial male. (C) A resident male *S. jarrovii* is attacking a male lizard that has been tethered to a point within the resident's territory. (After Pough and Andrews

ers rose to four times resting levels. Lactate concentrations were correlated with the intensity of the fight, which was measured as the number of bites per minute delivered by the territorial male.

Lactic acid metabolism

1985b; photograph by Harvey Pough.)

Most species of amphibians and reptiles become exhausted when they are forced to sustain intense levels of activity for more than 2–3 min. An exhausted lizard or frog is nearly inert, and an animal's inability to right itself when it is turned on its back is a common criterion of exhaustion in laboratory studies. Whole-body lactic acid concentrations at exhaustion approach 2 mg lactate/g body mass for some lizards, and concentrations exceeding 6 mg/g body mass have been reported for amphibians.

Maximum lactate concentrations measured in laboratory studies are higher than any reported for animals engaged in natural activities, and amphibians and reptiles may normally use their entire glycolytic capacity only in emergencies. Nonetheless, a submaximal use of glycolytic metabolism depletes muscle glycogen stores and reduces the capacity for additional activity. For example, the male S. jarrovii defending their territories in the previous example accumulated lactic acid concentrations averaging 0.653 mg/g body mass. Those lizards had used a substantial part of their muscle glycogen store and would have had a reduced capacity to defend their territories against another intruder until their muscle glycogen was replenished. Thus, the speed with which an animal can replenish glycogen may have a direct impact on its behavior.

Five minutes of running on a treadmill at speeds of 1.5 to 5 km/h exhausted desert iguanas (*Dipsosaurus dorsalis*). Glycogen was depleted in red and especially in white muscle, and lactate concentrations increased correspondingly. Following exercise, lactate concentrations declined and glycogen stores increased; 2 h later the glycogen content of red muscle was higher than it had been at the start of exercise, but glycogen stores in white muscle were still low (Gleeson and Dalessio 1990).

Reptiles and amphibians convert about 50% of the lactate back to glycogen in the muscles and oxidize less than 20% of it. This pattern is strikingly different from the metabolic fate of lactate in mammals, in which as much as 90% of the lactate formed in muscles during activity is oxidized to carbon dioxide and water. Muscle glycogen stores of mammals are replenished by glucose from the liver (Gleeson 1996).

Total ATP production and activity

Understanding the costs and benefits of relying on glycolysis to sustain activity requires a perspective that integrates long-term energy efficiency with short-term energy needs. The low energy requirements of amphibians and reptiles are associated with their ectothermy. Because they do not depend on metabolic heat production to raise their body temperatures, amphibians and reptiles have low resting rates of oxygen consumption and convert 40–80% of the energy in their food into new body tissue. In contrast, birds and mammals (endotherms) have high resting meta-



Figure 7.17 Oxidative and glycolytic ATP production by a running lizard and mammal. A desert iguana (*Dipsosaurus dorsalis*) synthesizes 32% more ATP in 30 seconds of activity than does a kangaroo rat (*Dipodomys merriami*), but glycolytic (anaerobic) metabolism accounts for 76% of the ATP production by the iguana compared with only 30% by the kangaroo rat. As a result, the lizard rapidly becomes exhausted while the kangaroo rat can continue to run. (After Ruben and Battalia 1979.)

bolic rates and use about 98% of the energy in their food for temperature regulation. Thus, the low resting metabolic rates of amphibians and reptiles promote efficient use of energy.

A different consequence of low resting metabolic rates is revealed during activity. Amphibians, reptiles, and mammals can increase their resting rates of oxidative metabolism about tenfold during activity. Because the resting metabolic rates of mammals are seven to ten times higher than those of amphibians and reptiles, however, the maximum rates of oxidative metabolism by mammals are also seven to ten times higher. As a result, mammals synthesize ATP via oxidative pathways more rapidly than do reptiles or amphibians.

By combining glycolytic and oxidative pathways of ATP synthesis, amphibians and reptiles achieve a short-term total metabolic capacity equivalent to that of a mammal (**Figure 7.17**). During 30 seconds of running, a desert iguana (*Dipsosaurus dorsalis*) produces 32% more ATP than a kangaroo rat (*Dipodomys merriami*)—but 76% of the lizard's ATP is derived from glycolytic metabolism, compared with only 30% for the mammal. The lizard depletes its muscle glycogen in about 5 minutes and must stop running, while the mammal can continue to run.

In general, reptiles and amphibians are intermittently active—they simply do not engage in behaviors that require sustained high levels of ATP synthesis. A lizard uses high levels of activity to sprint away from a predator, and power (total ATP production) for a few seconds is crucial. It doesn't matter that the lizard will be exhausted in 5 minutes, because long before that it will either have escaped or been captured by the predator.

7.4 Environmental Variables and Performance

In biology, performance means how well an organism carries out an activity—how fast it runs, how successfully it captures prey, how rapidly it grows, and so on. Both the physical and biological environments of an animal can affect performance in many ways, and the responses of amphibians and reptiles to these environments extend from the molecular level upward.

Effects of environmental conditions on adults

Because amphibians and reptiles are ectotherms, they cannot always maintain body temperatures within their set-point temperature range. At times they must function with body temperatures above or below the optimum. Amphibians face the additional challenge of evaporative water loss, and some amphibians are active at substantial levels of dehydration.

In general, capacity for performance initially increases as body temperature rises, reaches a maximum, and then declines. The Central American whiptail lizard (*Holcosus festivus*) provides an example of the effect of temperature on performance (van Berkum et al. 1986). The sprint speed of *H. festivus* is temperature-sensitive, reaching a maximum of about 2.3 m/s at a body temperature of 37.5°C (**Figure 7.18**). The optimum temperature for sprinting is close to the mean body temperature of *H. festivus* in the field (35.9°C), and a lizard with a body temperature anywhere between its lower and upper set points (34.5°C and 39.4°C) can achieve at least 90% of its maximum speed.



Figure 7.18 Temperature affects sprint speed and escape from predators. The speed at which the Central American whiptail lizard (*Holcosus festivus*) can sprint increases at body temperatures from 15°C to about 35°C and then declines. The lizard can achieve at least 90% of its maximum speed at body temperatures between about 34°C and 39°C. (After van Berkum et al. 1986.)

Sprinting is most critical for *Holcosus* when it is escaping from a predator. During Fredrica van Berkum's study, a *Holcosus* was captured by a snake that overtook the running lizard in a 6-m dash. Increasing the ability to escape from predators may be an important consequence of thermoregulation for many reptiles and amphibians. The sprint speed of Santa Fe land iguanas (*Conolophus pallidus*) increases as body temperature rises from 15°C to 32°C and is stable at higher temperatures. Galapagos hawks prey on juvenile iguanas (the adults are too large for the hawks to attack), and the ability of iguanas to escape is temperature-dependent. Iguanas escaped from only 33% of the attacks that were made when the body temperatures of the animals were 15°C, whereas they escaped from 81% of the attacks when their body temperatures were 32°C or higher (Christian and Tracy 1981).

Loss of body water can affect performance and amphibians, because of their permeable skins, are probably affected by dehydration more often than are reptiles. Many terrestrial amphibians undergo substantial changes in body water content on a daily basis, and these changes in hydration state affect locomotor performance. For example, dehydration reduces the jumping speed and endurance of leopard frogs (*Rana pipiens*). Fully hydrated frogs can travel nearly 35 m and sustain activity for 2.5 min, whereas frogs that have lost 30% of their body water travel only 12 m and become exhausted in just over 1 min (Moore and Gatten 1989).

Water balance and body temperature interact to determine the locomotor capacity of American toads (*Anaxyrus americanus*). The distance that toads could move in 10 min was measured in the laboratory at body temperatures from 15°C to 30°C and at hydration states from fully (100%) hydrated down to 70% of full hydration (Preest and Pough 1989). Not surprisingly, toads were able to hop farthest when they were fully hydrated and had a body temperature of 30°C. The distance they could cover decreased at lower body temperatures and lower hydration states (**Figure 7.19**).

Free-ranging toads were often active at body temperatures and hydration states substantially below the laboratory optimums, however. Body temperatures ranged from 29.0°C to 16.4°C and averaged 21.3°C, while hydration states ranged from full hydration to 82% of full hydration and averaged 93%.

This interaction between temperature and hydration state adds an important dimension to studies of performance. It means that there is no one optimum body temperature for performance—the body temperature that produces most rapid locomotion depends on hydration state. Rather than regulating only body temperature or only water content, ectotherms are probably making the best compromises possible among a series of ecological and physiological forces.

Effects of the nest environment

The temperature and moisture that reptile eggs experience in their nest can have long-term effects on the hatchlings



Figure 7.19 Both body temperature and hydration state affect locomotion by American toads (*Anaxyrus americanus***).** During laboratory tests, toads traveled farthest when they were 100% hydrated and had a body temperature of 30°C (black arrow). Lower body temperatures and lower hydration shortened the distance they could travel. Free-ranging toads never reached body temperatures above 29°C, however, and were usually less than fully hydrated. The mean state of toads in the field was 21°C body temperature and 90% hydration (red dot), which corresponds to a 25% reduction in locomotor capacity (open circle). (After Preest and Pough 1989.)

that emerge, a phenomenon called developmental plasticity (Deeming 2004; Shine 2004). Temperature-dependent sex determination is an example of developmental plasticity, as are differences in behavior of hatchlings that result from different conditions during incubation, and those topics will be discussed in Chapter 9. Here we will focus on examples of incubation conditions that affect performance.

The embryos of egg-laying reptiles metabolize yolk, using some of it as energy for metabolism and growth and converting the rest to fat. Temperature and moisture in the nest interact to determine how much yolk is metabolized and how that energy is divided between maintenance and growth. The uptake of water by eggs is related to the water potential of the substrate, temperature, and the proportion of the egg surface that is in contact with air in the nest chamber (reviewed by Packard 1999). The wettest substrate produces the largest hatchlings, and the driest substrate produces the smallest. Within any moisture regime, however, eggs incubated at low temperatures take up more water than eggs incubated at high temperatures. Field studies in which the temperature and water potentials in field nests



were related to water uptake by eggs confirm the relevance of these laboratory observations (Packard et al. 1999). In both the field and laboratory, water uptake affects the size of hatchlings, with better-hydrated eggs producing bigger hatchlings because more yolk is metabolized.

To test the effect of moisture during embryonic development on the performance capacity of hatchling turtles, snapping turtle (*Chelydra serpentina*) eggs were taken from natural nests and incubated in the lab in wet or dry substrates at 29°C (Miller et al. 1987; Miller 1993). Hatchlings from the wet substrate were larger than hatchlings from the dry substrate (**Figure 7.20A**). Furthermore, hatchlings from the wet substrate were able to run and swim faster than hatchlings from the dry substrate. By 50 days after hatching, turtles from the wet substrate swam 22% faster than turtles from the dry substrate (**Figure 7.20B**).

The strong locomotor capacities of hatchlings from wet nests may be important in their initial movement to water. Snapping turtle nests may be as far as several hundred meters from the nearest body of water, and hatchlings face desiccating conditions as they make the journey. Hatchlings from wet nests have two advantages over hatchlings from dry nests—they can crawl faster, and their higher initial body water content allows them to lose more water before dehydration diminishes their capacity for locomotion.



Figure 7.20 Incubation conditions affect the performance of hatchling snapping turtles (*Chelydra serpentina*).

(A) Eggs incubated in wet substrate (water potential –150 kPa) produced larger hatchlings than eggs from the same clutch incubated in dry substrate (–850 kPa). Hatchlings from the wet substrate were 18% heavier that those from the dry substrate when they emerged, and the difference in weight persisted for the 50-day duration of the study. (B) Hatchlings from the wet substrate swam 19% faster than those from the dry substrate when they were first placed in water a week after hatching, and the difference increased to 22% by the end of the study. (After Miller 1993; photograph by Gary C. Packard.)

These differences may increase the chances of reaching water successfully (Finkler 1999).

Amphibian eggs in terrestrial nests are affected by the amount of water available in the nest. Puerto Rican coquís (Eleutherodactylus coqui) lay eggs in fallen leaves and palm fronds, and the eggs are brooded nearly continuously by the male parent (see Figure 15.6). Coquí eggs increase in mass three- or fourfold during development by absorbing water from the gelatinous material that encloses them, and the size of the hatchling is determined in part by the amount of water absorbed. Eggs that do not increase in mass during development either die or produce small hatchlings. The egg jelly has a high water content when the clutch is laid but loses water by evaporation during the 15- to 20-day period of embryonic development. The additional water the eggs require is provided by the brooding male, either by osmotic flow through the male's skin or by the male urinating on the eggs (Taigen et al. 1984). Egg masses without an attending male either desiccate or are eaten by predators (see Chapter 8).

7.5 ■ Energy Costs of Natural Activities

It has been possible to measure the amount of energy that an amphibian or reptile uses to carry out some natural behaviors. Locomotion is a prominent feature of the lives of amphibians and reptiles, and the costs of hopping and



walking by anurans and of running and crawling by squamates have been measured. Measurements of the energy costs of consuming prey by lizards and of vocalizing by anurans have been particularly fruitful because they have allowed tests of hypotheses about optimal foraging and sexual selection. Field metabolic rates integrate the costs of all the activities an animal engages in and provide an energy budget showing the daily and annual cost of living.

Locomotion

The locomotor modes of amphibians and reptiles are diverse, and the net cost of transport (ml $O_2/g/km$) shows some variation among and within groups (**Figure 7.21**). Walking salamanders use substantially less energy than do frogs, either walking or hopping (Gatten et al. 1992).

Many species of lizards move in bursts, alternating brief periods of rapid movement with pauses. A study of the frogeyed gecko (*Teratoscincus przewalski*) showed that this behavior increases the distance a lizard can move before it is exhausted (Weinstein and Full 1999). In the field, frog-eyed geckos move intermittently, alternating rest periods with brief sprints at speeds that exceed their maximum aerobic speed. On a treadmill, geckos could travel 258 m before exhaustion when they alternated 15 s of sprinting at 0.9 km/h with 30 s of rest (i.e., an average speed of 0.3 km/h), whereas they could travel only 152 m when they moved continuously at 0.3 km/h.

Most species of snakes can shift among several forms of locomotion (see Chapter 10), and these different locomotor modes have different net energy costs. Lateral undulation by snakes is as energetically efficient as locomotion with limbs by lizards, but no more so (Walton et al. 1990).

Figure 7.21 Net energy cost of locomotion for amphibians and reptiles. Several types of locomotion are shown: walking/ running for lizards and salamanders, walking/hopping for frogs, and lateral undulations, concertina locomotion, and sidewinding for snakes. The dashed line shows the relationship for mammals. The energy cost of locomotion per unit body weight decreases as body size increases, and some modes of locomotion require more energy than others. For example, walking salamanders use less energy than hopping frogs. Laterally undulating snakes use the same amount of energy as walking lizards, but sidewinding snakes use less than half that energy. (After Walton et al. 1990.)

Concertina locomotion by black racers (*Coluber constrictor*) is about seven times as costly as lateral undulation by the same species. The net energy cost of transport for side-winder rattlesnakes (*Crotalus cerastes*) is less than half that of lateral undulation by the racers (Secor and Nagy 1994).

Feeding

An animal invests both time and energy in obtaining food, and either time or energy can be an ecologically important cost. Theoretical models of optimal foraging make predictions about an animal's predatory behavior. Observations of lizards were important in the development of optimal foraging theory (Schoener 1969), and measurements of the energy costs of prey handling by lizards have been used to test some optimal-foraging hypotheses.

The time and energy an animal needs to subdue and swallow a prey item can be determined by measuring oxygen consumption during feeding (Figure 7.22). Both the time and the energy used by the skink Chalcides ocellatus to crush and swallow a cricket increase as cricket size increases. More than 90% of the ATP used during feeding comes from oxidative pathways. Glycolysis makes an insignificant contribution to the total energy cost of lizards feeding on insects (Preest 1991), but it may be important for snakes (Cruz-Neto et al. 2001; Canjani et al. 2003). For example, when garter snakes (Thamnophis elegans) ate salamanders (Plethodon jordani), both animals accumulated substantial amounts of lactic acid as the snakes struggled to eat the salamanders and the salamanders tried to escape from the snakes (Feder and Arnold 1982). The unusual morphology of the lung of most snakes may be related to the difficulty of breathing when a snake is constricting or swallowing prey (Canjani et al. 2003).

The morphological characteristics of lizards and their prey affect the energy cost of feeding. A large-headed species of skink (*Plestiodon inexpectatus*) was able to eat crickets faster than a small-headed species (*Chalcides ocellatus*). *Plestiodon* used less energy in feeding than did *Chalcides* and were able to consume larger prey relative to their own body size (Andrews et al. 1987). Insects with heavy exoskeletons, such as beetles, are harder for lizards to eat than are soft-bodied insects; *Chalcides* required 50% more energy to


Figure 7.22 Energy cost of subduing and swallowing prey. (A) Skinks (*Chalcides ocellatus*) readily ate crickets in closed chambers that allowed researchers to measure how much oxygen the skinks consumed. (B) The amount of energy that skinks used to subdue and swallow crickets increased with the size of the cricket. There was no measurable energy cost for the smallest crickets. (After Pough and Andrews 1985a; photograph by Harvey Pough.)

> crush and swallow a beetle than to eat a softbodied insect larva (Grimmond et al. 1994).

> The net energy that a lizard or snake gains by eating a prey item can be calculated by subtracting the energy used during feeding from an estimate of the energy obtained by digesting the insect. In every case—even for a small skink eating a large beetle—these calculations show that the energy cost of prey handling is less than 1% of the energy gained by digesting the prey. Thus, the energy cost of feeding is trivial and probably is not a factor in determining what sizes of prey a lizard or snake attacks.

> Field metabolic rates of actively foraging lizards are more than 39% higher than those of sit-and-wait foragers. Much of this difference results from the cost of locomotion, despite the generally shorter activity periods of actively foraging species (Brown and Nagy 2007). The cost of movement averaged 19.6% of the total daily expenditure for 27 species of lizards (Christian et al. 1997). The daily energy expenditure of a coachwhip snake (Coluber flagellum), an actively foraging predator, is nearly 2.5 times that of the sidewinder rattlesnake (Crotalus cerastes), an ambush predator, and the daily energy intake of the coachwhip is also about 2.5 times that of the sidewinder. The cost of locomotion accounts for 18% of the daily energy expenditure of the coachwhip, compared with only 6% for the sidewinder, despite a shorter activity period for the coachwhip (3.9 h/day) than for the sidewinder (7.9 h/day). Thus, actively foraging species expend more energy searching for prey than do sitand-wait species, but this energy investment

Figure 7.23 Active foraging costs more and gains more.

An actively foraging predator, the coachwhip snake (*Coluber flagellum*), both uses and gains about 2.5 times as much energy daily as does an ambush predator, the sidewinder rattlesnake (*Crotalus cerastes*). (After Secor and Nagy 1994. Photographs: *C. flagellum*, © Danita Delimont/Alamy; *C. cerastes*, courtesy of Mark Fisher.)

pays off in a higher daily energy intake by actively foraging species (Figure 7.23).

Vocalization by anurans

Vocalizing during the breeding season is the hardest work most male anurans do in their lives, and the acoustic energy in frog calls is substantial (Prestwich 1994). Sound energy is expressed as decibels (dB), and sound-pressure levels of the calls of 42 species of frogs, most with body masses less than 10 g—and some as small as 2–3 g—averaged 102 dB (Wells 2007). The vocalizations of these frogs contained more energy than the calls of 17 species of songbirds (average 89 dB) that weighed an average of 23 g (Pough et al. 1992). Being in the middle of a dense chorus of frogs can be deafening.

The rates of oxygen consumption by calling frogs are substantially higher than the rates measured during even the most rapid locomotion exercise (**Figure 7.24**). Even the cost of building a foam nest by *Engystomops pustulosus* is only 45% of the cost of calling by this species (Wells 2007). Furthermore, nest building takes only an hour, whereas a male frog may call every few seconds for several hours during a night and return to the chorus night after night. The loudness of a male's call, the length of time that it can call during a night, and the number of nights it can spend in the breeding chorus all contribute directly to its success in obtaining a mate.





Vocalization by anurans is a dramatic exception to the generalization we made earlier that most amphibians and reptiles do not engage in activities that require sustained high levels of energy expenditure. The remarkable energy costs of vocalization by anurans are supported by a series of anatomical and biochemical specializations.

CHARACTERISTICS OF TRUNK MUSCLES The high rates of oxygen consumption by calling frogs are associated with morphological and biochemical characteristics of the trunk muscles, primarily the rectus abdominus, external oblique, and internal oblique. These specializations are found only in males and only during the breeding season. The trunk muscles of males undergo anatomical and biochemical changes before the breeding season starts, and regress to a resting state when the season is over. The most conspicuous change is hypertrophy of the trunk muscles responsible for vocalization. At the height of their development, just two trunk muscles-the internal and external obliqueaccount for 2-15% of the total body mass of males of nine species of frogs (Pough et al. 1992). The size of the trunk muscles relative to the size of the frog is roughly proportional to the calling effort measured as seconds of vocalization per night: males of species with high calling effort have larger muscles than males of species with lower efforts.

The trunk muscles of calling frogs are highly oxidative, with many mitochondria, high densities of capillaries, and high activities of two enzymes associated with oxidative metabolism, citrate synthase and β -hydroxyacyl coenzyme A dehydrogenase (Ressel 1996; Wells 2007).

Lipids provide 75–95% of the ATP used by species of anurans with high rates of vocalization, whereas glycogen appears to be important for species with lower rates of calling (Wells 2007). At the start of the breeding season, lipids account for as much as 45% of the volume of trunk muscles of male spring peepers (*Pseudacris crucifer*) and nearly that much in two species of Panamanian frogs (*Dendropsophus microcephalus* [formerly *Hyla microcephala*] and *Engystomops pustulosus*), all of which emit 3,000 to 6,000 notes per hour. In contrast, very little lipid is stored in the trunk muscles of the North American wood frog (*Rana sylvatica*), which



Figure 7.24 Energy cost of vocalization.

The energy cost of vocalization by eastern gray treefrogs (*Hyla versicolor*) increases as the rate of calling increases. (A) Researchers placed frogs in metabolism chambers in the field and measured oxygen consumption as the frogs called. (B) The resting rate of oxygen consumption is shown by the blue bar on the *y* axis. The metabolic rate increases as the rate of calling increases. At high calling rates, the rate of oxygen consumption exceeds that required for rapid activity (red bar). (After Taigen and Wells 1985; Photographs: A, Theodore L. Taigen; inset, David McIntyre.)

emits only 500 to 600 notes per hour (Bevier 1995; Wells and Bevier 1997).

ENERGETICS AND CALLING EFFORT Males of several species of anurans lose weight and deplete glycogen or lipid reserves during a night of calling and across the length of a breeding season. Anuran vocalization is a social behavior, and it is influenced by the presence and behavior of other male frogs. For males of anuran species with prolonged breeding seasons, the availability of receptive females at the breeding sites is what limits reproductive success. On a given night the number of males at a breeding site is usually much greater than the number of females, so only a few males are able to mate. A strongly skewed mating success is typical of male frogs-that is, most individuals never mate, and a few individuals achieve multiple matings. Under these conditions sexual selection should be intense, and male frogs should behave in ways that maximize their attractiveness to females, and hence their chances of mating (see Chapter 14).

Females of many frog species appear to make a choice among males, probably on the basis of one or more characteristics of their vocalizations. For example, female Dendropsophus microcephalus mate preferentially with males that call at high rates (Schwartz et al. 1995), and the calling rates of male D. microcephalus can exceed 6,000 calls per hour. Male frogs in a breeding chorus often respond to the presence of a female by increasing the energy output of their vocalization—by calling faster, by giving longer calls, or by adding additional elements to the call. When one male increases its calling effort, nearby males often follow suit, and these interactions among males can produce substantial variation in calling effort in different parts of a chorus. An analysis of one chorus of D. microcephalus found that the calling effort of individual males varied from 205 to 6,330 notes per hour, corresponding to a 300% variation in energy expenditure (Wells and Taigen 1989).

CHORUS TENURE AND MATING SUCCESS The number of nights a male anuran spends in a chorus is an important factor in determining whether it will get a mate (**Figure 7.25A**). In a 4-year study, Christopher Murphy (1994a,b) found that male barking treefrogs (*Hyla gratiosa*) average about 1 mating for every 5 nights in a chorus. The breeding season of *H. gratiosa* lasts for several months, but most male barking treefrogs call for only 1 to 3 nights (**Figure 7.25B**). These short chorus tenures are characteristic of anurans that call at high rates. The median chorus tenure for individual males among 20 species of anurans is only 20% of the breeding season.

Depletion of energy reserves was the most likely explanation for the short chorus tenures of male *Hyla gratiosa*. In two successive years Murphy captured male frogs as they left the breeding pond, placed them in cages and fed them crickets, and then released them. Control males were cap-



Figure 7.25 Mating success and chorus attendance. The amount of time spent in a breeding chorus is an important determinant of mating success for male barking treefrogs (*Hyla gratiosa*). (A) Average number of matings obtained by male frogs increased with the number of nights a male spent in the chorus. (B) Despite the importance of showing up, many male barking treefrogs spent only 1 night in the chorus, and the median chorus attendance (red arrow) was only 3 nights. (After Murphy 1994a,b; photograph © AGE Fotostock/Alamy.)

tured and held in cages but were not given crickets. Individuals that ate crickets returned to the chorus sooner than did controls (medians for the two years were 2.4 and 2.6 nights for fed males versus 4.0 and 5.5 nights for control males). The fed males also returned to the chorus more often than did the controls (medians of 4 and 5 nights for fed males versus 1 and 2 nights for controls).

Depletion of energy stores as a result of the high energy demands of vocalization may be a widespread phenomenon among male anurans. Individual variation in the vocal behavior of male anurans, such as adjusting calling patterns as chorus density changes or in response to the presence of females, allows them to use their limited energy stores effectively and may contribute to their success in attracting mates.

7.6 ■ Metabolic Depression: Aestivation, Hibernation, and Freezing

Extreme heat or cold can force amphibians and reptiles to cease activity and enter a dormant state for periods ranging from days to months. **Aestivation** is long-term dormancy during periods of heat or drought, whereas **hibernation** is dormancy during periods of cold and food scarcity (Withers and Cooper 2010). Dormancy is a regular part of the annual cycle for many amphibians and reptiles; some species spend as much as 10 months each year in dormancy (Pinder et al. 1992). Yellow mud turtles (*Kinosternon flavescens*) can remain dormant for 2 years (Rose 1980), and some Australian water-holding frogs (*Cyclorana platycephalus*) may be able to survive 5 years of dormancy (van Beurden 1980).

Extremely low temperatures pose an additional challenge for dormant animals—the risk of freezing. Most species of amphibians and reptiles choose hibernation sites below the frost line, which protects them from subzero temperatures, but some remain close to the surface where the ground freezes. These species either remain unfrozen at subfreezing temperatures (freeze resistance) or withstand freezing and thawing of their body tissues without damage (freeze tolerance) (Costanzo and Lee 2013).

Hibernation and aestivation

Aestivating and hibernating animals are inactive, neither eating nor drinking, so conservation of energy and water is critical. Metabolic rates during both aestivation and hibernation fall by 70% or more (Withers and Cooper 2010). These low metabolic rates prolong survival by conserving stores of lipids and glycogen and by reducing respiratory and urinary water loss. The reduction of metabolic rates during dormancy is anticipatory rather than the result of starvation, and the metabolic rates of aestivating and hibernating animals return to normal when they arouse.

Aestivating animals are often at or near the temperatures at which they are normally active, but their metabolic rates are nonetheless depressed. For example, the metabolic rate of Australian long-necked turtles (*Chelodina rugosa*) declined to 29% of resting rates after 2 weeks of aestivation at 30°C (Kennett and Christian 1994). After 10 weeks of aestivation at 25°C, the metabolic rate of Australian trilling frogs (*Neobatrachus centralis*) fell to 23% of the rate for nonaestivating frogs at the same temperature (Withers 1993).

Hibernating amphibians and reptiles show metabolic depression compared to non-dormant animals when both are measured at hibernation temperatures. The metabolic rates of hibernating European common frogs (*Rana temporaria*) were 38% of the rates for non-hibernators after two weeks at 3°C (Donohoe and Boutilier 1998) and the metabolism of hibernating male European lizards (*Zootoca vi-* *vipara*) was 35% of the non-hibernating rate after 2 months at 10°C (Patterson and Davies 1978).

The metabolic rate depression that occurs during aestivation and hibernation results from adjustments that extend from modification of gene expression and protein synthesis to modifications that change the activity of enzymes and the mass and structure of body tissues (Secor and Lignot 2010; Storey and Storey 2010; Storey 2015).

- Transcriptional controls alter the rates at which genes are transcribed to mRNA. For example, changes in histones (proteins that stabilize DNA) affect access of RNA polymerase to the promoter regions of genes. Despite the overall down-regulation of gene expression, selective up-regulation of genes that silence the expression of other genes occurs during aestivation and hibernation.
- 2. *Translational controls* alter the rates at which the ribosome/mRNA complex synthesizes proteins. Alterations in ribosomal initiating factors and microRNAs change the rates at which synthesis begins and the rate at which the protein is elongated.
- 3. *Posttranslational controls* alter the properties of proteins and their longevity. Reversible phosphorylation of proteins is a major component of metabolic depression, changing the activity and substrate affinity of enzymes and their susceptibility to allosteric activators and inhibitors. (Reversible phosphorylation of proteins is the underlying mechanism of many transcriptional and translational controls.) The longevity of a protein can be affected by addition of the small regulatory protein ubiquitin, and heat-shock proteins refold damaged proteins.
- 4. *Selective atrophy of tissues* accompanies metabolic depression. Digestive organs (stomach, small and large intestines, and the liver) decrease in mass, but the heart, lungs, and kidney show little change.

These mechanisms are broadly conserved across phylogenetic lineages and types of environmental stress. They are found in insects, mollusks, and all vertebrates, and they are employed in response to dehydration, osmotic concentration, and hypoxia as well as during aestivation and hibernation. Thus, these tissue and cellular defenses are pre-existing mechanisms that have been incorporated into amphibian and reptile responses to dormancy (Storey and Storey 2004).

Freeze resistance and freeze tolerance

Most amphibians and reptiles hibernate in sites where temperatures do not fall below freezing. Some species of frogs and aquatic turtles spend the winter beneath the ice in ponds in water temperatures around 4°C, and garter snakes (*Thamnophis sirtalis*) and rattlesnakes (*Crotalus viridis*) hibernating underground in Canada had body temperatures between 2° and 7°C (Macartney et al. 1989).

Other species remain close to the surface, however, where they are exposed to sub-zero temperatures. European lizards (*Zootoca vivipara*) hibernate in grass tussocks where temperatures fall as low as -4° C, and hatchling painted turtles (*Chrysemys picta*) overwinter in their nest where temperatures reach -10° C (Costanzo et al. 2000; Grenot et al. 2000). In Ohio, wood frogs (*Rana sylvatica*) hibernate beneath leaf litter on the forest floor, where their body temperatures fall to -7° C. In Alaska this species is exposed to minimum temperatures of -18° C (Costanzo et al. 2013; Larson et al. 2014). Two salamander species from Siberia (*Salamandrella keyserlingii* and *S. tridactyla*) have been reported to survive temperatures of -35° C (Berman et al. 2010).

Amphibians and reptiles that experience sub-zero temperatures during dormancy depend on one of two mechanisms to survive: freeze resistance or freeze tolerance (Costanzo and Lee 2013). Freeze-resisting species cool to a temperature below the freezing point of their body tissues without freezing, a phenomenon called **supercooling**. In contrast, freeze-tolerant species allow their body fluids to freeze, employing mechanisms that prevent ice crystals from damaging cells and molecules.

FREEZE RESISTANCE Increasing the concentration of body fluids lowers their freezing point and promotes supercooling. Glucose, glycerol, urea, and amino acids are molecules used for cryoprotection by freeze-resistant amphibians and reptiles. Freeze resistance is risky, however, because a supercooled fluid can flash-freeze spontaneously at any moment. The longer a supercooled organism remains at subfreezing temperatures, the greater becomes the chance that it will freeze. Ice nucleation causes flash-freezing, and ice nucleating bacteria and yeasts are found on the skin and in the gut. Ice crystals in the soil are nucleators if they penetrate the skin of a supercooled animal. Gray treefrogs (Hyla versicolor) that were cooled to -1.1 to -1.5°C on moist soil froze within 30 seconds after the supercooled soil was seeded with ice (Layne 1991). Their dry skins make reptiles less subject to seeding by external ice crystals than amphibians, and some species reptiles supercool to -5 or -10°C. In the laboratory hatchling painted turtles (Chrysemys picta) can remain unfrozen at temperatures as low as -20°C, but only if they are protected from external nucleation; supercooling in the field probably does not exceed -5°C (Costanzo et al. 2000; Packard and Packard 2004).

Thus, animals that depend on supercooling to avoid freezing are betting their lives (literally) that nucleation will not occur. Yarrow's spiny lizard (*Sceloporus jarrovi*) is found at high altitudes in the mountains of southern Arizona. Although temperatures fall well below freezing in winter, sunlight is intense and the lizards can bask and reach activity temperatures during the day. These lizards spend the nights in relatively shallow rock crevices where the temperature sometimes falls below 0°C. When that happens, the animals supercool. Laboratory studies have shown that the lizards can be chilled to -3° C without freezing—usually, that is. Freezing of a supercooled solution is an unpredictable event, and every spring there are some dead lizards in the crevices. Those are the ones that lost their bets.

FREEZE TOLERANCE Freezing is deadly for most animals because the formation of ice crystals damages intracellular structures. However, a few vertebrates, including about a dozen species of amphibians and reptiles, are able to tolerate repeated freezing and thawing (Pinder et al. 1992; Costanzo and Lee 2013). These animals have a complex biochemical response to freezing that protects intracellular structures from damage. Cells face two problems as an organism freezes: first, they are themselves at risk of freezing, and second, they risk dehydration. Cellular dehydration can occur when some of the water in the extracellular space freezes and the osmolality of the remaining extracellular water increases. This increased osmolality of the extracellular fluid draws water from cells unless it is counter-acted by a mechanism that *raises* intracellular osmolality.

The key to surviving freezing is to (1) initiate ice formation at temperatures high enough to avoid flash-freezing, and (2) control the size and distribution of ice crystals. Freeze-tolerant animals do not supercool far below the freezing points. Instead, they employ ice-nucleating molecules to initiate ice formation while the rate and location of crystallization can be controlled.

The mechanism of freeze tolerance of Rana sylvatica has been studied extensively (Costanzo et al. 2013). As its body temperature falls, R. sylvatica becomes immobile, and actual freezing of some tissue (usually the toes, seeded by ice-nucleating bacteria on the skin) is the stimulus for a protective response (Figure 7.26). As soon as the first freezing occurs. glycogen in the frog's liver is converted to glucose that is rapidly transported throughout the body. The process is remarkably fast-within 10 or 15 minutes after its toes start to freeze the frog has dispersed glucose throughout its body. The accumulation of glucose inside cells increases intracellular osmolality and lowers the freezing point of intracellular water. As water in the extracellular spaces turns to ice. the osmolality of the remaining extracellular fluid increases. The high concentration of glucose inside the cells prevents water from being drawn into the extracellular space by osmosis and also prevents the formation of ice crystals inside the cells.

Freezing takes about 24 hours for an adult wood frog About 65% of the water in a frog is frozen, and the frog becomes stiff (see Figure 7.26, center photograph). Respiratory movements, circulation, and heartbeat stop. Thawing follows a reverse sequence: the heartbeat resumes while some tissues are still frozen, and breathing and simple reflexes follow. Full restoration of locomotion and other behaviors requires a day or more. The frog can remain frozen for a week or two. If freezing is extended for longer periods, the probability of survival decreases, although frozen





wood frogs from Alaska have been known to survive for two months (Costanzo et al. 2013). At least in temperate regions, freeze tolerance probably allows animals to resume activity quickly in the spring, when cold and warm periods alternate.

Freezing and thawing are energetically costly processes for wood frogs (Sinclair et al. 2013). The metabolic rates of frogs rise as they cool toward freezing and increase dramatically during glycogenolysis. Another burst of metabolic activity occurs at the end of thawing as the frogs repair damage to cells and tissues. Each freeze–thaw cycle incurs these metabolic costs, and wood frogs near Ottawa, Canada undergo more than 20 freeze–thaw cycles in a winter. The high energy cost of repeated freezing and thawing is further evidence that the value of freeze tolerance for wood frogs lies in the advantage of overwintering close to the surface and resuming activity quickly in the spring rather than conserving energy during dormancy. frozen. For the next 10 hours the body temperature fell slowly, finally reaching the chamber temperature (-2.5°C). At this point, 65% of the body fluid was frozen and no additional freezing occurred. After 36 h the frog was moved back to the 4°C chamber and began to warm. Thawing is an endothermic (heatabsorbing) process, and the flattening of the temperature curve at 0°C represents the conversion of water in its frozen state to water in its liquid state. Physiological processes resumed at the times shown, and the frog was capable of locomotion at 60 h. (After Costanzo and Lee 2013; photographs by Janet M. Storey.)

7.7 Annual Energy Budgets

The resting metabolism or the cost of locomotion for a species can be measured in the laboratory at a particular temperature, but these measurements cannot readily be extrapolated to natural conditions. Free-ranging animals are exposed to variable temperatures, they alternate periods of activity and rest, and sometimes they are digesting food. Measuring the field metabolic rate—that is, the energy expenditure of a free-ranging animal—employs chemical tracers, and doubly labeled water is the method used most often (Buchowski 2014).

The term "doubly labeled" refers to water in which some hydrogen atoms (H) are replaced by deuterium (²H), and some oxygen atoms (¹⁶O) are replaced by oxygen (¹⁸O). A small amount of doubly labeled water is injected into an animal, and the disappearance of ²H and ¹⁸O is followed as the animal is recaptured at intervals. Oxygen is lost in both carbon dioxide and water, whereas H is lost only in water. Subtracting the rate of H loss from the rate of O loss provides an estimate of carbon dioxide production, and that value can be converted to an estimate of field metabolism.

Annual energy budgets of free-ranging animals can be constructed from measurements of field metabolism, and these studies reveal the impact of environmental conditions. Steven Beaupre (1995, 1996) studied mottled rock rattlesnakes (Crotalus lepidus) at two different elevations in Big Bend National Park, Texas (Figure 7.27). He found that temperature has an enormous effect on activity patterns, food intake, and the partitioning of energy between maintenance and production. Boquillas, the low-elevation site, is about 4°C warmer during the summer than the high-elevation site, Grapevine Hills. The body temperatures of free-ranging snakes were monitored by surgically implanting small temperature-sensitive radio transmitters in their bodies. The average body temperature of snakes at Boquillas was 29.9°C compared with 28.8°C at Grapevine Hills. Small as it is, that 1.1°C difference in average body temperature between the sites is statistically significant and has important biological consequences.

Temperature affects the energy balance of the rattlesnakes in three ways:

- 1. Snakes at Boquillas spend more time in underground shelters and less time searching for prey on the surface than do those at Grapevine Hills. Snakes at Boquillas were on the surface in only 33% of censuses, whereas snakes at Grapevine Hills were on the surface in 62% of censuses.
- 2. Because the snakes at Boquillas spend less time on the surface than do the snakes at Grapevine Hills, they feed less frequently. Snakes from Boquillas had fed recently only 44% of the times they were examined, compared with 90% of the time for snakes from Grapevine Hills.
- 3. Because body temperatures of snakes at Boquillas are high, their metabolic rates are high. As a result, approximately 31% of the annual energy expenditure of snakes at Boquillas is used for resting metabolism, compared with 19% for snakes at Grapevine Hills.

Because snakes from Boquillas captured fewer prey and used more energy for maintenance than did snakes at Grapevine Hills, the Boquillas snakes grew more slowly than those at Grapevine Hills. The number of segments in an unbroken rattle is an approximate measure of age, and a male mottled rock rattlesnake from Boquillas with 10 segments in its rattle weighed about 50 g, whereas a male snake of the same age from Grapevine Hills weighed about 125 g.

When the energy used at rest and during activity is subtracted from the total energy intake, the remaining energy



Figure 7.27 Annual energy budgets of mottled rock rattlesnakes (*Crotalus lepidus*) at two sites in Big Bend National Park, Texas. A 100-g adult male snake from Grapevine Hills (high-elevation site) devotes a larger proportion of its energy to active metabolism (hunting for prey) than does a similar-size snake at Boquillas (low-elevation site). As a result, snakes at Grapevine Hills are twice as likely to have food in their stomachs as are snakes at Boquillas. Because snakes at Grapevine Hills spend more time foraging and capture more prey, their annual total energy budget (1,116 kJ) is 70% greater than that of snakes at Boquillas (655 kJ). Higher food intake allows Grapevine Hills snakes to devote 64% more energy to growth than snakes at Boquillas (194 kJ vs. 118 kJ). (After Beaupre 1996.)

is available for growth. The growth component of the energy budget of a male snake is entirely somatic—that is, an increase in the size of that snake. Female snakes, however, devote some of the growth energy to reproduction. Female mottled rock rattlesnakes at Boquillas have less energy to devote to reproduction than do females at Grapevine Hills.

Quantifying energy budgets illuminates current aspects of the behavior and ecology of a species, and also suggests how climate change will affect populations of amphibians and reptiles. By the middle of this century, the mean temperature in Big Bend National Park is predicted to increase by 2–3°C (NOAA 2013). That change may further restrict the time that snakes at Boquillas can spend aboveground and will even reduce the activity of snakes at Grapevine Hills. As foraging time is reduced, energy intake will decrease, leading to reductions in growth rates and reproduction. Temperature changes of the magnitude predicted by the Intergovernmental Panel on Climate Change have already been responsible for the extinction of populations of Sceloporus lizards in the American Southwest and Mexico, and are predicted to have a worldwide impact (see Chapter 17) (Sinervo et al. 2010).

SUMMARY

Water and air are the respiratory media for aquatic and terrestrial animals, respectively, but all amphibians and some reptiles can use both media, often simultaneously.

Gas exchange takes place in the lungs (pulmonary gas exchange), at the skin surface (cutaneous gas exchange), and in the gills, pharynx, and cloaca.

Amphibians, and to a lesser extent reptiles, take up oxygen and release carbon dioxide through the skin.

Many aquatic amphibians have specialized structures—gills, skin folds, flattened tails, or elaborate fins—that increase the surface area available for gas exchange. Some salamander lineages are lungless, relying entirely on cutaneous and buccopharyngeal respiration.

Cutaneous gas exchange is significant for some aquatic reptiles, and appears to be correlated with the extent of aquatic specialization.

Although cutaneous gas exchange plays a role in respiration by aquatic turtles, the buccopharyngeal region and cloaca are more important sites of gas exchange than the skin is.

Most air-breathing animals rely on lungs: internal sacs of air that are ventilated by respiratory movements of the buccopharyngeal region and trunk.

The lungs of amphibians and reptiles range from simple sacs with few if any internal divisions, to complex structures with interior walls and passages that direct airflow and increase surface area.

Amphibians force air into the lungs by buccopharyngeal pumping (positive-pressure ventilation), Most amphibians use two-cycle ventilation in which exhaled air and inhaled air move in opposite directions with little mixing.

Reptiles suck air into the lungs by expanding the rib cage (negative-pressure ventilation). Squamates use trunk muscles to ventilate the lungs, whereas crocodylians also use the liver as a piston to compress and expand the lungs. Turtles use the viscera as a piston.

Most elongate reptiles, such as snakes and amphisbaenians, have only one functional lung.

The circulatory system carries oxygen from the sites of gas exchange to metabolically active tissues and brings carbon dioxide produced by metabolism to sites where it is released.

The circulatory system of lung-breathing amphibians and reptiles can be pictured as a figure eight, with the heart at the junction of the two loops. The pulmonary circuit receives oxygen-poor blood from the right side of the heart and sends it to the lungs. Oxygen-rich blood from the lungs returns via the left side of the heart and is pumped through the systemic circuit to the body.

The amphibian heart has a single ventricle, with a complex internal structure that minimizes mixing of oxygen-rich and oxygen-poor blood.

Turtles and squamates have a single ventricle anatomically, but ventricular contraction dynamically creates three chambers that separate oxygen-rich and oxygenpoor blood.

Crocodylians have an anatomical separation of the ventricle into two chambers.

Intracardiac shunts shift blood between the pulmonary and systemic circuits. A right-to-left shunt sends some of the oxygen-poor blood from the right atrium into the systemic circuit, and a left-to-right shunt sends some oxygen-rich blood into the pulmonary circuit.

The septum in the crocodylian ventricle precludes an intracardiac shunt, and an extracardiac shunt occurs through the foramen of Panizza, which connects the left and right aortas.

High-energy phosphate compounds stored in muscle cells power the first muscle contractions during activity, after which new ATP molecules are synthesized via oxidative (aerobic) and glycolytic (anaerobic) pathways.

Oxidative metabolism produces more ATP per substrate molecule than glycolytic metabolism (glycolysis) does, but there is a delay because glucose and oxygen molecules must be transported by the circulatory system. Glycolysis produces fewer ATP molecules per substrate molecule but uses an immediately available substrate—the glycogen stored in muscle cells.

Oxidative metabolism can be sustained for long periods, whereas glycolysis depletes muscle glycogen. The relative importance of oxidative versus glycolytic metabolic pathways in any given species is associated with the species' foraging behavior, diet, social behavior, reproductive mode, and defenses against predators.

An animal's metabolic rate is affected by many variables simultaneously.

Performance describes how effectively an animal engages in an activity—how fast it runs or swims, how rapidly it grows, how loudly it vocalizes, and so on. Both the physical and biological environments can affect an animal's performance.

In general, performance improves with increasing body temperature until a maximum is reached, then declines at higher temperatures. Body temperature and hydration display a synergism that makes it impossible to define a single temperature for optimum performance. Because of their permeable skin, amphibians are affected by dehydration more than reptiles are.

The temperature and moisture that reptile eggs experience in the nest can affect the phenotype of hatchlings, including their body size, sex, locomotor ability, growth rates, and behavior.

The energy costs of several natural activities of amphibians and reptiles have been measured, which in turn has allowed tests of hypotheses about optimal foraging and sexual selection.

Amphibian and reptilian modes of locomotion are diverse, and the net cost of transport shows variation among and within groups

The energy expended subduing and swallowing prey is small compared with the energy gained by digesting the prey, and most feeding is supported almost entirely by oxidative metabolism. Snakes are an exception not because they expend a great amount of energy while feeding, but because constriction and swallowing interfere with breathing.

Depletion of energy stores causes some male frogs to limit their calling activity, despite the strong positive relationship between calling performance and the number of times a male frog mates.

Dormancy is part of the seasonal cycle of many amphibians and reptiles. They aestivate to avoid heat or drought and hibernate during periods of cold.

During aestivation or hibernation, metabolic rate is depressed to about a quarter of the normal rate This depression results from changes in the rate of transcription of genes and synthesis of proteins, the functional properties and longevity of proteins, and the mass of tissues.

Hibernating amphibians and reptiles run the risk of freezing. Some species resist freezing by increasing the osmolal concentration of their body fluids and supercooling below the freezing points of their tissues. Others tolerate freezing by controlling the rate and location of ice crystal formation.

Measuring field metabolic rates and constructing energy budgets can help predict the effects of climate change on populations of amphibians and reptiles.

Temperature changes of the magnitude predicted by the Intergovernmental Panel on Climate Change have already been responsible for the extinction of populations of *Sceloporus* lizards in the American Southwest and Mexico, and are predicted to have a worldwide impact on amphibians and reptiles.

Go to the **Herpetology** Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

8 Reproduction and Life Histories of Amphibians

eproduction is by far the most conspicuous feature of amphibian biology, and most casual observers seldom encounter amphibians outside of the breeding season. Reproductive activities of many amphibians can be spectacular. Who would not be impressed by the sound of hundreds of male frogs gathered in a pond, calling to attract mates, followed by the appearance of enormous numbers of eggs and the eventual mass emergence of thousands of metamorphosing froglets? In many cultures the sudden appearance of amphibians after heavy rains, and their prolific reproduction, has made these animals symbols of fertility. The ancient Egyptians believed that frogs were generated by the coupling of land and water during the annual flooding of the Nile. The Egyptian goddess Heget functioned as a divine midwife and was depicted in paintings and sculpture with the head of a frog and the body of a woman. In the New World the ancient Maya considered frogs to be musical heralds, whose mating calls announced the coming of the rains that provided life-giving water for their crops.

Today children learn the basic life history of frogs, often through colorful books showing mating and the progression from large masses of aquatic eggs to tadpoles, metamorphosing juveniles, and adults. Similar diagrams of this amphibian life cycle appear in most introductory high school and college biology textbooks. Yet this highly simplified view of amphibian reproduction fails to capture the enormous diversity of reproductive modes in these animals (Crump 2015).

Many amphibians have external fertilization, whereas others fertilize their eggs inside the body of the female. The large masses of aquatic eggs depicted in illustrations of amphibian life cycles are characteristic of most pond-breeding species, but many other amphibians produce only a few eggs at a time and often do not lay them in water (Figure 8.1). Some of the most successful amphibians, including most plethodontid salamanders and Neotropical frogs in the families Eleutherodactylidae and Craugastoridae, have abandoned aquatic reproduction altogether and lay terrestrial eggs that undergo direct development into miniature adults. Some amphibians retain their eggs inside the reproductive tract of the female and give birth to live young; others provide elaborate forms of parental care, including transporting and feeding their offspring.

This chapter explores the diversity of amphibian reproductive modes and life histories, including the behaviors associated with mating, how eggs are fertilized, sex determination, development and metamorphosis of larvae, and parental care. Modes of communication used during courtship and mating will be discussed in more detail in Chapter 13, and the structure of amphibian mating systems and the criteria used by individuals to choose mates will be discussed in Chapter 14.

8.1 Sex Determination

What determines whether a developing embryo will become male or female? Testes (male gonads) and ovaries (female gonads) differentiate from bipotential gonads (Hayes 1998). That is, each individual has the capacity to develop either testes or ovaries. In some cases, sex is determined by environmental factors. For example, incubation temperature determines the sex of many reptiles (see Chapter 9). Sex in most vertebrates, however, is determined genetically.

In amphibians, as in mammals, the sex of an individual is determined by a mechanism known as **genotypic sex determination**, or **GSD**, which means sex is determined by the particular complement of genes received from each parent at the moment of fertilization. We are accustomed to thinking of the male as the heterogametic sex—the sex with different sex chromosomes, an X and a Y—but in birds the female is the heterogametic sex. Both male and female heterogamety occur among amphibians. Female heterogamety is the ancestral condition for frogs and salamanders. Male



Figure 8.1 Aquatic versus terrestrial eggs. (A) The microhylid frog *Chiasmocleis mantiqueira* ovipositing in water in the Brazilian rain forest. (B) Female *Bryophryne cophites* with directdeveloping terrestrial eggs. This species' habitat is the grass and shrublands of the Andes. (Photographs: A, Celio Haddad; B, Alessandro Catenazzi.)

heterogamety has evolved at least seven times, with only one subsequent reversal from male to female heterogamety (Hillis and Green 1990). Regardless of whether sex determination is regulated by the environment or by genes, ultimately the process is directed by expression of specific proteins and hormones during critical developmental stages (see Chapter 9).

Reproductive functions of amphibians, like those of many other vertebrates, can be drastically altered if the animals are exposed to exogenous hormones at critical stages of development. The genetically programmed sex can even be reversed (Hayes 1998). Laboratory experiments have revealed that sexual development can be disrupted by extremely low concentrations of pesticides such as atrazine the most heavily used herbicide in the United States (Hayes et al. 2002, 2006). Male African clawed frog (*Xenopus laevis*) tadpoles become hermaphrodites when exposed to atrazine, and their larynges become demasculinized. (See Chapter 17 for further discussion of the possible role of endocrine disruptors in amphibian population declines.)

8.2 Reproductive Cycles

Successful reproduction depends on the coordination of many internal processes and external events (Houck and Woodley 1995). Reproduction by amphibians is hormonally mediated, but external events such as rainfall serve as proximate stimuli. Males and females must be ready for mating at the same time. Environmental conditions includ(B)



ing moisture, temperature, and food availability must be suitable to ensure the successful development of embryos, larvae, and newly metamorphosed young. A complex network of neural and hormonal mechanisms is responsible for this coordination (**Figure 8.2**).

External factors such as weather conditions act as cues for the induction and release of reproductive hormones and for changes in the responsiveness of target organs to the presence of these hormones. Because temperature and photoperiod change predictably throughout the year, they play important roles in the timing of reproductive cycles. Rising temperatures and increasing day length, for example, stimulate gonadal activity. These are especially critical cues for temperate-zone species. Once an amphibian is hormonally ready to breed, it can respond to external cues such as rainfall. Rainfall acts as a strong stimulus for the breeding behavior of amphibians in both temperate and tropical zones (Wells 2007).

Some amphibians exhibit definite reproductive seasons. Most species in the temperate zones are highly seasonal, but the timing of reproduction varies. Some species breed only in late winter and early spring, others only during the summer, and others only during autumn. Seasonal breeders are also found in areas of the tropics that exhibit some seasonality in temperature and rainfall. Most of these species breed during the wet season, when ponds and shallow depressions fill with water, but some lay their eggs only during the dry season.

Other amphibians breed year-round. Continuous reproductive cycles are exhibited by some anurans that live in relatively aseasonal tropical habitats. Gonadal activity is high nearly year-round—or at least for a lengthy period, typically during the wet season. At Santa Cecilia in eastern Ecuador, at least 10 species are reproductively active throughout the year (Crump 1974). Another 8 species breed opportunistically following heavy rains at any time of the year. For most species with continuous reproductive cycles, we know that a given population breeds continuously, but



Figure 8.2 External and internal factors that influence

reproduction in amphibians. Environmental stimuli include abiotic factors (light, heat, moisture), the physical and biological environments (space, habitat, food), and the social environment (behavior, population density, position of an individual in the social structure of the population). These stimuli trigger nerve impulses that are integrated largely in the hypothalamus of the brain. The hypothalamus produces gonadotropin-releasing hormone (GnRH), which causes the pituitary to release follicle-stimulating hormone (FSH) and luteinizing hormone (LH). These substances in turn stimulate the gonads to produce eggs and sperm and to release sex steroids (estrogens and testos-terone). The sex steroids affect the development of secondary sexual characters and reproductive behavior. (After Houck and Woodley 1995.)

we do not know how often individual females lay eggs within a year.

Although it appears that most individual female amphibians lay eggs at least once each year, a few species breed only every other year. Various explanations have been suggested for biennial cycles:

- The animals may be restricted by short activity seasons, especially in the temperate zones.
- Although males may be reproductively active each year, females of some species may be unable to store enough energy for egg production.

- If males and females migrate long distances to and from breeding sites, the added cost in time and energy may preclude annual reproduction.
- Females of many plethodontid salamanders that provide prolonged parental care to direct-developing eggs have biennial cycles (Houck 1977), suggesting that parental care is so energetically costly that females cannot breed every year.

We know much less about the reproductive activities of caecilians than we know about anurans and salamanders. Presumably all members of Ichthyophiidae are oviparous (Wilkinson and Nussbaum 1998). For all ichthyophiids for which information is available, the female guards eggs in terrestrial chambers until they hatch as larvae; the larvae then develop in water or semiaguatic conditions until they metamorphose. Anecdotal reports suggest that in India, breeding in Ichthyophis is related to the monsoon season, but until recently there was no quantitative study of the reproductive biology of any oviparous caecilian. Alexander Kupfer and colleagues (2004) studied a population of Ichthyophis cf. kohtaoensis* from northeastern Thailand to determine breeding seasonality and other aspects of reproduction in this species. Egg laying, parental care, and larval hatching were closely correlated with the monsoon rains (Figure 8.3). Egg clutches and guarding females were found only during the rainy season. In Sri Lanka, early clutches of Ichthyophis glutinosus were found at the onset of the monsoon (Breckenridge and Javasinghe 1979). In Brazil, however, the aquatic, viviparous species Typhlonectes compressicaudus appears to give birth at the end of the dry season (Moodie 1978).

8.3 Modes of Fertilization

Although external fertilization is the ancestral condition among amphibians, internal fertilization has evolved independently in most salamanders, a few species of frogs, and all caecilians. Sperm competition may occur during external fertilization if several males simultaneously release sperm onto the eggs of a female (see Chapter 14) (Halliday 1998). Sperm competition also is possible with internal fertilization, if more than one male mates with a female, and particularly if the female can store sperm for an extended period.

Internal fertilization by salamanders

Most salamanders have internal fertilization. Our current understanding of salamander phylogeny suggests that internal fertilization evolved only once in the common ancestor of all of the derived salamander families (the Salamandroidea), although the phylogenetic position of the

^{*} The designation "cf." means "compare." In the context here, it indicates a possible identity, and that the species' identification is uncertain.



Figure 8.3 Timing of oviposition by a caecilian in northeastern Thailand. In 1999, females of *Ichthyophis* cf. *kohtaoensis* laid their first egg clutches about 4 weeks after the onset of the monsoon season. In 2000, the earliest oviposition was about

Sirenidae is not fully resolved (see Chapter 3). The mode of sperm transfer is similar in all of the derived salamander families. The major innovation in the evolution of salamander reproductive modes was the **spermatophore**. The spermatophore, which is produced by male cloacal glands, consists of a gelatinous base that supports a cap containing the spermatozoa (**Figure 8.4**). Salamanders with external fertilization have cloacal glands, but in these species glands apparently produce pheromones to attract females. This ancestral function is retained in derived salamander families with internal fertilization, but in these groups cloacal glands have taken on the secondary function of spermatophore production (Sever 2003).

The evolution of the spermatophore had a profound effect on the reproductive biology and social behavior of salamanders. Females of some species can retain viable sperm in their reproductive tracts for months or even longer. This sets the stage for the separation of mating from oviposition, something that is virtually nonexistent among anurans, except for *Ascaphus*. Many North American plethodontid salamanders engage in courtship in both the fall and spring but lay eggs only in late spring and early summer



7 weeks after the beginning of the monsoon. In 2001, the monsoons were late and sparse; many fewer females laid eggs, and they began to oviposit about 3 weeks after the start of the monsoon. (After Kupfer et al. 2004.)

(Houck 1977). This separation of courtship and oviposition allows females to make use of hidden oviposition sites that are not necessarily good courtship sites. Internal fertilization also sets the stage for the evolution of female parental care, because the male is not present when eggs are laid (Nussbaum 1985, 2003). The relatively high cost of spermatophore production may limit the rate at which spermatophores can be produced (Marks and Houck 1989). This cost may have resulted in selection for increased efficiency of spermatophore transfer, which in turn has led to the evolution of elaborate forms of courtship seen in many salamanders (Halliday 1990) (see Chapters 13 and 14).

Males of most salamanders court a female and deposit one or more spermatophores on the substrate—the ground, the bottom of a pond, or a rock. The female then moves over the spermatophore and picks up the sperm with the lips of her cloaca (see Chapter 14). Among *Euproctus*, the male salamander grabs a female either by biting her or by encircling her with his tail. He then places spermatophores on the female's body, pushing them into her cloaca with his feet, or directly on her cloaca (Thiesmeier and Hornberg 1990). The cloaca of male *Euproctus* is elongated into a coni-



(B)



Figure 8.4 Spermatophores deposited by Ambystoma

maculatum. (A) Male salamanders deposit spermatophores on the substrate (often the bottom of a pond), from which they are taken directly into the oviducts by the courted female.
(B) One of the spermatophore-bearing branches in (A) was removed from a pond in order to obtain a clearer photograph.
(C) Close-up of *A. maculatum* spermatophore, showing the gelatinous base supporting a cap filled with spermatozoa.
(Photographs: A,B © Mike Marchand; C by David McIntyre.)

cal shape that may facilitate placement of spermatophores in the female's cloaca.

Once sperm enter the female's cloaca, they are stored in **spermathecae**, clusters of tubules that connect to the cloaca. The walls of the spermathecae of some species provide nutritional secretions that sustain the sperm for some time, but most species probably do not retain sperm capable of fertilizing eggs for more than a few months. In many ambystomatid salamanders, sperm remains viable for no more than a few days, and eggs are laid shortly after mating. In contrast, many plethodontids lay eggs long after mating, so sperm must remain viable for several months. Because females can mate with several different males, there is the potential for direct sperm competition, and fertilization by multiple males has been detected in several species (Halliday 1998; Sever 2003).

External fertilization by salamanders

The Cryptobranchids, a basal lineage that includes the giant salamanders (see Figure 3.6), are among the few salamanders with external fertilization. Males of these species are highly territorial and defend nest sites underneath submerged rocks. Small males have been observed entering the nests of larger males when females were laying eggs, presumably to release sperm onto the eggs (Kawamichi and Ueda 1998).

Female hynobiid salamanders lay eggs in sacs (see Figure 8.10). Males clasp the egg sacs and release sperm onto them; they often aggressively defend the egg sacs from other males (Tanaka 1989). A possible transition from external to internal fertilization is seen in the hynobiid genus *Ranodon*, which has a spermatophore-like mode of sperm deposition but retains external fertilization: the male deposits a large, gelatinous sperm mass under a rock in a stream, and the female deposits her eggs on top of this mass.

The mode of fertilization in the Sirenidae has long been a mystery. These salamanders were assumed to have external fertilization because males lack the specialized glands found in other salamanders that produce spermatophores, and females lack spermathecae (Houck and Arnold 2003; Sever 2003). Only recently, however, has actual sirenid mating behavior been observed. Males construct a nest from aquatic plants and aggressively defend the nest as a territory. When a female enters the nest, the male engages in complex courtship behavior involving tail movements and tactile stimulation of the female. When the female is ready to lay eggs, she places her cloaca near the top of the nest and releases eggs individually into the nest. The male then releases sperm onto the eggs. As in the cryptobranchids, the male remains at the nest after the eggs are fertilized. He guards the eggs and aerates them with vigorous fanning of his tail (Reinhard et al. 2013).

External fertilization by anurans

Most anurans have external fertilization. Males reduce opportunities for sperm competition by clasping females in a position known as **amplexus**, which allows the male to place his cloaca close to that of the female as gametes are released, thereby reducing the chances of other males fertilizing the eggs. Often the male receives the eggs in a sort of basket formed by his hindlegs, thereby ensuring that the eggs are fertilized immediately after being released (**Figure 8.5**). In some species, the whole process of oviposition takes only a few minutes. In other species, especially those that attach eggs individually to aquatic plants, the process can take up to several hours (Wells 2007).

The way in which the male clasps the female differs among families. The ancestral condition for anurans is inguinal amplexus, with the male clasping the female around her waist (Figure 8.6A). Fertilizing the eggs requires the male to arch his back to align his cloaca with that of the female. All of the morphologically primitive groups of frogs have ingui-



Figure 8.5 Oviposition and external fertilization by anurans. A pair of American bullfrogs (*Rana catesbeiana*) depositing a surface film of eggs. The male's hindlegs form a basket near the female's cloaca to receive and fertilize the eggs. This entire sequence took less than 3 minutes. (Photographs by Kentwood D. Wells.)

(A)

(C)

nal amplexus, including *Ascaphus, Leiopelma, Rhinophrynus,* and the families Bombinatoridae, Discoglossidae, Pelobatidae, Pelodytidae, Pipidae, Myobatrachidae, and Sooglossidae (Wells 2007). Some of the more derived frog groups also have inguinal amplexus, although it is not always clear whether this represents retention of the ancestral condition or secondary evolution of it. For example, at least two species of *Osornophryne* and two species of *Incilius* have inguinal amplexus. These species exhibit extreme sexual dimorphism, with the female being much larger than the male, perhaps making it difficult for the male to clasp the female around





Figure 8.6 Amplexus positions of anurans. (A) Inguinal amplexus by the Mexican burrowing frog (*Rhinophrynus dorsalis*). The male clasps the female around her waist. (B) Axillary amplexus by the North American wood frog (*Rana sylvatica*). The male clasps the female behind her front legs. (C) Cephalic amplexus by a dendrobatid frog (*Colostethus panamensis*) from Panama. The male clasps the female along the sides of her jaws. (Photographs: A, Kristiina Hurme; B, Nicole Friedenfelds; C, Kentwood D. Wells.)

her body (Novak and Robinson 1975; Ruiz-Carranza and Hernández-Camacho 1976; Graybeal and de Queiroz 1992). Several genera of frogs found in the cold regions of southern South America, including *Eupsophus* and *Batrachyla*, also retain inguinal amplexus (Formas 1976; Formas and Vera 1980). The tiny toads in the family Brachycephalidae have unusual mating behavior: the male initially clasps the female in the inguinal region, but shifts to clasping her around her head as the eggs are fertilized (Pombal et al. 1994).

Most derived anuran families have axillary amplexus, in which the male clasps the female behind her front legs (Figure 8.6B). Typically the male holds the sides of the female, often using enlarged nuptial pads to keep a firm grasp. In some species, such as the North American wood frog (Rana sylvatica), the male wraps his front legs around the female's body and interlocks his thumbs, enabling him to repel other males that attempt to mate with the female (Howard and Kluge 1985). Amplexus has been highly modified or lost altogether in some anurans, especially those that lay terrestrial eggs. The ancestral condition for dendrobatid frogs appears to be cephalic amplexus, in which the male clasps the female loosely while lying on her back, with the longest digits of his front feet pressed against the sides of her head (Figure 8.6C). Some of the more derived dendrobatids have lost amplexus. In some species, the male and female press their cloacae together while facing away from one another, while in others, males release sperm onto the eggs after they have been laid in a terrestrial nest (Zimmermann 1990). The male of some mantellid frogs from Madagascar lies on top of the female's head and apparently releases sperm that runs down her back onto the eggs (Blommers-Schlösser 1975). Female Nyctibatrachus petraeus (Nyctibatrachidae), a species from India, lay eggs on leaves overhanging small streams or on rocks. Once the eggs have been deposited, the males sit on the eggs (sometimes in groups) and fertilize them without amplexus (Kunte 2004).

Internal fertilization by anurans

Internal fertilization has evolved independently several times among frogs. The only frogs with internal fertilization that lay eggs in large bodies of water are the tailed frogs (*Ascaphus*) from western North America (**Figure** **8.7A**). These are perhaps the most primitive living frogs, yet their mode of fertilization is highly derived, perhaps an adaptation to breeding in rapidly flowing water. The cloaca of the male has been modified to form a permanently extended copulatory organ. *Ascaphus* are the only anurans with internal fertilization that have true inguinal amplexus. During mating, the copulatory organ is bent forward and inserted into the female's cloaca while the male clasps her around the waist. Mating can last up to 90 hours and can occur weeks or months before oviposition (Sever et al. 2003; Stephenson and Verrell 2003).

Internal fertilization has been described for two species of Eleutherodactylus from Puerto Rico. The first of these, E. jasperi is viviparous, retaining fertilized eggs in the oviducts and giving birth to small froglets (M. H. Wake 1978). Mating behavior has not been observed, however, and unfortunately this species is now thought to be extinct. E. coqui also has internal fertilization, but it retains the normal mode of terrestrial oviposition and direct development seen in other Eleutherodactylus. The male rests on top of the female in a sheltered nest but does not actually clasp her in amplexus. The female loops her hindlegs over those of the male in a reverse hindleg clasp (Figure 8.7B). Mating may last more than 2 hours before oviposition begins. The female normally lays her eggs with the male still resting on her back, but fertile eggs are laid even if the male is removed (Townsend and Stewart 1986). A similar reverse hindleg clasp also has been observed in a closely related species, E. johnstonei, that has external fertilization (Bourne 1997). These observations suggest that this unusual form of amplexus evolved before internal fertilization did.

Other examples of internal fertilization by anurans occur in African bufonids. An unusual clade of African toads that includes the genus *Nectophrynoides* and its close relatives exhibits a continuum of reproductive modes from strictly oviparous to fully viviparous and with both external and internal fertilization (M. H. Wake 1980). In some species the male's cloacal opening faces downward to facilitate internal fertilization when the cloacae of the male and female are pressed together. The male of another African bufonid

Figure 8.7 Internal fertilization by

anurans. (A) Male of the tailed frog *Ascaphus montanus* showing the copulatory organ. (B) Reverse hindleg clasp in a pair of Puerto Rican coquís (*Eleuthero-dactylus coqui*), a position that allows the male and female to press their cloacae together for sperm transfer. (Photographs: A, Wayne Van Devender; B, Daniel S. Townsend.)



(B)



with internal fertilization, *Mertensophryne micranotis*, also has a modified cloaca, with unusual spines that may facilitate copulation with the female (Grandison and Ashe 1983).

Internal fertilization by caecilians

All caecilians have internal fertilization, but the mode of fertilization is quite different from that of salamanders. In male caecilians, the cloaca is modified into a copulatory organ, the phallodeum. This structure normally is folded back inside the cloaca but is everted during mating by contractions of muscles in the body wall and cloaca (M. H. Wake 1992). Fluid for transporting the sperm is provided by paired Müllerian glands, which are not found in any other vertebrates (M. H. Wake 1981). Mating behavior has seldom been observed in caecilians, even in captivity, so details of courtship and copulation are largely unknown. We also know nothing about how long viable sperm can be retained in the female's reproductive tract, although female caecilians lack a specialized sperm storage organ like that found in salamanders.

8.4 ■ Hybridogenesis and Kleptogenesis

Although most amphibians produce haploid eggs and sperm that unite to form diploid offspring, others have unusual forms of reproduction, which often are associated with elevated ploidy levels (meaning individuals have extra sets of chromosomes, producing triploid, tetraploid, or even pentaploid adults). Some amphibians have a reproductive system known as **hybridogenesis**, in which the genome of the female parent passes unchanged from one generation to the next. Hybrid females mate with males of one of the parental species and produce individuals with an intermediate phenotype. However, the paternal genome is discarded at the time of gametogenesis, and the gametes produced by the hybrid female contain only the maternal genome.

Another unusual form of reproduction by amphibians is **kleptogenesis** (from the Greek *kleptos*, "thief"). Kleptogenesis, found in some salamanders of the genus *Ambystoma*, also involves females that steal genomes from males of other species, but in this case there is not a common genome that is inherited clonally (Bogart and Bi 2013). There are three possible ways in which sperm is involved in these chromosomally atypical forms of reproduction: (1) sperm simply initiates development of the embryo, but the sperm's genetic material is not incorporated into the embryo's genome; (2) sperm is sometimes incorporated into the embryo's genome, resulting in offspring with a higher ploidy level; or (3) the sperm genome replaces one of the original genomes in the hybrid offspring.

The European waterfrog complex

Hybridogenetic reproduction by European waterfrogs of the *Pelophylax esculentus* complex has been studied extensively. *P. esculentus* (formerly *Rana esculenta*), the common edible frog of Europe (**Figure 8.8**), was first described by Linnaeus in the 18th century, but it was not until the 1960s that Leszek Berger (1977) discovered that populations of this frog in Poland were derived from hybrid matings between the pool frog (*P. lessonae*) and the marsh frog (*P.*

> *ridibundus*). Such matings produce both male and female hybrid frogs. Populations of hybrids can occur with both parental species, but this situation is rare because the ecology of the parental species differs. *P. lessonae*, the smaller of the two species, lives in small bodies of water during the spring and summer and hibernates on land during the fall and winter. In contrast, *P. ridibundus* lives in rivers and lakes and hibernates in water. Hybrids are found in intermediate

Figure 8.8 Hybridogenetic water-

frogs. A chorus of edible frogs (*Pelophylax esculentus*), a hybridogenetic species produced by mating between *P. lessonae* and *P. ridibundus*. In some parts of Europe, hybrid genotypes coexist and mate with one of the parental species, whereas populations in parts of northern Europe consist of nearly all hybrid genotypes. (Photograph by Uli Reyer.)



habitats, most commonly in association with only one parental species, with which they interbreed (Graf and Polls Pelaz 1989).

Populations of *Pelophylax* vary in their genetic makeup across Europe. The most common situation in central and western Europe is for the *esculentus* genotype (LR) to occur with *lessonae* (*LL*). In this system the *lessonae* genome (*L*) is discarded before meiosis when LR esculentus females form eggs. The *ridibundus* genome (R) that remains is then duplicated. During normal meiosis, haploid eggs are formed; when they are combined with lessonae sperm (L), the esculentus genotype (LR) is reconstituted. In some populations in eastern Europe, P. esculentus is associated with P. ridibundus (RR). In that case, the lessonae genome (L) is maintained in esculentus eggs more often than the ridibundus genome (R). Recent research has examined the ecological factors that account for the widespread success of the esculentus genotype in much of Europe. This form should be at some disadvantage because it is dependent on one of the parent species for successful reproduction and cannot reproduce itself independently. Yet in many populations, the esculentus genotype appears to be the most successful form. The esculentus tadpoles tolerate a wider range of physical conditions in ponds (Tunner and Nopp 1979) and are superior competitors to

Figure 8.9 A close phylogenetic relationship of unisexual *Ambystoma* and *A. barbouri* can be inferred from the mitochondrial genome. Five species of *Ambystoma* are involved as sperm donors in a kleptogenesis system. (A) Left to right: *A. jeffersonianum*, *A. tigrinum*, *A. laterale*, and *A. texanum*. (B) *A. barbouri*. (C) Phylogeny showing unisexual individuals as a sister group to *A. barbouri*, based on mitochondrial DNA. Mitochondrial DNA from *A. barbouri* is present in all uni-

the tadpoles of the parental genotype (*lessonae*) with which they most often are associated (Semlitsch and Reyer 1992; Semlitsch 1993). The *esculentus* tadpoles also have higher survival in permanent ponds with fish than do *lessonae* tadpoles, which are highly vulnerable to fish predation (Anholt et al. 2005). Both forms continue to persist through a combination of mating preferences by females for *lessonae* males and patterns of migration between neighboring populations (Hellriegel and Reyer 2000; Som et al. 2000).

Kleptogenesis among Ambystoma

Some salamanders in the genus *Ambystoma* in eastern North America display a unique and complex reproductive system (Bogart 2003). Virtually all-female populations of salamanders have a wide distribution around the Great Lakes and the northeastern United States and Canada. These females must mate with males of a sympatric bisexual species in order to reproduce. Males of five different species can be sperm donors for these females: *A. jeffersonianum, tigrinum, laterale, texanum,* and *barbouri* (Figure 8.9A,B). As in the waterfrog complex, the unisexual populations of females are sexual parasites on the sperm donor species. The actual mechanism is slightly different, however, in that *Ambystoma* has no clonally inherited genome.

The production of all-female hybrids does not appear to be an ongoing event, but rather the result of an ancient hybridization event between a male *A. laterale* (a species that breeds in temporary ponds) and a female *A. barbouri* (a stream-breeding species). The history of this event is preserved in the maternally inherited mitochondrial DNA of the unisexual species, all of which have *barbouri* mitochon-



sexuals, supporting origin of unisexual populations from an ancient hybridization event between a male *A. laterale* and a female *A. barbouri*, two species that are not currently sympatric. Numbers along branches indicate probabilities of support for the relationships from Bayesian (left) and bootstrap (right) analyses. Branch length are estimated using the Bayesian results. (After Bi and Bogart 2010; photographs by James Bogart.) drial DNA as well as *laterale* DNA in their nuclear genomes (**Figure 8.9C**). The unisexual populations have females with varying complements of chromosomes, but triploid individuals predominate. The wide distribution of triploid unisexuals may result from their hybrid origin, which is thought to give them a wider ecological niche than those occupied by the parental diploid species. Their offspring further benefit from being fertilized by males of a local species, which may be best adapted to the local habitat (Bogart 2003; Bogart et al. 2007; Bi and Bogart 2010; Bogart and Bi 2013).

8.5 Reproductive Modes

Most amphibians are oviparous (egg-laying) and lay jelly-covered eggs in water. These eggs exhibit only limited resistance to desiccation. The only extraembryonic membrane in an amphibian egg is the yolk sac, which encloses the yolk, a nutrient substance consisting of lipoproteins, phosphorylated proteins, and glycogen. Yolk is synthesized in the mother's liver, drawing on stored lipids (a process called **vitellogenesis**), and is transported by the circulatory system to the maturing eggs. In most amphibians, the yolk supports embryonic development until the eggs hatch into larvae that can acquire their own food. The condition whereby embryos receive all their nutrition from yolk reserves within the egg is called **lecithotrophy** (from the Greek *lecithoi*, "yolk," and *trophos*, "nourish").

Amphibians reproduce in an amazing variety of ways. Some tropical frogs lay terrestrial eggs that give rise to larvae that remain in the nest throughout development and subsist entirely on yolk reserves without feeding; others have larvae that remain on the body of a parent while using up yolk reserves (Thibaudeau and Altig 1999). Some species skip the larval stage altogether by laying eggs from which miniature adults hatch. In species with direct development, large yolk reserves nourish the embryos throughout their development inside the egg, and some yolk may remain when the eggs hatch into terrestrial juveniles.

Some amphibians are viviparous; they give birth to live young. Fetal nutrition in viviparous species can come entirely from lecithotrophy or can be provided from the mother (matrotrophy, from the Latin *mater*, "mother"), as for example from oviductal secretions. Some viviparous species combine lecithotrophy and matrotrophy.

Reproductive mode refers to the type of embryonic and larval development, the site of egg deposition, egg and clutch size characteristics, and type of parental care, if any (Duellman and Trueb 1986). The ancestral reproductive mode in amphibians is assumed to include aquatic deposition of eggs, larval development, and absence of parental care. All three orders of amphibians include species that have aquatic, partially aquatic, and terrestrial forms of reproduction. Ecological and evolutionary aspects of direct development, viviparity, and parental care will be discussed further in Sections 8.6 and 8.7.

Caecilians

Because of the secretive nature of caecilians, not much is known about their reproductive biology (see Gomes et al. 2012 for a review). In fact, life histories are known for fewer than half of the described species (M. H. Wake 2006). Caecilian modes of reproduction include egg-layers with freeliving larvae, direct developers, and live-bearing species. So little is known about reproduction in caecilians that the proportion of oviparous species is debated; estimates range from 50% to 80% (M. H. Wake 1977; Wilkinson and Nussbaum 1998; Exbrayat 2006).

OVIPARITY Oviparous caecilians lay eggs on land. Only females are known to attend the eggs. Some species lay eggs that hatch into aquatic larvae that wriggle to water where they develop for a year or so before metamorphosing and returning to land; others deposit eggs that undergo direct development. Females coil around their eggs and presumably protect them from predators and from drying out. Marvalee Wake (1986) speculated that females of all oviparous caecilians attend their eggs.

A novel behavior associated with parental care, **dermophagy** (from the Greek root *derm*, "skin"), has been reported for *Boulengerula taitana*, a direct-developing oviparous caecilian from Kenya, Africa (Kupfer et al. 2006, 2008). Females guard their eggs in terrestrial nests. The young hatch with specialized dentition, which they use to tear off and eat the outermost layer—the stratum corneum of their mother's skin. The stratum corneum is normally composed of squamous keratinized cells, but in brooding females it thickens and fills with lipid inclusions, providing a rich supply of nutrients for the young. This nursing behavior is costly for the mothers, as shown by a lower body mass to total length relationship and lower fat body volume of females attending young compared with nonattending females.

VIVIPARITY In viviparous caecilians, the eggs are retained in the female's reproductive tract until development is complete; after the yolk has been depleted the young feed on maternal secretions. For example, larvae of *Dermophis mexicanus* are retained in the oviduct of the female for 11–12 months (M. H. Wake 1993). The larvae use their yolk stores for the first 3 months of development. When the yolk is exhausted, the larvae feed on a lipid-rich material that is secreted by the proliferated and vascularized oviductal epithelium. Larvae use their fetal dentition (which are epidermal structures on the lips, not true teeth) to graze on the epithelium.

Salamanders

Most salamanders are oviparous. Stanley Salthe (1969) divided the reproductive modes of salamanders into three categories: pond breeding (mode I), stream breeding (mode II), and nonaquatic eggs (mode III), although his category III can be divided into several subcategories (**Table 8.1**).

TABLE 0.1 Modes of egg deposition and development in salamanders				
Egg deposition site	Larval development	Selected examples		
Aquatic eggs				
Still water (I) ^a	Larvae feed in ponds	Sirenidae; some hynobiids, some ambystomatids, some salamandrids, and some plethodontids		
Flowing water (II) ^a	Larvae feed in streams	Cryptobranchus (Cryptobranchidae), Necturus (Proteidae), Dicamptodon (Dicamptodontidae), Rhyachotriton (Rhyacotritonidae); some hynobiids, some ambystomatids, some salamandrids, and some plethodontids		
Nonaquatic eggs (III) ^a				
Terrestrial nest	Larvae feed in ponds	Ambystoma opacum, A. cingulatum (Ambystomatidae)		
Terrestrial nest	Larvae move to water	Hemidactylium, some Desmognathus (Plethodontidae)		
Terrestrial nest	Nonfeeding larvae in nest	Desmognathus aeneus (Plethodontidae)		
Terrestrial nest	Direct development	Desmognathus wrighti, Plethodon, Ensatina, some bolitoglossines (Plethodontidae)		
Arboreal nest	Direct development	Aneides lugubris, some bolitoglossines (Plethodontidae)		
Retained in oviducts	Birth to larvae, or terrestrial young	Salamandra, Mertensiella (Salamandridae)		

TABLE 8.1 Modes of egg deposition and development in salamanders

*Roman numerals identify Salthe's (1969) modes of salamander reproduction.

Egg size varies among these three groups. Stream-breeding salamanders lay larger eggs than do pond-breeding species, perhaps reflecting the higher oxygen concentrations in streams than in ponds (Bradford 1990). In addition, the food available to stream-dwelling larvae often comes in relatively large packages, such as aquatic insects, that can be eaten only by large larvae, whereas the food of ponddwelling larvae is zooplankton and other small prey (Nussbaum 2003). Salamanders that lay eggs on land produce even larger eggs than do stream dwellers, with the advantage that a large egg has a small surface-to-volume ratio and thus loses water slowly.

Parental attendance of eggs occurs in at least 72 species of salamanders (Crump 1995, 1996). In some cases, the eggs are aquatic (*Andrias, Cryptobranchus, Dicamptodon*, *Hynobius, Eurycea, Gyrinophilus, Leurognathus, Pseudotriton, Necturus, Proteus, and Siren*). The remaining instances of egg attendance involve terrestrial eggs.

EGGS IN WATER Many salamanders lay their eggs directly in water. Some, such as many hynobiids, ambystomatids, and salamandrids, deposit eggs in still water, including ponds, swamps, seepage areas, and pools in streams (mode I). Some of these species deposit eggs scattered on the substrate; others lay their eggs in clumps, often attached to emergent vegetation or submerged logs or branches (Figure 8.10A). Other salamanders—cryptobranchids, proteids, dicamptodontids, and some salamandrids, plethodontids, and hynobiids—lay their eggs in flowing water, from mountain streams to large rivers (mode II) (Figure 8.10B).

(A)



(B)



Figure 8.10 Salamander eggs laid in water (reproductive modes I and II). (A) An egg mass of the spotted salamander (*Ambystoma maculatum*) represents reproductive mode I, pond breeding. (B) Illustrating mode II, stream breeding, the egg sacs of *Hynobius kimurae* are typically deposited underneath rocks in running water. These eggs have been removed from the water for photographic purposes. (Photographs: A, Kurt Schwenk; B, Alan H. Savitzky.) Most of these species hide their eggs under rocks, logs, or tree roots, which presumably helps protect them from predators as well as preventing them from being washed away in the currents.

EGGS OUT OF WATER Salamanders from several families have independently evolved reproductive modes that entail deposition of eggs out of water (reproductive mode III) but retention of an aquatic larval stage. This happens in a variety of ways. For example, female marbled salamanders (Ambystoma opacum) lay their eggs in the autumn in low-lying depressions that will flood during winter rains; females stay with their eggs until the depressions flood, at which time the eggs hatch at an advanced stage and the larvae complete development in the water (Figure 8.11A). Female four-toed salamanders (Hemidactylium scutatum) lay their eggs in sphagnum moss over or next to standing water. After hatching, the larvae drop into the water and complete development. Female Echinotriton andersoni lay their eggs under leaf litter near water. After hatching, the larvae wriggle in the mud until they enter the pond or puddle where they complete larval development.

Some salamanders have become completely independent of standing or running water for reproduction. Many plethodontids deposit their eggs on land, where the eggs undergo direct development (**Figure 8.11B**). Species with direct development deposit large, unpigmented eggs in hidden locations such as inside hollow logs, in cavities in the ground, and under mats of vegetation. Correlated with the large egg size, development in these species is prolonged. In most species, the female remains with the eggs. Plethodontids evolved direct development in North America before invading Central and South America. Their success in moist tropical habitats, especially montane regions that lack ponds, may be due to their reproductive mode (D. B. Wake 1987). Furthermore, direct development may have allowed plethodontids to invade a variety of habitats, from relatively dry areas to wet cloud forests (Wake and Hanken 1996).

VIVIPARITY Although most salamanders have internal fertilization, viviparity is confined to the Salamandridae (Wells 2007). Over much of the range of the European fire salamander (Salamandra salamandra), females retain relatively large numbers of eggs in an enlarged portion of the oviduct. During their development in the oviduct, the embryos derive nutrition from their yolk reserves. Once the yolk is used up, the larvae are born and complete their larval development in water. In some populations, however, females retain only a few embryos. After these embryos use up their yolk reserves, they hatch but remain in the oviduct and feed on the remains of unfertilized eggs. The mother gives birth to nearly or fully metamorphosed juveniles. In S. atra, only one egg is fertilized in each oviduct. The remaining eggs disintegrate and are eaten by the two developing larvae. Later during development, the two larvae use specialized teeth to scrape nutritious material from the epithelium of the mother's uterus.

WITHIN-GENUS VARIABILITY IN REPRODUCTIVE MODE

Some salamander genera, such as the dusky salamanders (*Desmognathus*), exhibit considerable variation in reproductive mode. For decades, it was assumed that direct development of terrestrial eggs was the derived life history in *Desmognathus*, but molecular phylogenetic studies have shown that the genus evolved from a clade of directdeveloping species. Thus, species with aquatic larvae have secondarily reverted to this life history (Titus and Larson 1996; Chippindale et al. 2004; Mueller et al. 2004; Kozak et al. 2005).







Figure 8.11 Salamander eggs laid out of water (reproductive mode III). (A) A female marbled salamander (*Ambystoma opacum*) lays terrestrial eggs that eventually will be flooded, allowing the larvae to develop and feed in standing water. (B) Egg mass of the arboreal salamander *Bolitoglossa*

rufescens with the mother in attendance. This species has direct development, bypassing the aquatic larval stage. (Photographs: A, Wayne Van Devender; B, © Robin Moore/National Geo-graphic Society/Corbis.)





(C)



Anurans

The reproductive modes of frogs are more diverse than those of caecilians and salamanders (**Table 8.2**, page 300). Anurans deposit their eggs in many forms. Ronn Altig and Roy McDiarmid (2007) described five categories of ovipositional modes: various arrangements of independent eggs, three-dimensional arrangements, floating arrangements, froth nests, and linear arrangements. Oviposition in ponds and swamps is assumed to be the ancestral mode of reproduction, and it is currently widespread in large families such as ranids, bufonids, and hylids. Even among pondbreeding anurans, there is considerable variation in the way eggs are deposited.

EGGS AND LARVAE IN WATER The ancestral mode of reproduction for anurans is assumed to be some form of aquatic oviposition, probably in standing water (e.g., Duellman and Trueb 1986). Aquatic reproduction is widespread across families and occurs in diverse habitats, from small temporary pools to permanent lakes. The wide range of physical and biological characteristics of these habitats has undoubtedly shaped many aspects of anuran reproduction. For example, differences in the structure of the egg mass are related to oxygen availability because the jelly

(B)



Figure 8.12 Frog egg masses in water. Egg mass structure is often related to oxygen content of the water. (A) Communal egg mass of the wood frog (*Rana sylvatica*). Such compact clumps are common in cold, well-oxygenated water. (B) The thin film of the egg mass of the green frog (*Rana clamitans*) is more common in warm, poorly oxygenated water. (C) A foam nest being constructed by túngara frogs (*Engystomops pustulosus*) on a pond in Panama. Air bubbles in the foam provide the eggs with oxygen and keep the mass afloat. (Photographs by Kentwood D. Wells.)

layers of the egg form a barrier to the diffusion of respiratory gases (Seymour and Bradford 1995). Species that breed in cold, well-oxygenated water often lay eggs in compact clumps surrounded by a thick jelly coat and even form large communal egg masses (**Figure 8.12A**). Species that lay eggs in warm or poorly oxygenated water often lay small eggs that are attached individually to plants, distributed in long strings, or deposited in a thin film on the water surface, maximizing exposure of individual eggs to the air (**Figure 8.12B**).

Some frogs, especially in the families Leptodactylidae and Myobatrachidae, lay eggs in foam nests floating on the water surface (Figure 8.12C). The eggs are surrounded by air bubbles that not only provide some oxygen for the eggs but also keep them from sinking into poorly oxygenated deeper water (Seymour and Roberts 1991). In leptodactylids, the foam is formed during amplexus as the male kicks his hindfeet and whips up the eggs and mucus from the female with his sperm. In myobatrachids, the female beats the water with her front feet as the eggs are laid. As bubbles rise from underneath the female, they combine with mucus secretions to form a mass of foam in which the eggs are suspended. As in salamanders, frogs that lay eggs in flowing water, such as tailed frogs (Ascaphus), have relatively large eggs compared with those of pond-breeding species (Brown 1989). The stream-breeding frogs Crossodactylus gaudichaudii and Hylodes asper lay their eggs in excavated subaquatic chambers that probably help prevent the

TABLE 8.2 Modes of egg d	eposition and development of anura	ns ^a
Egg deposition site	Tadpole development	Examples
Aquatic eggs		
Still water	Feeding in ponds	Rana (Ranidae), Bufo (Bufonidae)
Flowing water	Feeding in streams	Ascaphus (Ascaphidae), Atelopus (Bufonidae)
Subaquatic chamber	Feeding in streams	Crossodactylus, Hylodes (Hylodidae)
Basin near water	Feeding in ponds or streams	Hypsiboas boans (Hylidae)
Subterranean nest	Feeding in ponds or streams	Aplastodiscus leucopygius (Hylidae)
Tree hole, bromeliad	Feeding in water	Anotheca (Hylidae), Mertensophryne (Bufonidae)
Water-filled depression	Nonfeeding in water	Eupsophus roseus (Alsodidae), Leiopelma (Leiopelmatidae)
Tree hole, leaf axil	Nonfeeding in water	Anodonthyla (Microhylidae), Dendrophryniscus (Bufonidae)
Flowing water	Develop in mother's stomach	Rheobatrachus (Myobatrachidae)
Bubble nest floating on ponds	Feeding in ponds	Chiasmocleis leucosticta (Microhylidae)
Foam nest floating on ponds	Feeding in ponds	Physalaemus (Leptodactylidae)
Foam nest floating on still water	Feeding in slow-moving water	Limnodynastes interioris (Limnodynastidae)
Foam nest in basin	Feeding in ponds	Leptodactylus podicipinus (Leptodactylidae)
Foam nest in water of terrestrial bromeliads	Feeding in ponds	Physalaemus spiniger (Leptodactylidae)
Dorsum of female	Feeding in ponds	Pipa carvalhoi (Pipidae)
Dorsum of female	Direct development	Pipa pipa (Pipidae)
Nonaquatic eggs		
Terrestrial nest	Feeding in ponds or streams	Pseudophryne (Myobatrachidae)
Ground or rock above water	Feeding in water	Phrynomedusa appendiculata (Hylidae), Hemisus (Hemisotidae)
On rocks, in rock crevices, or on tree roots above water	Feeding in water film or in water- land interface	Cycloramphus, Thoropa (Cycloramphidae)
Terrestrial nest	Feeding, carried to water by adult	Allobates (Aromobatidae), Dendrobates, Oophaga (Dendrobatidae)
Terrestrial nest	Nonfeeding in nest	Zachaenus parvulus (Cycloramphidae), Leiopelma (Leiopelmatidae)
Terrestrial nest	Nonfeeding, on dorsum or in pouches of adult	Rhinoderma darwinii (Rhinodermatidae), Assa darlingtoni (Myobatrachidae)
Terrestrial nest	Direct development	Pristimantis (Craugastoridae), Eleutherodactylus (Eleutherodactylidae)
Leaves over still water	Feeding in water	Phyllomedusa (Hylidae)
Leaves over flowing water	Feeding in water	Hyalinobatrachium (Centrolenidae)
Water-filled cavities in trees	Feeding in water	Nyctimantis rugiceps (Hylidae), Acanthixolus (Hyperoliidae)
Arboreal nest	Direct development	Ischnocnema nasuta (Brachycephalidae), Platymantis (Ceratobatrachidae)
Foam nest on ground	Feeding in ponds	Members of the <i>Physalaemus signifer</i> group (Leptodactylidae)
Foam nest in basins	Feeding in ponds or streams	Leptodactylus (Leptodactylidae)

TABLE 0.2 (Continued)				
Egg deposition site	Tadpole development	Examples		
Foam nest in subterranean nest	Feeding in ponds	Leptodactylus fuscus (Leptodactylidae), Heleioporus (Limnodynastidae)		
Foam nest in subterranean nest	Feeding in streams	Leptodactylus cunicularius (Leptodactylidae)		
Foam nest in burrow	Nonfeeding in burrow	Adenomera (Leptodactylidae)		
Arboreal foam nest	Feeding in ponds	Chiromantis (Rhacophoridae)		
On male's legs	Feeding in ponds	Alytes (Alytidae)		
Female dorsal pouch	Feeding in ponds	Gastrotheca (Hemiphractidae)		
Female dorsum or pouch	Nonfeeding tadpoles in bromeliads or bamboo	Flectonotus, Fritziana (Hemiphractidae)		
Female dorsum or pouch	Direct development	Hemiphractus, Stefania (Hemiphractidae)		
Eggs hatch into tadpoles while in oviducts	Feeding in small marginal pools	Limnonectes larvaepartus (Dicroglossidae)		
Eggs retained in oviducts	Nutrition provided by yolk	Eleutherodactylus jasper (Eleutherodactylidae)		
Eggs retained in oviducts	Nutrition provided by secretions	Nimbaphrynoides occidentalis (Bufonidae)		

TABLE 8.2 (continued)

Data from Haddad and Prado 2005, Duellman and Trueb 1986, Iskander et al. 2014.

^aOnly a few examples are given for each mode. Not all members of a genus necessarily exhibit the same reproductive mode, and some genera are represented by more than one mode.

eggs from drifting downstream (Weygoldt and de Carvalho e Silva 1992; Haddad and Giaretta 1999).

A shift from depositing eggs in ponds or streams to breeding in small pools or on land is a common theme in the reproductive biology of anurans (Wells 2007). Re-

duced predation on eggs and larvae is probably a major benefit of this shift to oviposition sites that lack fish and some other predators found in large permanent bodies of water. Many tropical frogs lay eggs in small bodies of water, sometimes with volumes no greater than a teacup. Certain Neotropical treefrogs, such as *Hypsiboas boans*, *H. faber*, and *H. rosenbergi*, lay eggs in basins constructed by the male at the edge of a stream (**Figure 8.13**). Other tropical anurans, such as frogs in the genus *Eupsophus*, lay eggs in small water-filled depressions on the ground. Other species breed in water that collects in hollow logs on the forest floor or in natural containers such as the seed

Figure 8.13 A shift in the landward direction.

A shift from depositing eggs in ponds or streams to depositing egg masses in transient pools or on land can be seen in anuran evolution. The neotropical treefrog *Hypsoboas faber* lays eggs in a nest constructed by the male at the edge of a stream. The male seen here is guarding a clutch of eggs. (Photograph by Celio Haddad.) husks of Brazil nuts (Caldwell 1993). These small bodies of water often have little food for developing tadpoles. Some species have solved this problem by supplying their eggs with abundant yolk, which allows the tadpoles to develop without feeding (Crump 1989). Male *Aplastodiscus leuco*-



pygius construct subterranean nests, and females deposit eggs in a layer floating on water in the nest. Later, the nest floods, the roof collapses, and the tadpoles are washed into ponds or streams (Haddad and Sawaya 2000).

Frogs in several families lay eggs in water that collects in the leaf axils of bromeliads and other plants or in tree holes. For example, many hylid treefrogs, including all of the species found in Jamaica, are bromeliad breeders. A rhacophorid treefrog from Taiwan, Kurixalus eiffingeri, places its eggs inside bamboo stumps just above the water level. After the eggs hatch, the tadpoles drop into the water to complete development (Kam et al. 1997). Phrynobatrachus guineensis in West Africa has a similar reproductive mode. It lays eggs on the sides of tree holes and in waterfilled nut capsules on the forest floor (Rödel 1998). As in species that breed in small pools, tadpoles that develop in bromeliads, tree holes, and similar breeding sites often are faced with a shortage of food and oxygen. In many species the tadpoles do not feed at all, but in others they are opportunistic predators. Some species have gone even further and eat eggs provided by the mother (see below). Tadpoles in bromeliads and tree holes usually develop lungs very early and become obligate air-breathers because the oxygen content of the water in such sites is very low (Lannoo et al. 1987).

EGGS ON LAND, LARVAE IN WATER Some frogs lay their eggs on land, and the tadpoles get washed into water after they hatch. Male Leptodactylus bufonius construct mud nests by the edges of depressions (Figure 8.14A). The frogs deposit and fertilize eggs in a foam nest inside the mud nest and the female builds a cap over it. Eventually, rains break the nest apart and the tadpoles are washed into the pond. Species of Geocrinia and Pseudophryne lay their eggs on the ground, in burrows, or in depressions. Heavy rains flood the sites and stimulate the eggs to hatch. The tadpoles then complete development in the newly formed ponds. Physalaemus spiniger has three reproductive modes (Haddad and Pombal 1998). When a pond contains water, the frogs construct foam nests on the water surface. If a pond basin is dry, the frogs construct foam nests either in humid places on the ground near the pond depression, or in water that accumulates in the axils of terrestrial bromeliads. In these latter two situations, rainwater presumably washes the hatchling tadpoles into the newly formed pond.

Some frogs lay their eggs on vegetation but retain an aquatic tadpole stage. As the eggs hatch, the tadpoles drop into the water from vegetation that overhangs ponds or streams and complete a life cycle similar to that of typical pond- or stream-breeding frogs (Figure 8.14B). Groups with this type of life history include centrolenids, phyllomedusine hylids such as Agalychnis, and other hylids. The hylid Dendropsophus ebraccatus exhibits plasticity in its reproductive mode, sometimes laying eggs on vegetation above water and sometimes submerged in the water; eggs develop successfully under both conditions (Touchon and Warkentin 2008). The choice is influenced by the amount of shade above the breeding site. In shaded habitats, eggs are frequently deposited out of water, whereas in habitats exposed to the sun they often are deposited in the water. This plasticity seems to be maintained by the balance of mortality risks: desiccation of eggs out of water versus aquatic

(A)



Figure 8.14 In some species, eggs are laid on land, but larvae develop in water. (A) An uncapped mud nest of Leptodactylus bufonius. Eggs mature within a foam nest. Larvae are washed into ponds when rains break the mud nest apart. (B) Some treefrogs lay eggs on leaves or other vegetation over-



hanging water. The hatchlings drop into the water, where they complete a life cycle similar to that of pond- or stream-breeders. This egg mass was laid by a female Dendropsophus brevifons, native to Ecuador. (Photographs: A, Martha L. Crump; B, © Morley Read/Alamy.)

predators in the water (Touchon 2012). Rhacophorid treefrogs usually lay their eggs in foam nests overhanging temporary ponds. In the African genus *Chiromantis*, these nests provide protection from desiccation in the tropical sun (Seymour and Loveridge 1994).

NONAQUATIC LARVAE AND DIRECT DEVELOPMENT

Many frogs have eliminated an aquatic larval stage altogether. Tadpoles of a few species, including the dendrobatid *Anomaloglossus stepheni*, remain in a terrestrial nest without feeding until metamorphosis (Juncá et al. 1994). Eggs of other species, such as frogs in the families Eleutherodactylidae and Craugastoridae, undergo direct development and hatch into small froglets. Much of the ecological success of these groups may be attributable to their reproductive mode, which allows them to occupy terrestrial and arboreal habitats not available to frogs with aquatic larvae.

In the Eastern Hemisphere, the closest ecological equivalents of eleutherodactylids and craugastorids are microhylids from lowland and montane forests of New Guinea and northern Australia. One of the most bizarre of all frogs is the Australian turtle frog (*Myobatrachus gouldii*), which lives almost entirely underground in very dry deserts. The turtle frog lays direct-developing eggs buried more than a meter beneath the surface (Roberts 1981).

PARENTAL CARE An estimated 10 to 20% of anuran species provide parental care (Crump 1995; Balshine 2012). Care includes egg attendance, transport of eggs, attendance of tadpoles and/or young, transport of tadpoles and/ or young, and feeding of tadpoles. Egg attendance is the most common form of parental care by frogs, and it may be provided by the male, female, or both, depending on the

species (**Figure 8.15A**). Although attendance of aquatic eggs is uncommon, it occurs in a few species, such as *Hypsiboas* (Hylidae) and *Nectophryne afra* (Bufonidae) (Scheel 1970). We will mention a few examples of parental care here to illustrate the diverse behaviors that are part of anuran reproductive modes, and will examine various aspects of the evolution of parental care in Section 8.7.

Direct development of eggs into miniature froglets, without a free-living larval stage, is sometimes associated with parental care (Figure 8.15B). For example, some eleutherodactylids and craugastorids attend their eggs. Females of the Jamaican cave-breeding frog (*Eleutherodactylus cundalli*) and males of two species of microhylids from New Guinea, *Liophryne schlaginhaufeni* and *Sphenophryne cornuta*, transport the froglets on their backs (Bickford 2002).

Male African bullfrogs (*Pyxicephalus adspersus*) remain with their tadpoles until metamorphosis and defend them against potential predators. They also construct channels to free the tadpoles from entrapment in small pools (Kok et al. 1989). Another African frog, *Hemisus marmoratus*, lays eggs in burrows. The female remains with the eggs until they hatch and then digs a channel that allows the tadpoles to escape from the burrow. If a suitable pool is not available nearby, the female leads her tadpoles through a channel until they reach water (Kaminsky et al. 1999). In the New World, females of several *Leptodactylus* species also remain with their tadpoles (**Figure 8.16**) (Hurme 2014). All of these frogs are large, and an adult can protect its tadpoles from some predators and physical hazards. Female *Leptodactylus podicipinus, Leptodactylus* aff. *latrans*,

(B)

(A)



(A) A male *Hyalinobatrachium bergeri* attends an egg clutch. (B) Two species of *Bryophryne* (Strabmantidae) in which adults attend direct-developing eggs. A female *B. nubilosus* is seen attending her eggs in the top photo. The bottom photo shows *B. hanssaueri* eggs and hatchlings. (Photographs by Alessandro Catenazzi.)





(A)



Figure 8.16 Reproduction in *Leptodactylus insularum*. (A) Foam nest, with male and female in amplexus. (B) Female in the middle of her clutch of newly hatched tadpoles. Adults of this species are relatively large and able to offer substantial protection to their tadpoles. (Photographs by Kristiina Hurme.)

and *Leptodactylus* aff. *leptodactyloides** connect water bodies by digging channels to their shoals of tadpoles. This maternal behavior potentially provides tadpoles with access to new feeding areas and prevents predation and desiccation. Female *Leptodactylus* aff. *latrans* also defend their offspring by jumping at predatory snakes, birds, and conspecific males that approach the shoals of tadpoles (Rodrigues et al. 2011).

Newly hatched dendrobatid tadpoles wiggle onto the back of a parent, who transports them from a terrestrial oviposition site to water bodies ranging from streams to small pools in tree holes or in the axils of bromeliads, depending on the species (**Figure 8.17**). The ecology and behavior of parental care provided by dendrobatids have been studied by many researchers; see Summers and Tumulty 2014 for a recent review and a discussion of the evolution of parental care in this family.

Two intriguing aspects of parental care of some dendrobatids include the feeding of unfertilized (nutritive) eggs by the female to the tadpoles (e.g., Brust 1993; Stynoski 2009; Stynoski et al. 2014) and biparental care (e.g., Caldwell and de Oliveira 1999; Tumulty et al. 2014). Several frogs in other families have independently evolved the behavior of feeding tadpoles with unfertilized eggs, including the Neotropical hylids *Osteopilus brunneus* from Jamaica (Thompson 1996) and *Anotheca spinosa* from Central America (Jungfer 1996); the leptodactylid *Leptodactylus fallax* (Gibson and Buley 2004); and the Asian rhacophorids *Kurixalus eiffingeri* (Kam et al. 1997) and *Rhacophorus vampyrus* (Vassilieva et al. 2013). (B)



Some amphibians complete embryonic and larval development on or within the body of one of the parents but outside the reproductive tract. In Hemiphractus, Cryptobatrachus, and Stefania, the direct-developing eggs are attached to the back of the female with mucus (Duellman and Hoogmoed 1984; Jungfer and Boehme 1991; MacCulloch and Lathrop 2002). In *Gastrotheca*, the eggs are enclosed in a dorsal pouch and either fully developed froglets or well-developed larvae are released to complete their development in water (Figure 8.18A) (Duellman et al. 1988). In Fritziana and Flectonotus, the mother carries her eggs in a dorsal pouch and later releases tadpoles into bromeliads or bamboo stems containing water (Figure 8.18B. In the aquatic Suriname toad (Pipa; Figure 8.18C), when the eggs are released during amplexus, the male presses them against the female's back, where they become enveloped as her dorsal skin hypertrophies. Male



Figure 8.17 Dendrobatid frogs transport their tadpoles from a terrestrial oviposition site to a body of water. Here a male *Ameerega parvula* carries tadpoles on his back. (Photograph by Alessandro Catenazzi.)

^{*}The designation "aff." means "affinity to"—that is, the species is related, but not identical, to the binomial name indicated.

(A)

(B)

Figure 8.18 Some frogs brood eggs outside the female reproductive tract.

(A) Female *Gastrotheca excubitor* with a newly emerged young on her back; the direct-developing offspring has emerged from her dorsal pouch. (B) Female *Flec-tonotus fitzgeraldi* with eggs in her dorsal pouch. (C) Female *Pipa carvalhoi* with eggs embedded in her dorsal skin. (D) The male Darwin's frog (*Rhinoderma darwinii*) broods its tadpoles in its vocal sac. (Photographs: A, Alessandro Catenazzi; B, Kentwood D. Wells; C, © Natural Visions/ Alamy; D, Martha L. Crump.)

1983). Froglets emerge from the female's mouth following metamorphosis (**Figure 8.19**). Hormones released by the young suppress secretion of hydrochloric acid during brooding. The mother's digestive tract returns to normal and she resumes feeding after the young are released (Tyler et al. 1983). Both species of *Rheobatrachus* are believed to be extinct, not having been seen since the mid-1980s (but see Section 17.8).

BIRTH OF TADPOLES *Limnonectes larvaepartus*, a fanged frog from the Indonesian island of Sulewesi, gives birth to tadpoles. Fertilization is internal, and the tadpoles develop in the oviducts until they have exhausted their supply of yolk, at which point they are born. The tadpoles complete development in small pools of water on the margins of streams (Iskander et al. 2014).

VIVIPARITY At least nine species of anurans retain their developing young in their oviducts until birth (Lehtinen and Nussbaum 2003). The young of seven of these are nourished entirely by yolk reserves (lecithotrophy), and the other two are nourished at least in part by maternal secretions (matrotrophy).

8.6 ■ Evolution of Direct Development and Viviparity

Although large egg size is not an absolute prerequisite for the evolution of direct development (Callery et al. 2001), direct-developing eggs are typically much larger than eggs that hatch as larvae (Salthe and Duellman 1973), and large egg size has been suggested as the ancestral point of departure for the evolution of direct development (see Figure 8.21) (Wake and Hanken 1996). Direct-developing eggs generally are endowed with large yolk reserves, which nourish the



Darwin's frogs (*Rhinoderma darwinii*) brood their tadpoles in their vocal sacs (**Figure 8.18D**).

A unique brooding strategy has been employed by *Rheobatrachus*, the gastric-brooding frogs of Australia. In both species of this genus, the female swallows her eggs and broods them in her stomach (Tyler and Carter 1982; Tyler



Figure 8.19 Birth of a gastric-brooding frog (*Rheobatra-chus silus***).** Embryonic development in this species (extinct since 1983) lasted 36–43 days, at which time the young passed through metamorphosis in their mother's stomach and emerge from her mouth as fully developed froglets. (Photograph © Michael Tyler/Science Source.)

young during their prolonged development. Direct development has evolved independently in several lineages (Duellman and Trueb 1986; Duellman 2007). These species are usually found in moist habitats such as wet tropical rain forest and cloud forest, and their eggs are usually protected by heavy capsules that retard water loss. The ecological significance of direct development is that amphibians that are not dependent on standing water for reproduction are able to move into habitats that otherwise would be unavailable to them.

Herpetologists have long assumed that the amphibian reproductive modes we see today represent stages in an incomplete linear sequence of steps toward greater independence from open water, with direct development at the end of the spectrum (e.g., Lutz 1948). Views on the evolution of reproductive modes have changed recently, however. For example, direct development was thought to have evolved multiple times within the Plethodontidae (Wake and Hanken 1996). Recent analyses, based on a phylogeny using molecular data, suggest that a complex life history has reevolved from direct-developing ancestors (see Section 8.5).

Likewise, recent studies have challenged our thinking about the evolution of anuran reproductive modes. Ivan Gomez-Mestre and colleagues (2012) documented about 48 independent origins of terrestrial reproduction and about 19 for direct development. Contrary to the accepted dogma, frogs may frequently have bypassed seemingly intermediate stages in the evolution of direct development.

Retention of developing embryos within the female reproductive tract has evolved independently in all three amphibian orders. The comparatively small number of origins of embryo retention suggests that the costs may outweigh the benefits for most taxa. Embryo retention reduces total reproductive output because it usually limits reproduction to one clutch per season. Furthermore, clutch size is usually lower than in oviparous species because space within the female may be limited. Additionally, if gravid females cannot move as rapidly as nongravid females, they may be more vulnerable to predators.

David Gower and colleagues (2008) reported viviparity in *Gegeneophis sechachari*, a small caecilian from India. This is the only caecilian genus that contains both oviparous and viviparous species. The Gower et al. study indicates that viviparity in caecilians evolved independently at least four times, and there is no indication that oviparity has ever re-evolved once viviparity was established.

Comparative studies indicate that viviparity evolves through gradual increases in the length of time eggs are retained in the oviduct (Guillette 1987). One set of specializations enhances gas exchange between maternal and fetal tissues. During the evolution of these reproductive modes, the thickness of the jelly layers of the amphibian egg is reduced. The total length of blood vessels in the oviduct and in the respiratory structures of embryos is increased. Previously existing larval structures are modified and used for respiration. Larvae of viviparous species have greatly elaborated and highly vascularized gills or tails.

8.7 Evolution of Parental Care

As we saw in Section 8.5, some caecilians, salamanders, and anurans provide parental care for their eggs and/or young. Parental care generally is correlated with large egg size, but which came first evolutionarily? The answer has been controversial (see Shine 1978; Nussbaum 1985, 1987, 2003), but the most recent analysis (Summers et al. 2006) suggests that evolution of large egg size typically precedes parental care, at least in frogs.

Parental care by caecilians and salamanders consists only of egg attendance, whereas the forms of parental care by frogs are exceedingly diverse. The term "parental care" is generally used for any type of parental investment in offspring after the eggs have been deposited or the young have been born (Clutton-Brock 1991), though some authors define parental care as any investment in offspring that occurs after fertilization (e.g., including nest building and viviparity) (Lehtinen and Nussbaum 2003; Balshine 2012; Smiseth et al. 2012). Parental care presumably increases survivorship of the young, but it usually entails a cost to the caregiver. We would thus expect parental care to evolve only if a parent is able to increase offspring survival enough to offset the costs involved (Clutton-Brock 1991; Lehtinen and Nussbaum 2003; Royle et al. 2012).

Benefits of parental care

How does parental care increase offspring survivorship? Consider egg attendance. Attendant female Ambystoma opacum roll the eggs, which decreases fungal growth (Croshaw and Scott 2005). Attendance of direct-developing eggs by Cophixalus parkeri decreases the risk of fungal growth and also protects against conspecifics that eat the eggs (Simon 1983). Male Hypsiboas rosenbergi often guard their nests from intruding male conspecifics (Kluge 1981). Some attendant salamander parents likewise protect against predators. Another function of egg attendance is aeration of aquatic eggs, as in Nectophryne afra (Scheel 1970) and Proteus anguinus (Salthe and Mecham 1974). Parents may manipulate the eggs, thus preventing developmental abnormalities caused when the embryo rests in the same position throughout development, as in Desmognathus ochrophaeus (Forester 1979). Male Liophryne schlaginhaufeni transport young on their backs, and the froglets hop off at different places in the habitat. Thus, the young may benefit from reduced competition for food, lower predator pressure, and reduced levels of inbreeding (Bickford 2002).

Parental behaviors may reduce the risk of desiccation for eggs deposited on land. In *Desmognathus ochrophaeus*, the female reduces the rate of water loss by decreasing the exposed surface area of the egg mass (Forester 1984). In some dendrobatid frogs, the parent releases water from its bladder onto the eggs (Weygoldt 1980, 1987). Likewise, the terrestrial, direct-developing eggs of *Eleutherodactylus coqui* are kept hydrated by the attendant male (Taigen et al. 1984), who also guards the eggs against predators (see Figure 15.6) (Townsend et al. 1984). Female *Chiromantis hansenae* attend their eggs, which are deposited on leaves overhanging pools of water. Egg survivorship is significantly enhanced by attendance of the female through prevention of water loss (Poo and Bickford 2013).

The benefit of parental care has been documented in various species of centrolenids that lay their eggs on vegetation above water. For example, experiments suggest that attendance by male Hyalinobatrachium valerioi increases embryonic survivorship by reducing egg predation and preventing desiccation (Vockenhuber et al. 2009). Likewise, egg attendance by male H. fleischmanni reduces embryonic mortality. Males of this species modify their parental behavior in response to environmental moisture, exhibiting higher levels of attendance in drier years than in wetter years (Delia et al. 2013). Parental care to prevent desiccation appears to be so critical that H. fleischmanni embryos hatch earlier than normal if males abandon the clutches (Delia et al. 2014). The benefit of egg attendance by male H. orientale varies with the season (Lehtinen et al. 2014). During the wet season, egg attendance decreases the risk of predation by arthropods, whereas during the dry season it decreases the risk of mortality from desiccation. During both seasons, egg attendance significantly increases offspring survivorship (Figure 8.20).





Costs of parental care

The fact that most amphibians do not exhibit parental care suggests that the behavior involves costs to the parents that may outweigh the enhanced survival of offspring (Crump 1995, 1996; Lehtinen and Nussbaum 2003; Balshine 2012). Reduced reproductive output is one such cost. Species that exhibit parental care usually produce fewer eggs per clutch than do related species lacking parental care (Salthe and Duellman 1973). Furthermore, time and energy spent on parental care may limit opportunities for additional matings (Kluge 1981; Townsend 1986).

Another cost may be decreased food intake for the caring parent. Parents typically do not eat when they are guarding nests or eggs, and females that remain with their clutch produce fewer clutches overall than do non-caring females.

Reduced survival of the parent is another potential cost. Remaining with the eggs could increase an individual's vulnerability to predation. Because most amphibians are small and have ineffective defenses against vertebrate predators, parental care could increase the risk of their own death without saving their eggs or young.

Who cares?

Which parent cares, the mother or the father? We would predict that parental care is most likely to evolve in the sex that is more closely associated with the eggs (Gross and Shine 1981). When fertilization is external, either the female or male may be the caregiving parent, since both are present when the eggs are laid. In this case, the relative costs and benefits of parental care appear to determine who cares. For example, male frogs tend to be the caregivers when eggs are laid in the male's territory and he can continue to attract and mate with additional females while guarding eggs. By contrast, females tend to be the caregivers when the calling site of the male and the oviposition site are in different places, as in species that have internal fertilization (Lehtinen and Nussbaum 2003; Wells 2007).

8.8 ■ Egg Size and Clutch Size

A female can produce a clutch consisting of a few large eggs, many small eggs, or some intermediate combination. Amphibians have played an important role in empirical studies that have tested theoretical ideas, both because amphibians are relatively easy to work with and because, as a group, they exhibit a wide range of clutch and egg sizes. *Eleutherodactylus limbatus*, an 11- to 12-mm frog from Cuba, produces one large egg at a time, and the 14-mm *Noblella pygmaea* from southern Peru produces two eggs, each about 4 mm in diameter (**Figure 8.21**). At the other extreme, American bullfrogs (*Rana catesbeiana*), which measure 10–15 cm as adults, produce over 20,000 tiny eggs per clutch. Larger egg size and smaller clutch size has been



Figure 8.21 Large egg size has evolutionary implications. This female *Noblella pygmaea* from Peru is about 14 mm in total length and produces a clutch of only two large, direct-developing eggs. Large egg size is linked to direct development and, in some lineages, to parental care. (Photograph by Alessandro Catenazzi.)

correlated with direct development and parental care (see Sections 8.6 and 8.7).

The size of the egg affects offspring survival by influencing the embryo's size, shape, growth, and developmental rates (Kaplan and King 1997). Larger eggs typically result in larger hatchlings (Salthe and Duellman 1973). Various investigators have concluded that hatchlings from larger eggs should experience increased fitness because of their larger initial size, faster growth rates, faster developmental rates, or some combination (e.g., Kuramoto 1978; Crump 1984; Kaplan and King 1997). However, producing small eggs allows larger clutch sizes and potentially more offspring that survive to adulthood.

Reproductive mode, and thus the site of egg deposition and larval development (aquatic vs. terrestrial), is associated with differences in egg and clutch size (Salthe 1969; Salthe and Duellman 1973). Generally, species that lay eggs in water and have aquatic larval development produce large clutches of small eggs. However, there is considerable variability in egg size associated with oxygen availability. Cold-water habitats usually have higher levels of dissolved oxygen than warm-water habitats. Species that lay their eggs in oxygen-poor water, such as tropical ponds, typically have smaller eggs than species that breed in cold water; the larger surface-to-volume ratio of small eggs allows greater uptake of oxygen.

Species that oviposit out of water generally produce fewer, larger eggs than species that lay eggs in water. Terrestrial eggs usually have longer developmental times, larger hatchlings, and more advanced hatchlings than aquatic eggs. The increased investment per offspring (large eggs, parental care, or both) presumably increases the survival of eggs enough to compensate for the smaller number of offspring produced. Within a given reproductive mode, there is considerable variability among species in clutch and egg size, suggesting that multiple selective forces and constraints mold these life-history characteristics.

Variability in egg size

The optimal combination of egg and clutch size is one that maximizes the total number of surviving offspring. Nonetheless, there is considerable variability within a species, and there may not be an optimal egg size (Bernardo 1996). Egg size variability has been documented among populations (e.g., Berven 1982; Bruce and Hairston 1990; Kaplan and King 1997), within populations (e.g., Kaplan 1980; Travis 1983; Crump 1984; Williamson and Bull 1989, 1995; Kaplan and King 1997), and within individual clutches (e.g., Crump 1981, 1984; Williamson and Bull 1995; Kaplan and King 1997). What does all this variability mean?

A range of egg sizes within a given clutch may be advantageous. For example, variance in food availability is associated with success of different-sized eggs for the California newt (Taricha torosa) (Kaplan 1985). When excess food is available, larvae that hatch from relatively large eggs metamorphose sooner and at larger sizes than those that hatch from relatively small eggs. When food is limited, however, larvae that hatch from small eggs metamorphose considerably earlier than larvae from large eggs. Thus, large eggs should be favored over small eggs when food is abundant because large eggs hatch sooner and produce larger metamorphs. When food is limited, however, the slow development of larvae from large eggs exposes them to predators for longer periods and puts them at risk of dying if their pond dries out before they have metamorphosed. Thus, small eggs should be favored over large ones when food is scarce.

Another situation expected to select for variable intraclutch egg size is unpredictable environments, such as temporary ponds (Crump 1981; Yeager and Gibbons 2013). In a favorable environment, small eggs might survive, and a female could increase her fitness by producing many small eggs. In an unpredictable environment, a female might be expected to hedge her bets—that is, produce a range of egg sizes that might increase the chance that some offspring will survive. The largest offspring, hatching from larger eggs (with the potential to be better competitors and able to metamorphose faster and leave the pond earlier) might have increased survivorship if conditions are unfavorable. Of course, the disadvantage of producing all large eggs is that the female can produce fewer of them, thus the advantage of a range of egg sizes.

8.9 ■ Complex Life Cycles, Larval Development, and Metamorphosis

Despite the great diversity of reproductive modes in amphibians, the trait that sets many amphibians apart from other terrestrial vertebrates is having a complex life cycle in which a free-living aquatic larva metamorphoses into a terrestrial or semiaquatic adult. There are, however, considerable differences in patterns of development among the three major lineages of amphibians.

Complex life cycles

A complex life cycle enables an animal to exploit resources in more than one environment. Tadpoles are essentially eating machines that exploit seasonally abundant food resources in aquatic habitats (Wassersug 1975; Wilbur 1980). The shift to more terrestrial habits that accompanies metamorphosis in most anurans can be seen as a shift in ecological niche, with adults being exposed to different food resources, different growth conditions, and different kinds of predators than the aquatic larvae (Werner 1986). In animals such as salamanders, which have morphologically similar larvae and adults, the ability of each life-history stage to exploit resources efficiently in its respective environment is constrained by genetic correlations between larval and adult morphology. Larval and adult diets are likely to be similar in groups that have similar larval and adult morphology.

Theoretical models suggest that natural selection can favor disruption of genetic correlations between larval and adult morphology and lead to divergence that enables each stage to use very different resources. This process can result in dramatic shifts at metamorphosis, as in the transition from herbivorous tadpoles to carnivorous adult anurans (Ebenman 1992). Once this type of complex life cycle is established, it may be more evolutionarily stable than the type of life cycle seen in salamanders, and less likely to evolve toward reduction of either the larval or adult morphology (Hanken 1999). Indeed, caecilians have larvae most similar in morphology to adults, and many lineages lack the larval stage. In contrast, anurans have larvae that are least similar to adults, and most lineages retain the larval stage. Salamanders are intermediate in degree of similarity between larvae and adults. Most major lineages (families) of salamanders retain the larval stage, and some actually retain some larval features as adults (paedomorphosis; see Section 8.10), but in most species of plethodontids, the larval stage has been lost and embryos undergo direct development.

Larval development of caecilians

Most caecilians lack an aquatic larval stage, and when it is present, the larvae hatch at a very advanced stage, with lungs already well developed. External gills disappear within a few days, but open gill slits are retained, probably because they facilitate prey capture in water (see Chapter 11). Aquatic larvae have lateral line systems and tail fins that are lost at metamorphosis except in permanently aquatic species. The dentition of larval caecilians is similar to that of adults, and ossification of the skeleton occurs early. By the beginning of metamorphosis, most of the cartilage forming the neurocranium has been replaced by bone (Breckenridge et al. 1987). Some caecilian larvae tend to be more amphibious than fully aquatic, foraging in shallow water and even emerging periodically onto exposed mud (Himstedt 1991; Verdade et al. 2000).

Larval development of salamanders

The larval development of most salamanders is similar, although there are differences in the developmental stage at which larvae hatch and the length of the larval period. The three species of *Amphiuma* are unusual in having an abbreviated larval period. Females lay eggs in burrows that they excavate, and the eggs hatch into aquatic larvae when the burrows are flooded. The larvae hatch at an advanced stage of development and lose their gills in about 2 weeks, essentially becoming miniature adults (Gunzburger 2003). Most other salamanders with complex life cycles have much longer larval periods and go through a more pronounced metamorphosis.

Larval salamanders have prominent external gills, tail fins, and lateral line organs. Gills and tail fins are larger in pond-dwelling larvae than in those that live in the running water of streams and brooks (Figure 8.22). Most salamander larvae develop all four limbs shortly after hatching, and they soon begin to search for food. The larvae have a distinctive larval dentition. They are strictly carnivorous, feeding on zooplankton when they are small and gradually shifting to larger prey as they grow. Large individuals of some species become predators on relatively large invertebrates, and even on members of their own species (see Chapter 11). Some of the obvious events that occur with metamorphosis include resorption of the gills, closure of the gill slits, resorption-or at least reduction-of the tail fin, and development of the stratified epithelium of the skin. Changes may occur in the head as well, including tooth maturation and development of eyelids and a fleshy tongue. The simple flap of connective tissue that acts as a valve in closing the internal nares may be replaced at metamorphosis by a more sophisticated structure that is operated by smooth muscle fibers. Because larval salamanders are carnivorous like adults, metamorphosis does not include major changes in the digestive system (Reilly 1994).

Larval development of anurans

Because of their distinctive appearance and feeding habits, larval anurans are called tadpoles. The exact stage at which a tadpole hatches varies among species; generally the hatchlings of aquatic-breeding species emerge from (A) Pond-dwelling larvae

(B) Stream/brook-dwelling larvae



Figure 8.22 Morphological types of salamander larvae.

All larval salamanders have external gills, tail fins, and lateral line organs. (A) Pond-dwelling larvae have large gills and high tail fins. Oxygen levels are low in ponds, and the larvae use tail fins to swim in the still water (B) Stream-dwelling larvae have small gills and low tail fins. Running water is well oxygenated, and the larvae crawl among rocks on the stream bottom rather than swimming. (After Wells 2007.)



their protective jelly capsules at earlier stages than those that develop out of water (for example, on leaves above a pond). After hatching, many species of tadpoles remain motionless for a few days while they absorb their yolk stores (Figure 8.23). The operculum (a flap of skin) grows over the gills, forming an opercular chamber that encloses the gills, and the eyes and mouth become functional. At this point the tadpoles begin to feed. Almost all tadpoles are suspension feeders that capture small particles from the water on specialized food traps as water passes through the oral cavity and gill chambers and exits through the spiracle. Most tadpoles are strictly or primarily herbivorous, but many consume animal matter opportunistically, and some have evolved into specialized carnivores (see Chapter 11). McDiarmid and Altig (1999) provide a detailed review of tadpole biology.

Metamorphosis of anurans is associated with dramatic morphological and physiological changes. The transition from a suspension-feeding tadpole to a carnivorous adult requires major modifications

Figure 8.23 Embryonic and larval development of wood frogs (*Rana sylvatica***).** (A) Embyros in an underwater egg mass; the gills are just starting to develop. (B) Newly hatched tadpoles have external gills and are largely immobile, remaining on or near the egg jelly and living off their remaining yolk reserves. (Photographs by David McIntyre.)

of the digestive tract (Hourdry et al. 1996). For example, the long, coiled tadpole intestine changes to the shorter adult gut, and a true (acidic) stomach develops. Tadpole mouthparts disappear and are replaced by jaws, teeth, and (in almost all species) a tongue. Moveable eyelids form, and the lungs become fully developed. The vertebral column and limb bones ossify, and skin glands and a stratified epithelium develop. The legs develop at similar rates, although the front legs are not visible at this stage because they develop inside the opercular chamber. During metamorphosis, the front legs erupt through the opercular wall and the tail is resorbed.

Hormonal control of metamorphosis and developmental plasticity

The timing of critical events in amphibian development and metamorphosis is ultimately under hormonal control. Larval development involves two processes: growth (increase in size) and differentiation (structural changes leading to metamorphosis). The two processes are controlled by different hormones. Growth is largely regulated by growth hormone secreted by the pituitary gland, whereas differentiation is regulated by thyroid hormones and corticosteroids.

Early in development the thyroid gland is relatively small and inactive. Corticotropin releasing factor (CRF) produced by the pituitary gland regulates release of thyroid-stimulating hormone (TSH) and adrenocortitropic hormone (ACTH). TSH regulates production of thyroid hormones (T_3 and T_4) by the thyroid gland while ACTH regulates production of corticosteroids by the interrenal glands of the kidney. Initially, the part of the hypothalamus that releases CRF is very small, but this region increases in size and activity in response to low levels of thyroid hormones (T_3 and T_4) in the blood. Circulating levels of thyroid hormones increase during development and peak at metamorphosis, as does the sensitivity of peripheral tissues to thyroid hormones (**Figure 8.24**).

Until recently it was not clear how environmental variables interact with this hormonal control system to control plasticity in the timing of metamorphosis. Recent work has shown that CRF provides the critical link between certain kinds of environmental stress, such as pond drying, and the hormonal regulation of metamorphosis. Stress increases production of CRF, which in turn increases production of corticosteroids. Higher levels of corticosteroids in the blood increase the rate of conversion of a relatively inactive form of thryoid hormone, thyroxine (T_4) , to a more biologically active form, triidothryonine (T_3) . It is T_3 that actually initiates metamorphosis. Field studies have shown that circulating levels of CRF and corticosterone increase dramatically in response to both pond drying and increased density of competitors, and laboratory studies show that both tadpoles and salamander larvae accelerate metamorphosis when treated with CRF (Denver 2013). These experiments demonstrate a physiological mechanism for the plasticity in timing of metamorphosis originally predicted by an ecological model put forth in 1973 by Henry Wilbur and James Collins (see p. 312).

The ecology of metamorphosis

Although there is a basic similarity in the life cycles of many amphibians, there is considerable variation among species in the duration of the larval period and size at metamor-



Figure 8.24 Production and regulatory interactions of hormones during tadpole metamorphosis. CRF (cortico-tropin releasing factor) from the hypothalamus causes the pituitary gland to release both TSH (thyroid-stimulating hormone)

and ACTH (adrenocorticotropic hormone). TSH causes the thyroid gland to release thyroid hormones (T_3 and T_4). Corticosteroids promote conversion of T_4 to T_3 . (After Denver et al. 2002.)

phosis. For example, American bullfrogs (*Rana catesbeiana*) can require more than 2 years to reach metamorphosis, and tailed frogs (*Ascaphus*), which develop in cold mountain streams, require 3 years. In contrast, some spadefoot toads (*Scaphiopus*) require only 8 days to reach metamorphosis. What accounts for this variation?

Werner (1986) argued that over evolutionary time, the timing of metamorphosis for a given species reflects the trade-off between growth and mortality in the aquatic and terrestrial environments. When growth conditions are good in the aquatic environment and mortality is lower than in the terrestrial environment, selection will favor a prolonged larval period. In contrast, if mortality increases in the aquatic environment, larvae may be better off if they metamorphose and emerge onto land. Bullfrogs typically breed in permanent ponds that are unlikely to dry up. Bullfrog tadpoles often grow large enough to escape many predators, and in addition they are distasteful to large predators such as fish. Such larvae can safely remain in a pond for several years before emerging at a relatively large size that is advantageous in facing the rigors of terrestrial life. Many spadefoot toads, on the other hand, breed in ephemeral desert pools that disappear within a few weeks. Even if food resources are abundant, larval periods must be short enough to allow the toads to escape the drying ponds, no matter how risky the terrestrial environment may be. Selection has favored very rapid development and metamorphosis at a small size.

This pattern is apparent even when comparing different species of spadefoot toads and their close relatives. North American spadefoot toads in the genera *Scaphiopus* and *Spea* (Scaphiopodidae) have shorter larval periods than Old World spadefoot toads in the genus *Pelobates* (Pelobatidae), and much shorter than the sister group to Pelobatidae, the parsley frogs (Pelodytidae) (**Figure 8.25**). These differences in larval period are evident even when the species are raised under the same conditions. A phylogenetic analysis indicated that very short larval periods are a derived trait in the North American clade, an adaptation to breeding in much more ephemeral water than do *Pelobates* and *Pelodytes* (Buchholz and Hayes 2002; Gomez-Mestre and Buchholz 2006).

DENSITY-DEPENDENT VARIATION IN LARVAL GROWTH **AND DEVELOPMENT** The typical duration of the larval period and size at metamorphosis for a given species are determined over evolutionary time by selective pressures imposed by the environment in which that species breeds. Nevertheless, many species exhibit considerable variation in both the timing of metamorphosis and the size at which transformation occurs, even in the same pond. In a now classic paper, Henry Wilbur and James Collins (1973) developed a model to explain individual variation in length of larval periods and size at metamorphosis. They postulated that each species has a minimum size that must be reached before metamorphosis can occur, as well as a maximum size at which it no longer is efficient to remain in the larval stage. They argued that when growth conditions are poor, larvae should metamorphose near the minimum size, but when conditions are good, they should continue growing until they reach the maximum size (Figure 8.26). At the population level, larvae growing under favorable conditions will almost always reach a large size, and variation in size at metamorphosis in a given pond will be minimal. When growth conditions are poor, either because of limited food resources or high densities of larvae, the first larvae to reach the minimum metamorphic size should immediately transform and leave the pond. Those left behind may experience reduced competition and therefore may be able to reach a larger size at metamorphosis.

Since the Wilbur-Collins model was developed, an enormous number of experimental studies have verified its



Figure 8.25 Spadefoot toads exhibit considerable variation in life histories. (A) *Scaphiopus couchii* breeds in ephemeral rain pools in the deserts of southwestern North America. *S. couchii* has one of the shortest larval periods of any anuran—as little as 8 days from hatching to metamorphosis. (B) Members of the North American genus *Spea*, such as *Spea hammondii*, are

less desert-adapted, breed in longer-lasting temporary ponds, and have larval periods of up to 4 weeks. (C) Old World spadefoot toads such as *Pelobates syriacus* breed in even longer-lasting ponds and have longer larval periods (up to 7 weeks). (Photographs by Wayne Van Devender.)



Figure 8.26 The Wilbur–Collins model of larval development and metamorphosis. The model postulates that larvae must reach a minimum size (*b*) before they can undergo metamorphosis. Metamorphosis must occur before the larvae reach a maximum size (b + c) at which it is no longer efficient to remain in the larval stage. The probability of undergoing metamorphosis depends on larval body size (*W*) and size-specific growth rate (dW/dt). If larvae have reached a body size that exceeds the minimum size for metamorphosis (W > b), but have not reached the maximum larval size (b + c), then they are expected to continue growing if recent growth rates are high (dW/dt > g, where *g* is some function of current body mass). If recent growth rates are low (dW/dt < g), then larvae are expected to metamorphose. (After Wilbur and Collins 1973.)

major predictions (see Alford 1999 for a review). For both anuran and salamander larvae, individuals raised at high density in the laboratory, in artificial ponds such as cattle tanks, or in field enclosures typically exhibit slower growth rates, longer larval periods, and smaller size at metamorphosis than do individuals raised at low density (Figure 8.27A). Manipulation of food resources while larval density is kept constant produces similar results, with larvae raised at low food levels exhibiting slower growth and smaller size at metamorphosis (e.g., Travis 1984; Semlitsch 1993). Some studies have shown evidence of competitive release after some larvae either left the pond or died. For example, Semlitsch and Caldwell (1982) found that spadefoot toad (Scaphiopus holbrookii) tadpoles reached larger metamorphic size at high densities than at intermediate densities because the high mortality that occurred at high densities reduced competition for the survivors.

In species that breed in ephemeral ponds containing few resources, the ability of larvae to escape drying ponds may be limited by a scarcity of food. The tadpoles of desert-dwelling spadefoot toads such as *Scaphiopus couchii* frequently die in drying pools, which often are little more than rain-filled depressions in the soil. Newman (1987) provided supplemental food to some tadpoles in natural ponds, and this resulted in faster growth and larger size at metamorphosis than in ponds without added food. Those toads with supplemental food were more likely to escape the ponds before they dried up completely (**Figure 8.27B**). Studies of salamander larvae have produced similar results. *Ambystoma* larvae raised at high density in artificial pools or enclosures in natural ponds and lakes exhibit slower growth and smaller size at metamorphosis than those raised at low densities (Semlitsch 1987a; Brunkow and Collins 1996). The effect of density can vary among years, however, especially in natural ponds. In experiments with *A. opacum* larvae in large pond enclosures, high density resulted in longer larval periods in some years but not in others, but larvae raised at high density were consistently smaller at metamorphosis.



Figure 8.27 Representative growth curves for tadpoles raised at different densities. (A) Growth curves (expressed as body weight) for wood frog (*Rana sylvatica*) tadpoles at initial densities of 50, 150, and 1,200 individuals raised in pens in natural ponds. (B) Growth curves for tadpoles of the spadefoot toad *Scaphiopus couchii* in high- and low-density natural ponds. In the high-density condition, the pond that did not receive added food (red curve) failed to produce any metamorphs before the pond dried up. (Data from Wilbur and Collins 1973; Newman 1987; Wells 2007).
Small metamorphic size can have profound effects on adult fitness. *A. opacum* that metamorphosed at a small size had smaller lipid stores than did those that metamorphosed at a large size, and they were smaller when they returned to the pond as adults. This difference, in turn, can affect reproductive success, because large females typically lay more eggs than do small females (Taylor and Scott 1997).

PLASTICITY IN LARVAL GROWTH AND DEVELOPMENT

The negative effects of high density or low food resources on larval growth and development are not surprising, but



a key prediction of the Wilbur–Collins model of metamorphosis is that larvae will exhibit plasticity in the timing of metamorphosis and respond to changes in growth conditions by speeding or delaying transformation. Consequently, the most direct tests of the model are experiments in which environmental conditions are altered during larval development.

Several experiments have shown that reducing food rations partway through larval development results in longer larval periods and smaller size at metamorphosis, but timing of metamorphosis and size at metamorphosis may not respond in exactly the same way to changes in resource levels. In an experiment with three species of spadefoot toads (Scaphiopus couchii, Spea hammondii, and Spea intermontana), Morey and Reznick (2000) removed all food at different stages of development. Tadpoles that were starved early in development failed to reach metamorphosis, but those starved at later stages sped up development and reached metamorphosis. Scaphiopus couchii, which has the shortest larval period of any North American anuran, exhibited the greatest capacity to complete metamorphosis after being deprived of food relatively early in development. Presumably a high degree of developmental plasticity is advantageous for S. couchii because it breeds in the most unpredictable ponds.

Some amphibian larvae can respond to drying conditions by increasing their rate of development and reaching metamorphosis early. This type of plasticity is expected to be most pronounced in species that breed in ponds that tend to dry up every year. Spadefoot toad tadpoles can reduce the length of the larval period by as much as 50% in response to pond drying. Laboratory experiments with Spea hammondii showed that decreasing water level alone could induce early metamorphosis, even when temperature and food resources were kept constant (Figure 8.28) (Denver et al. 1998). Several other anurans exhibit some capacity to shorten the larval period in response to pond drying, but none approaches the plasticity of spadefoot toad tadpoles. For example, larval periods for Epidalea (formerly Bufo) calamita tadpoles were only about 3% shorter in drying ponds than they were in ponds that did not dry (Tejedo and Reques 1994). Larval periods for Rana blairi tadpoles were 8% shorter in drying ponds than in ponds that did not dry (Ryan and Winne 2001).

Figure 8.28 Reducing water depth causes spadefoot toads to metamorphose earlier and at smaller body

sizes. Each experiment began with a water depth of 10 cm. That depth was either maintained throughout the period of development or was reduced at different rates (gradual to drastic) to a final depth of 0.5 cm. (A) The age at which tadpoles metamorphosed decreased by 20%, from an average of 40 days when water depth remained constant at 10 cm to 32 days for the most rapid depth-reduction rate. Similarly, body mass at metamorphosis (B) decreased by 55%, and snout-vent length (C) decreased by 15%. (After Denver et al. 1998.)





Experimental work with *Ambystoma talpoideum*, a salamander that breeds in ponds of varying degrees of permanence, also revealed a capacity to adjust the length of the larval period. Larvae raised in artificial ponds with short drying times metamorphosed earlier and at a smaller size than did those raised in ponds with longer drying times (**Figure 8.29A**). The experimental results were consistent with year-to-year variation in time of drying and time of metamorphosis in two natural ponds (**Figure 8.29B**).

8.10 Paedomorphosis

Paedomorphosis—the retention in adults of a derived species of characters that appeared during larval development in ancestral species—has occurred repeatedly over the course of amphibian evolution. Salamanders in the genus *Ambystoma* present some of the best-known examples of paedomorphic life histories. The tiger salamander (*A. tigrinum*) and the Mexican salamander or axolotl (*A. mexicanum*) are closely related species (**Figure 8.30**). *A. tigrinum* typically passes through an aquatic larval stage and metamorphoses to a terrestrial adult before the gonads mature.





Figure 8.30 Paedomorphosis in *Ambystoma.* (A) The paedomorphic Mexican salamander, or axolotl (*A. mexicanum*). (B,C) The tiger salamander (*A. tigrinum*) is a non-paedomorphic relative of A. *mexicanum*, with distinct larval (B) and adult (C) life stages. (Photographs by Wayne Van Devender.)

A. mexicanum, in contrast, fails to metamorphose fully, and the gonads mature while the body remains in the larval form. Undergoing metamorphosis is the ancestral condition for Ambystoma, and A. tigrinum retains the ancestral condition of metamorphosis. The retention of larval morphology in sexually mature A. mexicanum is the derived condition. A. mexicanum is paedomorphic, resembling the juvenile form of its tigrinum-like ancestor. This change is the result of a recessive genetic trait with a major effect on larval development becoming fixed in the A. mexicanum population (Voss and Shaffer 1997).

Because the developmental mechanisms that produce paedomorphosis are so general, distantly related paedomorphic salamanders have features in common. For example, the highly paedomorphic *Pseudobranchus* and *Siren* (Sirenidae) and *Necturus* (Proteidae) retain large external gills, and have pointed snouts because the maxillary bones do not form. (The two maxillae are among the last bones to appear during the development of the non-paedomorphic salamander skull, and development of these species is truncated before the maxillae appear.) The evolution of paedomorphosis can be understood in the framework of ecological niche shifts proposed by Werner (1986) to explain variation in the timing of metamorphosis. Specifically, paedomorphosis can be favored when the larval aquatic habitat is more stable or more



Figure 8.31 A genetic component to paedomorphosis of mole salamanders (Ambystoma talpoideum). Larvae were collected from a relatively permanent pond (Ellenton Bay) and a temporary pond (Sun Bay), and replicate groups of larvae (groups I and II) were established in large tanks. The water depth in half of the tanks was decreased, simulating a pond drying, while the water level in the remaining tanks was kept at a constant depth. Larvae from Ellenton Bay (the permanent pond) developed as paedomorphs more often than larvae from Sun Bay in both sets of tanks, indicative of a genetic distinction between the two populations. (After Semlitsch and Gibbons 1985.)

productive than the terrestrial habitat of adults, which in turn can result in higher growth rates and lower mortality in the aquatic environment than in the terrestrial environment. Some salamanders exhibit considerable plasticity in the degree to which adults are paedomorphic (Denoël et al. 2005). The best-studied example is Ambystoma talpoideum, which breeds in a variety of habitats, from ponds that dry up every year to those that dry every few years (Semlitsch 1985). In temporary ponds, all individuals exhibit the ancestral life history in which larvae hatch in the spring and metamorphose in response to drying of the pond in the summer. Individuals that hatch in more permanent ponds, however, frequently delay metamorphosis and breed as larvae, later metamorphosing into terrestrial adults. These individuals achieve increased reproductive success because they reproduce much earlier than do metamorphosing adults (Ryan and Semlitsch 1998). The proportion of paedomorphic larvae can be increased by rearing the larvae in artificial ponds that do not dry out (Semlitsch 1987b). There are genetic differences in paedomorphic tendencies among nearby populations, however. Larvae derived from populations with a high proportion of paedomorphic individuals are more likely to become paedomorphic than are larvae from populations that exhibit little tendency toward paedomorphosis in the wild (Figure 8.31).

Among plethodontid salamanders, paedomorphosis is strongly associated with life in caves and occurs exclusively in the spelerpine clade (Spelerpini), which includes the genera *Eurycea*, *Gyrinophilus*, *Pseudotriton*, *Stereochilus*, and *Urspelerpes* (the last consisting of a single species, *U. brucei*, considered the sister taxon of the large genus *Eurycea*). Many spelerpine salamanders undergo normal metamorphosis, but paedomorphic life histories occur in some species of *Eurycea* and *Gyrinophilus* (Figure 8.32).

The Edwards Plateau in central Texas, a region of limestone caves and underground springs, is a hot spot for the evolution of paedomorphosis in Eurycea. Phylogenetic studies have shown that paedomorphic life histories evolved independently multiple times in this genus (Bonett et al. 2013), usually in association with subterranean life in caves Food resources in caves are dependent on energy input from the outside, and most of these resources are found in the water. The terrestrial portions of caves offer relatively little for metamorphosed adults to eat. Paedomorphosis thus is favored, because larval forms can feed in the water more effectively than can metamorphosed individuals. In addition to paedomorphic traits such as retention of external gills. cave-dwelling salamanders often exhibit adaptations to life in dark environments, including loss or reduction of eyes and loss of skin pigment (pigmentation serves to protect animals from the sun's UV radiation). One surprising result of phylogenetic studies using DNA sequencing is that metamorphic life histories seem to have re-evolved in several clades of Eurycea from a paedomorphic life history-a rare example of reverse evolution (Bonett et al. 2013).









Figure 8.32 Paedomorphosis in plethodontid salamanders is associated with cave-dwelling. The only plethodontids displaying paedomorphosis belong to the clade Spelerpini. (A) *Gyrinophilus subterraneus* sometimes lives in caves. It has a very long larval period and reaches a large size before undergoing metamorphosis. (B) *Eurycea tynerensis* is a surfacedwelling salamander from the Ozark Plateau with some paedomorphic populations. (C) *Eurycea wallacei* is a blind paedomorphic salamander found in deep wells and caves. (D) *Eurycea rathbuni* lives in caves and springs. Both *E. wallacei* and *E. rathbuni* lack pigment and functional eyes, and adults retain external gills. (Photographs by Wayne Van Devender.)

SUMMARY

All amphibians studied so far have genotypic sex determination; that is, sex is determined at the moment the egg is fertilized by the particular complement of genes received from the parents.

Both male and female heterogamety occur in amphibians.

An individual's genetically programmed sex can be reversed by exposure to exogenous hormones at critical stages of development.

Amphibian reproductive cycles are variable and depend on both internal processes (e.g., hormones) and external events (e.g., rainfall, temperature, and food availability).

Some species, especially those in seasonal temperate areas, have definite reproductive seasons, which often, but not always, correspond with the warm, rainy period of the year.

Other species, including many that live in relatively aseasonal tropical habitats, breed year-round.

Individual amphibians may breed more than once per year, once per year, or less often.

Some amphibians have internal fertilization, whereas others have external fertilization.

External fertilization is presumed to be the ancestral condition for all amphibians and is retained in most anurans, but all caecilians and most salamanders have internal fertilization.

The spermatophore is a major evolutionary innovation of salamanders that allows internal fertilization of eggs, often at a time distinct from that of oviposition. Most salamanders have elaborate courtship that ensures the efficient transfer of spermatophores to the female.

The only salamanders with external fertilization are the cryptobranchids, sirenids, and hynobiids. There is the potential for direct sperm competition if more than one male fertilizes the eggs. Males guard oviposition sites, or in hynobiids, egg sacs, from other males.

Most anurans have external fertilization. Males reduce opportunities for sperm competition by clasping females in amplexus, which allows the male to place his cloaca close to that of the female as gametes are released.

The ancestral form of amplexus is inguinal amplexus: derived forms include axillary amplexus and cephalic

(A)

amplexus. Internal fertilization has evolved independently in a few anuran families, including ascaphids, bufonids, and eletherodactylids.

Some amphibians have unusual modes of reproduction that involve exchange of genomes between species and often the evolution of polyploidy and unisexual populations.

The European waterfrog complex is an example of hybridogenesis, with polyploid individuals produced by hybridization between *Pelophylax lessonae* and *P. ridibundus*. Polyploid hybrids usually mate with males of a parental species, but the genome of the male is not incorporated into the offspring.

Unisexual populations of salamanders in the genus *Ambystoma* reproduce through kleptogenesis, stealing genomes from sperm donor males of several species.

■ Amphibians exhibit a wide diversity of reproductive modes, varying in types of embryonic and larval development, sites of egg deposition, egg and clutch size, and parental care.

Most amphibians are oviparous and lay their eggs in water. Some deposit their eggs out of water, and many of these have direct development.

Some amphibians give birth to live young. In some species, the young obtain all their nutrition from their yolk reserves (lecithotrophy); in others, the young are nourished by maternal secretions (matrotrophy) after they exhaust their yolk reserves.

An estimated 50%–80% of caecilians are oviparous; the other species are viviparous. The young of viviparous species use specialized fetal dentition to consume maternal secretions.

Most species of salamanders are oviparous; some have a larval stage and others have direct development; some oviparous species attend their eggs. A few species of salamanders are viviparous.

The reproductive modes of frogs are more diverse than those of caecilians and salamanders; many species have eliminated the aquatic larval stage, and many of these species have direct development. Several species are viviparous.

Herpetologists once assumed that the modes seen today represent stages in an incomplete linear sequence of steps toward greater independence from open water, with direct development at the end of the spectrum, but that viewpoint has been modified in recent years.

Recent studies have suggested that within the Plethodontidae, the larval stage has re-evolved from directdeveloping ancestors. Contrary to the accepted dogma, recent research suggests that frogs frequently have bypassed seemingly intermediate stages in the evolution of direct development.

Although some species in each order of amphibians provide parental care for their eggs or young, most amphibians do not exhibit parental care.

Parental care by caecilians and salamanders consists only of egg attendance.

Parental care by frogs is exceedingly diverse and includes attendance of eggs, transport of eggs, attendance of tadpoles or young, transport of tadpoles or young, and feeding of tadpoles.

Parental care presumably increases offspring survivorship, but it entails a cost (e.g., reduced opportunities for additional matings, decreased food intake, greater vulnerability to predation). Parental care is expected to evolve if it increases offspring survival enough to offset the costs involved.

In frogs, evolution of large egg size typically seems to precede parental care.

Clutch and egg size affect offspring survival by influencing an embryo's size, shape, growth, and developmental rates.

Many factors, including female body size, reproductive mode, and food availability, influence clutch and egg size.

There is a trade-off between producing many small eggs and fewer larger eggs.

Although the optimal combination of egg and clutch size is one that maximizes the total number of surviving offspring, there is considerable variability in egg size within populations of a given species and even within a clutch. A range of egg sizes may be advantageous in unpredictable environments.

Complex life cycles represent a shift in ecological niche from the larval to the adult stage, enabling animals to exploit distinctly different resources at different life-history stages.

Although the aquatic larval stage has been lost repeatedly in amphibian evolution, many amphibians retain the ancestral condition of a complex life history with a distinct larval stage that metamorphoses into an adult.

Caecilians exhibit the least dramatic metamorphosis; in those species with aquatic larvae, the larvae are almost fully developed when they emerge from the egg, and the larval period is short.

Larval salamanders develop functional legs well before metamorphosis and undergo a relatively simple change to the adult morphology by losing their external gills and some other larval features. Anurans undergo the most dramatic metamorphosis, from largely herbivorous suspension-feeding tadpoles to terrestrial, carnivorous adults.

Amphibians often exhibit considerable plasticity in growth and development, prolonging the larval stage when growing conditions in the aquatic environment are favorable, and shortening the larval stage when conditions in the aquatic environment are unfavorable.

Population density, food availability, temperature, and persistence of the aquatic environment all can affect the length and plasticity of the larval period.

Amphibians that breed in ephemeral rain pools, such as spadefoot toads, have extremely short larval periods and metamorphose at a relatively early stage of development. Amphibians that breed in permanent water often have prolonged larval periods, sometimes lasting several years.

Paedomorphosis, the retention in adults of a derived species of characters that appeared during larval development in ancestral species, has occurred repeatedly in the evolution of amphibians.

Many examples of paedomorphosis in amphibians result in morphological changes in certain structures that enable amphibians to adapt to new kinds of environments.

Paedomorphosis occurs in several species of salamanders but is unknown in anurans.

Go to the **Herpetology** Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

9 Reproduction and Life Histories of Reptiles

Some reptiles are largely solitary in their habits and seldom encounter, let alone interact with, other members of their species. Others are highly social and interact with conspecifics on a daily basis; individuals recognize each other, and may be part of a dominance hierarchy or have long-term pair bonds. Regardless of the nature of day-to-day social interaction, the annual cycles of nearly all reptiles include at least one social event, mating.

From this perspective, mating can be viewed as the pivotal event of reproduction. Physiological, morphological, and behavioral events that lead up to mating include the maturation of gonads, development of secondary sexual structures, and courtship. Surprisingly, even all-female species engage in mating behaviors. Mating by some species is associated with high levels of gonadal activity, whereas in others it occurs when levels of sex steroids are low and the gonads are undeveloped. In this latter situation, mating is not followed immediately by fertilization, and sperm are stored for later use. The events that follow mating include fertilization and embryonic development; parental care of eggs and offspring may occur as well.

Reproduction is only one aspect of an organism's life history. Life histories track the progression of individuals from hatching or birth to death. Important life-history traits include: schedules of reproduction, survival, and growth; mode of reproduction; and body size at maturity and when growth is asymptotic. Life histories are shaped by trade-offs between traits such as the rate of reproduction and the probability of survival. An important aspect of current studies of the evolution of life histories is elucidation of the physiological mechanisms of such trade-offs.

9.1 Sex Determination

Reptiles exhibit more diverse mechanisms of sex determination than any other vertebrates except fish. Some species have **genotypic sex determination (GSD)**, and either males (XY) or females (ZW) can be the heterogametic sex (although sex chromosomes are not always morphologically distinct). More enigmatically, however, sex determination can be environmental, with an individual's sex resulting from the temperatures that the embryo experienced during development. Observations in the early 1970s suggesting the existence of **temperature-dependent sex determination (TSD)** were met with skepticism, but a decade later the evidence was overwhelming and TSD had been documented in many reptilian taxa (Bull 2004).

While GSD and TSD were initially considered to be dichotomous, recent studies indicate that other environmental factors can influence sex determination in both cases. The scincid lizard Bassiana duperreyi, for example, has GSD judging by its male heteromorphic sex chromosomes. Nonetheless, at relatively low incubation temperatures, sex ratios are male-biased (Radder et al. 2009), while relatively large eggs produce hatchlings with female-biased sex ratios at a range of incubation temperatures (Shine et al. 2002). And although the lizard Gekko japonicus clearly has TSD, sex ratio in this species is influenced secondarily by egg size at intermediate incubation temperatures (where the sex ratio is 1:1). The mechanistic connection between sex and egg size for G. japonicus may be the amount of estrogen and testosterone deposited in the yolk by the female (Ding et al. 2012).

Species with TSD exhibit three basic responses when eggs are incubated at constant temperatures in the laboratory (**Figure 9.1**).

Figure 9.1 Three patterns of response in reptiles with temperature-dependent sex determination. Pattern Ia: males are produced at low incubation temperatures and females at high temperatures. Pattern Ib: males are produced at high temperatures and females at low temperatures. Pattern II: males are produced at intermediate temperatures and females at both low and high temperatures. (After Bull 1983.)



80 Graptemys ouachitensis Pelomedusa Percentage male 60 subrufa 40 20 0 23 25 27 29 31 33 35 Incubation temperature (°C)

100

Figure 9.2 TSD patterns illustrate taxon-specific pivotal temperatures. At the pivotal temperature at which the sex of the Ouachita map turtle (*Graptemys ouachitensis*, a crypto-dire with Pattern Ia TSD) shifts from male to female—around 30°C—the sex of the African helmeted turtle (*Pelomedusa sub-rufa*, a pleurodire with Pattern II TSD), shifts in the opposite direction, from female to male. The sex of *P. subrufa* shifts from male to female at a higher temperature (around 33°C). (After Ewert et al. 2004.)

- 1. Pattern Ia: males produced at cooler temperatures, females at warmer temperatures
- 2. Pattern Ib: females produced at cooler temperatures, males at warmer temperatures
- Pattern II: females produced at both cooler and warmer temperatures, males at intermediate temperatures

These patterns are not distributed randomly. Crocodylians exhibit Pattern II, the tuatara (*Sphenodon punctatus*) exhibits Pattern Ib, turtles exhibit either Pattern Ia or Pattern II, and squamates exhibit all three (Valenzuela and Lance 2004). For all three patterns, however, the transition between female-biased and male-biased sex ratios usually occurs over a few degrees of temperature and may be quite abrupt, as seen for two species of turtles in **Figure 9.2**. The **pivotal temperature** is the constant temperature that results in the production of equal numbers of males and females.

Mechanisms of sex determination

The proximate mechanisms of sex determination and sex differentiation of all vertebrates are based on a common toolbox of regulatory gene networks (Place and Vance 2004). The most fundamental difference between reptiles with GSD and TSD is the mechanism that commits the differentiation of gonads irrevocably into testes or ovaries (reviewed by Warner 2011). For reptiles with GSD, sex determination presumably parallels that of mammals, in which a gene located on the Y chromosome and known as *Sex-determining region* (*Sry*) initiates a cascade of events that results in the development of testes. Ovaries develop in the absence of *Sry*, which is why individuals with two X

chromosomes become females. For reptiles with TSD, the temperature-sensitive period begins prior to differentiation of the gonads and extends to the time when their differentiation into testes and ovaries is evident—roughly the middle third of embryonic development.

Temperature presumably affects the expression of genes that convert the steroids deposited in the egg yolk by the mother from one form to another. The steroid precursor of the gonad-differentiating hormones is testosterone. At temperatures that produce males, the enzyme 5α -reductase is induced and converts testosterone to dihydrotestosterone. Dihydrotestosterone binds to androgen receptors on the undifferentiated gonads and triggers their differentiation into testes, which in turn produce additional androgens. These events feed back to increase expression of the gene that produces 5α -reductase, which in turn results in a cascade of events leading to the differentiation of the structures involved in male reproduction.

At temperatures that produce females, the enzyme aromatase is induced, and it converts testosterone to estradiol (an estrogen). Estradiol binds to estrogen receptors on the undifferentiated gonads, triggering their differentiation into ovaries, which in turn synthesize more estrogen. Estrogen production causes a positive feedback that induces additional aromatase production. Once again, the result is a cascade of events, in this situation leading to differentiation of the remaining structures involved in female reproduction.

Adaptive significance of GSD and TSD

Understanding the adaptive significance of the different forms of sex determination has been a challenging research goal for decades. Phylogenetic analyses provide a broadscale perspective on the evolution of TSD and GSD (Figure 9.3). GSD is the ancestral state for vertebrates (Janzen and Krenz 2004; Gamble 2010), while TSD is the probable ancestral state for reptiles (with birds exhibiting an evolutionary reversal to GSD). This conclusion is based on the observation that crocodylians, tuatara, and a majority of turtles exhibit TSD.

The ancestral state of sex determination for squamates is controversial because the mode of sex determination in key taxa is unknown and the deep branches of squamate phylogeny are yet to be resolved (Janzen and Phillips 2006; Gamble 2010). Nonetheless, phylogenetic analyses suggest that TSD may also be the ancestral state for squamates, with snakes exhibiting a reversal to GSD (Pokorna and Kratochvil 2009). Whether or not TSD is the ancestral state for squamates, most squamates are characterized by GSD, and multiple independent transitions between TSD and GSD have occurred in groups such as agamids and gekkotans (Gamble 2010).

GSD conveniently produces the 1:1 sex ratio predicted by Fisher's sex ratio theory: a female should produce equal numbers of male and female offspring when the cost of producing each of the two sexes is similar (Fisher 1930). Life history and environmental circumstances that favor short- and long-term deviations in sex ratio in GSD systems also have a firm theo-



Figure 9.3 Phylogenetic distribution of sex-determining mechanisms in extant tetrapods. Only lineages for which information is available are shown. Yellow branches identify clades where only genetic sex determination (GSD) is currently known. The sex-determining chromosome combinations (XY, ZW) are given when known. Red branches identify clades with temperature-dependent sex determination (TSD), with observed types of TSD (see Figure 9.1) indicated. Clades in which both GSD and TSD occur are shown in green, and the occurrence of parthenogenesis within a clade is indicated by the black hatch marks (records of facultative parthenogenesis are excluded). Branch lengths do not reflect divergence ages or evolutionary rates. (Data from The Tree of Sex Consortium 2014.)

retical basis (Trivers and Willard 1973), and an understanding of the evolution of XY and ZW genetic systems from TSD is emerging (Adkins-Regan and Reeve 2014).

In contrast to that of GSD, the adaptive significance of TSD remains unclear (Bull 2004; Valenzuela 2004). Among many hypotheses proposed to date, that of Eric Charnov and James Bull (1977) has the most general applicability. The Charnov–Bull model proposes that TSD will be advantageous if males and females have their highest fitness associated with different incubation temperatures. For example, Pattern Ia produces males at low temperatures and females at high temperatures. Under the Charnov–Bull model, males that develop at low temperatures should have higher fitness than males that develop at high temperatures, and conversely, females that develop at high temperatures should have higher fitness than females that develop at low temperatures.

That prediction is straightforward, but testing it is difficult. If low temperatures always produce males and high temperatures always produce females, how can one determine if males produced at high temperatures are less fit than males produced at low temperatures? Turk Rhen and Jeff Lang (1995) knew that male hatchling snapping turtles (*Chelydra serpentina*), a Pattern Ia species, grow faster than females. But do males grow faster because they are produced from eggs that experience low temperatures or because incubation at low temperatures produces hatchlings that grow fast regardless of sex?

To resolve this question, Rhen and Lang manipulated the hormonal environment of eggs to reverse the normal effects of temperature on sex determination. Eggs were treated with an aromatase inhibitor to produce males at the high temperatures that normally produce females, and with estradiol to produce females at the low temperatures that normally produce males. The researchers thus were able to compare the growth rates of male and female hatchlings that were produced from eggs incubated at both high and low temperatures. They found that growth rates dur-





in similar directions for males and females. (B) Observations on captive jacky dragons (*Amphibolurus muricatus*) support the Charnov–Bull model. Male fitness, as indexed by the total number of offspring produced during three reproductive seasons, was the highest for individuals incubated at 27°C (left) and female fitness was the highest for individuals incubated at higher and lower temperatures (right). These results match the predictions in the leftmost panel of (A). (After Warner and Shine 2008a; photograph © Melva/Fotalia.) ing the first 28 weeks of life were related only to incubation temperature, irrespective of sex. That is, hatchlings from eggs incubated at low temperatures always grew faster than hatchlings from eggs incubated at high temperatures. Rhen and Lang concluded that males grow more rapidly than females because males are produced at low incubation temperature, not because they are males. Their results are thus in accord with the Charnov–Bull model. The results do not, however, indicate why rapid growth benefits males more than females.

Dan Warner and Richard Shine (2008a) tested the predictions of the Charnov-Bull model for jacky dragons (Amphibolurus muricatus), an agamid lizard with TSD Pattern II (Figure 9.4A). Because jacky dragons have a short lifespan, Warner and Shine were able to assess the lifetime fitness of individuals hatched from eggs incubated at three temperature regimes: 23°C, 27°C, and 33°C, all ± 5°C (Figure 9.4B). These three regimes would normally produce females, equal numbers of males and females, and females, respectively. Warner and Shine used hormone manipulations to produce males at all three temperatures. Hatchings were released into large outdoor enclosures under seminatural conditions where they were monitored for 3.5 years. Sex per se did not directly affect hatchling phenotypes or survival, but incubation temperature had a large affect on lifetime reproductive success. Males from eggs incubated at 27°C-a temperature that normally produces males-sired more offspring over the three reproductive seasons than did males from eggs incubated at 23°C or 33°C, temperatures that normally produce females. In contrast, females from eggs incubated at 23°C or 33°C had more offspring than females incubated at 27°C. This pattern fits predictions of the Charnov-Bull hypothesis: the fitness of each sex is matched to the temperature that normally produces that sex.

Eggs in natural nests experience a daily variation in temperature, so the patterns of sex ratio exhibited under constant temperature conditions in the laboratory are not necessarily the same as those exhibited under natural conditions (Georges et al. 2004). Observations of the jacky dragon illustrate this phenomenon (Warner and Shine 2011). Eggs that were incubated in the laboratory at a constant 25°C produced female-biased clutches, but when the daily temperature cycle was set to vary between 17° and 33°C, clutches became more male-biased. In contrast, eggs incubated at a constant 28°C produced nearly equal numbers of males and females, but with a temperature variation from 20° to 36°C, sex ratios became more female-biased.

Mean nest temperatures of jacky dragons increase during the breeding season and also become less variable. As a result of the interacting effects of mean temperature and variance in temperature, approximately equal numbers of male and female hatchlings are produced during a breeding season. These data emphasize that realistic tests of the adaptive significance of TSD must incorporate information about the effects on sex ratio of both the mean nest temperature and the variance in temperature.

Ecological consequences of TSD

Beyond the challenges of understanding the evolutionary basis for the mode of sex determination in reptiles, the immediate ecological consequences of TSD are considerable. Climate change, including warmer temperatures in many parts of the world, is likely to have a negative impact on many reptiles (Huey et al. 2009; Sinervo et al. 2010), and species with TSD may be especially at risk. For example, 94% of the hatchlings produced over 3 years at one of the major nesting beaches of the loggerhead sea turtle (*Caretta caretta*) were females (Mrosovsky 1994). Because sand temperatures at nest depth remained above the pivotal temperature for most of the three nesting seasons, few males were produced. The narrow range of pivotal temperatures of sea turtles in general (29–30°C) suggests that global warming will have negative consequences on their populations.

While geographic and intrapopulation variation in the pivotal temperature of some species indicates genetic variation on which selection can act in the long term (Rhen and Lang 1998; Ewert et al. 2004), the pace of temperature change under global warming may be too rapid to allow long-lived TSD species such as freshwater turtles and tuatara to avoid extinction through genetically based shifts in their thermal physiology.

TSD species may be able to avoid or reduce bias in sex ratio in response to climate change by adjusting their nesting behavior, at least in the short term (Refsnider and Janzen 2012). To study how a TSD species compensates for variation in climate, researchers in Australia examined nesting parameters of the water dragon Physignathus lesueurii at sites ranging from Cairns in the north to Canberra in the south (Doody et al. 2006). Mean soil temperature at nest depth during the warmest month of the year is 30°C in Cairns and 23°C in Canberra. The researchers found that female water dragons at southern (cool) locations selected unshaded nest sites with high incident radiation, whereas females at northern (warm) locations selected shaded nest sites with low incident radiation. As a result of this behavioral compensation by females, the mean temperatures of nests were the same in the north and south.

Not all species can mitigate climate change behaviorally. Even though female *Bassiana duperreyi* in Australia dug deeper nests and deposited eggs more than a month earlier in 2006–2007 than they did in 1998–1999, the increase in ambient temperature during the intervening decade still produced a 1.5°C increase in nest temperature. As a result, nest temperatures shifted above 20°C—the threshold below which *B. duperreyi* exhibits TSD and the sex ratio is male-biased. Above 20°C, sex is determined genetically and males and females are produced in equal proportions (Telemeco et al. 2009). Increased nest temperatures affect a broad spectrum of phenotypic attributes for *B. duperreyi* and other reptiles. This means that climatic change is likely to have diverse and disruptive impacts on reptiles in general.



Figure 9.5 Hybrid origin of parthenogenetic Aspidosce-

lis species. (A) New species of *Aspidoscelis* are the result of hybridization. *Aspidoscelis neomexicana* (center) arose from a hybridization event involving a female *A. tigris* (top) and a male *A. inornata* (bottom). (B) In typical (canonical) meiosis, a single round of DNA replication is followed by two consecutive divisions that result in a haploid (1*n*) gamete (the oocyte). Crossing over during synapsis generates recombinant chromatids. (C) Meiosis in parthenogenetic *Aspidoscelis* produces a 2*n* egg and maintains heterozygosity. Premeiotic DNA endoreplication allows meiosis to begin with a 4*n* rather than 2*n* comple-

ment. Doubling of chromosomes to 8*n* allows either pairing of homologous (red–blue combinations) or of sister (red–red or blue–blue) chromosomes. Homolog pairing and recombination results in some loss of heterozygosity in the mature oocyte. In contrast, recombination between pairs of sister chromosomes maintains heterozygosity at all loci. Parthenogens exhibit only the latter of these two possibilities. In (B) and (C), only one of two daughter cells from the first division and one of four oocytes from the second division are shown. (After Lutes et al. 2010; photograph by W. B. Neaves.)

The great majority of reptiles reproduce sexually. The benefit of sexual reproduction is that genetic variability is generated by recombination during meiosis, and natural selection can operate on that genetic variation. Nonetheless, about 40 species of squamates in 7 families exhibit asexual reproduction (see Figure 9.3), producing offspring that are genetic clones of their mothers. Most squamates that reproduce asexually are agamid, gekkotan, lacertid, and teiid lizards, but asexuality has been reported in other lineages as well (Kearney et al. 2009). The only snake with asexual reproduction is the typhlopid *Indotyphlops* (formerly *Rhamphotyphlops*) *braminus*. This earthworm-sized "flowerpot" snake has become wideby distributed throughout the tropics as the result of human horticultural activities, and because it is unisexual, a single female can be the founder of a new population.

Like the unisexual amphibian species described in Chapter 8, most unisexual species of squamates share three features (Dawley and Bogart 1989): (1) they originate from hybridization of two or three species; (2) all individuals are female; and (3) reproduction is via clonal inheritance. Unlike amphibians, however, unisexual reptiles do not require sperm to initiate or sustain embryonic development. The form of asexual reproduction in reptiles is **parthenogenesis**: a female animal produces female offspring through a process that does not involve fertilization (i.e., the fusion of gametes from two individuals) (Stenberg and Saura 2009).

Whiptail lizards (Teiidae) in the genera *Aspidoscelis* of the southwestern United States, Mexico, and Central America and *Cnemidophorus* of South America (Reeder et al. 2002) are among the best-studied examples of asexual reproduction by squamates. About one-third of the 50 species of *Aspidoscelis* and *Cnemidophorus* reproduce asexually and unisexual species can be diploid or triploid (Wright 1993).

Diploid unisexual species are the product of hybridization between two bisexual species. Triploid unisexual species are the product of hybridization between a diploid unisexual individual and a male of one of the parental bisexual species or of a third species. The hybrid origin of these and other unisexual species is well documented. Genetic analyses can often identify which bisexual species were parents of the unisexual species as well as the sex of the participating individuals. For example, the unisexual *Aspidoscelis neomexicana* is the result of hybridization between a male *A. inornata* and a female *A. tigris*, and as **Figure 9.5A** shows, is a phenotypic intermediate of its parental species.

Once hybridization occurs, a new reproductively isolated species is formed because hybrid individuals subsequently produce eggs that are genetically identical to their somatic cells. We do not know whether all or only a few hybrid females have the ability to reproduce asexually, nor have we identified the mechanism that shifts reproduction from sperm-dependent to sperm-independent in a single generation (Neaves and Baumann 2011). We do know, however, the mechanism by which diploid (and, by extension, triploid) eggs are produced by *Aspidoscelis* (Cuellar 1971; Lutes et al. 2010). The basic meiotic process is not altered. Rather, chromosomes are replicated prior to meiosis so that cells enter meiosis with an 8*n* chromosome complement (**Figure 9.5C**). The end product of meiosis is thus a 2*n* egg. An evolutionarily important aspect of this process is that the genetically identical sister chromosomes pair prior to the first meiotic division, thus eliminating the possibility of recombination between the genetically dissimilar homologous chromosomes (Lutes et al. 2010). The result is that the heterozygosity resulting from the initial hybridization event is fixed—that is, it persists from generation to generation.

Additional insight into the process by which unisexual species are formed comes from studies of Caucasian rock lizards (*Darevskia*; Lacertidae). Phylogenetic analyses show that the production of unisexual species may be constrained by genetic factors (Murphy et al. 2000). For example, unisexual species are the result of hybridization between members of only two of the three clades of bisexual rock lizards. Moreover, for the five unisexual species, the male is always from one of the clades and the female is from the other. These patterns of origin of asexual reproduction are probably not due to chance. This means that only specific hybridization events represent genetic combinations that produce new asexual lineages.

Unisexual species are of recent origin, perhaps within tens of thousands of years (Moritz et al. 1992). The youthfulness of unisexual lineages matches the expectation that unisexual species will not persist as long as sexual species because, without recombination, new favorable gene combinations cannot arise. The lack of recombination is not an immediate problem for unisexual species, as they are highly heterozygous as a result of their hybrid origins. They will, however, lose fitness more rapidly than sexual species when the environment changes. Unisexual species fill weedy ecological niches (e.g., short-lived habitats) compared with their sexual relatives, and are successful in the short term. They are commonly found in ecotonal habitats, high latitudes and elevations, dry areas, islands, and associated with disturbed habitats and human habitation (Kearney et al. 2009). Heteronotia geckos illustrate this general pattern. The genus is associated with arid environments, but unisexual lineages are found in more arid areas of central Australia than are their sexual parents (Kearney et al. 2003). On a finer spatial scale, coexisting species of Aspidiscelis exhibit high niche overlap and, while unisexual and sexual species may differ in physiological traits, the differences do not vary in any consistent manner (Kearney et al. 2009).

The absence of fertilization in unisexual species does not mean that sexual behavior cannot occur. Unisexual *Aspidoscelis* sometimes engage in pseudocopulation, a behavior in which one female plays the role of the male and the other the female (**Figure 9.6**). Courtship and copulatory behaviors of unisexual *Aspidoscelis* are almost identical to those of closely related sexual species. The same phenomenon, how-





ever, sometimes occurs between females of sexual species of lizards, as it does in dogs, cattle, and other organisms. The continuation of sexual behavior by unisexual species is consistent with the observation that courtship behavior of sexual species of vertebrates enhances gonadal activity (Crews and Moore 1993).

The occasional production of offspring by long-isolated females in captivity was previously attributed to sperm storage. Now that diagnostic genetic analyses are possible, **facultative parthenogenesis** has been documented in 15 species of snakes and 2 species of monitor lizards (*Varanus*) (Kearney et al. 2009). Two cases of facultative parthenogenesis in the wild have been reported: A female water moccasin (*Agkistrodon piscivorous*) and a female copperhead (*A. contortrix*) each gave birth to a single male offspring that had the same microsatellite genotype as its mother over all loci sampled. The chance that these offspring resulted from sexual reproduction is less than 1 in 40 million for the water moccasin, and less than 1 in 1 quadrillion for the copperhead (Booth et al. 2012).

The apparent rarity of facultative parthenogenesis suggests that it is an occasional genetic aberration rather than a mechanism that is advantageous when a female is isolated from potential mates, as in colonization of an island by rafting.

9.3 Reproductive Modes

Reptiles exhibit two reproductive modes, **oviparity**, or egg laying, and **viviparity**, or live bearing. At one time, the term ovoviviparity was used to characterize live-bearing species whose embryos were nourished from materials deposited in the yolk prior to ovulation (**lecithotrophy**), while the term viviparity was restricted to species whose embryos were nourished from materials provided after ovulation via some form of placentation (**placentotrophy** or **matrotrophy**). Because live-bearing species actually represent a continuum between lecithotrophy and placentotrophy, all live-bearing reptiles are best characterized as viviparous (Blackburn 1993, 1994).

Oviparity is the ancestral reproductive mode for vertebrates and for reptiles (Lee and Shine 1998). Among reptiles, all crocodylians and birds, turtles, and the tuatara (Sphenodon punctatus) are oviparous, as are most squamates. Among squamates, viviparity has had more than 100 independent origins, and about 20% of squamate species are viviparous (Shine 1985; Blackburn 1999). Some squamate families are entirely oviparous (e.g., Helodermatidae, Leptotyphlopidae, Pygopodidae, Pythonidae, Teiidae, and Varanidae), others are entirely viviparous (e.g., Acrochordidae, Aniliidae, Shinisauridae, Uropeltidae, and Xantusiidae), and some include both modes of reproduction (e.g., Anguidae, Boidae, Chamaeleonidae, Colubridae, Lacertidae, Phrynosomatidae, Scincidae, and Viparidae). Studies of the evolution of viviparity have focused on closely related oviparous and viviparous species or populations because these taxa represent the most recent origins of viviparity.

Oviparity: Eggshells, eggs, and nests

Reptile eggs are characterized by a sturdy shell that provides mechanical protection for the embryo and makes eggs resistant to water loss while allowing passage of respiratory gases and water vapor. The eggshell has two layers, a mineral layer on the outside and an organic layer beneath (Packard and DeMarco 1991). The mineral layer consists of calcium carbonate (typically in the form of aragonite in turtles and calcite in crocodylians and squamates). The mineral layer is often organized into discrete **shell units** that represent the growth of crystals that form the outer surface of the shell. The organic layer, or **shell membrane**, is formed from multiple layers of proteinaceous fibers.

The structure and relative thickness of the mineral layer and the shell membrane differ considerably among the major groups of reptiles (Figure 9.7). The rigid-shelled eggs produced by crocodylians, some turtles, and some gekkotans have a thick mineral layer made up of closely spaced shell units and a thin shell membrane. The shell units extend into the shell membrane and firmly connect the two layers. In contrast, the flexible-shelled eggs of some turtles and most squamates have a thin mineral layer and thick shell membrane. The mineral layer of these eggshells is not organized into structural units but is deposited on the shell membrane in irregularly placed nodules or plaques that may follow the orientation of the underlying fibers. The flexible-shelled eggs of the tuatara differ from those of squamates in that the shell units of the tuatara egg extend into the shell membrane and attach the two lavers.

Not surprisingly, the structure of the shell has a functional relationship to the movement of water into or out of

Figure 9.7 Structure of reptilian eggshells. These

schematic diagrams show cross sections of some representative reptilian eggshells. (A) Flexibleshelled egg of a snapping turtle (Chelydra serpentina). (B) Rigidshelled egg of a soft-shell turtle (Tryonyx spiniferus). (C) Rigidshelled egg of a crocodylian (Alligator mississippiensis). (D) Flexible-shelled egg of a tuatara (Sphenodon punctatus). The shell has features of both rigid- and flexible-shelled eggs of squamates. (E) Rigid-shelled egg of a tokay gecko (Gekko gecko). The tip (i.e., the inner aspect) of each shell unit is composed of fine, needlelike crystals. (F) Flexibleshelled egg of the zebra-tailed lizard (Callisaurus draconoides). (After Packard and DeMarco 1991.)





Shell units are nodular and regularly shaped, and the mineral layer and shell membrane are about equal in thickness.

(C) Crocodylian



Shell units are wedge-shaped and the shell membrane is thin relative to the mineral layer. The conical tip of a shell unit encloses membrane fibers, anchoring the mineral layer to the membrane.

(E) Lizard (rigid shell)



Shell units are poorly defined. The shell membrane is very thin relative to the mineral layer. The mode of attachment between the mineral layer and the shell membrane has not been determined. (B) Turtle (rigid shell)



Shell units are tall, columnar, and abut tightly. The shell membrane is thin relative to the mineral layer. Shell units extend a short distance into the shell membrane and enclose membrane fibers, thereby attaching the mineral layer and the shell membrane.





The mineral layer consists of irregularly shaped shell units that extend deep into the shell membrane.

(F) Lizard (flexible shell)



The mineral layer lacks shell units. It is thin and rests on the outer surface of the thicker underlying shell membrane; it does not enclose fibers of the membrane.

the egg (Deeming and Unwin 2004). At the time of oviposition, the rigid-shelled eggs of crocodylians, tuatara, and turtles contain all the water that the embryo will need to complete development. Water movement between the egg and its environment is slight in these taxa. In contrast, the flexible-shelled eggs of most squamates contain relatively little water at oviposition, and these eggs must take up water from the environment for successful development. Their shells stretch as the eggs double or even quadruple their mass during development.

Eggs of reptiles vary considerably in size and shape (Iverson and Ewert 1991). The largest eggs, at about 300 g, are laid by large species of pythons, and the smallest, at less than 0.1 g, are laid by tiny species of *Brookesia* chameleons and *Sphaerodactylus* geckos. Reptilian eggs can be characterized as symmetrical ellipsoids, although shape ranges from spherical to elongate and is related to the functional requirements of egg production and oviposition. Lukás Kratochvíl and Daniel Frynta (2006) argue that the rigidshelled eggs of sphaerodactylid, gekkonid, and phyllodactylid geckos are spherical because this shape minimizes the calcium required to produce an egg, and that the flexibleshelled eggs of eublepharid, carphodactylid, diplodactylid, and pygopodid geckos are elongate because this shape maximizes the volume of an egg (and thus the size of the hatchling) that can pass through the pelvic aperture. The egg of the Mbanja worm lizard (*Chirindia ewerbecki*), an amphisbaenid, is 15 times longer than it is wide, and both the egg and the lizard are exceptionally elongate (Iverson and Ewert 1991; Branch 1988).

One of the important behavioral components of successful reproduction is the selection of a nest site where physical conditions will remain suitable during incubation. Eggs may be buried in a mound of decaying vegetation (crocodylians), placed in a constructed nest in the ground (most turtles and lizards), casually buried in debris or secluded in cavities in the ground or in trees (many snakes), or glued to a surface (gekkotans with rigid-shelled eggs).

Once oviposition occurs, the eggs of most reptiles are on their own. To a great extent their success depends on the nest site selected by the female, so it is no surprise that females are selective about where they place their eggs. Females may dig test nests at several locations before they commit to a nest site (Warner and Shine 2008b), and they may migrate considerable distances to nesting areas (Werner 1983; Ferrara et al. 2013). In laboratory studies, gravid females exhibit strong preferences for particular temperature and moisture regimes in their choice of nest sites (Warner and Andrews 2002). The cues used for nest site selection may also include the presence of eggshells or previously laid eggs (Radder and Shine 2007; Mateo and Cuadrado 2012).

Characteristics of viviparous species

If an oviparous female is unable to oviposit at the normal time, embryonic development does not proceed normally. When the eggs are eventually laid, embryos have developmental abnormalities or are dead, and the severity of the impact on development depends on the length of egg retention (Mathies and Andrews 1999; Parker and Andrews 2006). Clearly, viviparous reproduction requires more than simply retaining embryos inside the female until development is complete. Indeed, viviparity is associated with a suite of physiological and morphological adaptations that facilitate embryonic development in the uterine environment.

The **corpus luteum** (plural *corpora lutea*) is a structure formed in all vertebrates from the walls of the ovarian follicle after ovulation. Corpora lutea secrete progesterone, a hormone that inhibits the contractions of the uterine wall that would expel eggs from the oviduct. This secretory activity of the corpus luteum is usually limited to the preovulatory period in oviparous species, but remains active after ovulation in some viviparous species, thus maintaining gestation (Guillette 1987).

Viviparous species also exhibit several features that enhance gas exchange between the mother and the embryos, especially during the last half of development, when the metabolic needs of embryos increase dramatically. Eggshells of viviparous species are extremely thin; the mineral layer is absent, and if the shell membrane is present at all, it is only a few microns thick.



Figure 9.8 Arrangement of the extraembryonic membranes of an oviparous and a viviparous skink. Drawings are of the late growth phase (see Table 9.1, p. 337). (A) The vascularized chorioallantoic membrane of the oviparous eastern three-lined skink (*Bassiana duperreyi*) extends to the abembryonic pole. Its close proximity to the shell facilitates gas exchange between the embryo and the nest environment. The connection of the embryo and the allantoic sac is not illustrated, but the development of the allantois is shown in Figures 9.15 and 9.16. (B) The egg of the viviparous metallic skink (*Niveoscin*-

cus metallicus) is bounded externally by the uterus; a thin shell membrane is present, but only early in development. The chorioallantoic membrane and uterus are in direct contact on the embryonic pole of the egg, forming a chorioallantoic placenta. On the abembryonic pole, a nonvascular membrane composed of ectoderm and endoderm (the omphaloplure) interfaces with hypertrophied epithelial cells of the uterus and tissues associated with the yolk sac to form a yolk sac placenta (the omphaloplacenta). (After Stewart 2013.) Vascularization of the extraembryonic chorioallantois membrane increases commensurately with growth of the embryo toward the end of gestation (Parker et al. 2010). The vascularized tissues of the uterine wall and chorioallantoic membrane are closely adpressed and form a chorioallantoic placenta (**Figure 9.8**). The chorioallantoic placenta functions largely in gas exchange, and in highly placentotrophic species it also appears to transport nutrients to the embryo. A placenta formed from the yolk sac is a feature unique to squamates (Stewart 2013) and is implicated in nutrient secretion by the uterus and nutrient absorption by embryonic tissues (Thompson et al. 2006).

While the yolk is the source of nutrients (lecithotrophy) for all oviparous species and most viviparous squamates, nutrients including amino acids and inorganic ions are transferred to the embryo from the mother, and nutrient transfer can make up a nontrivial fraction of the caloric and nutrient requirements of embryos (Blackburn 2000; Thompson and Speake 2006; Stewart 2013). At its extreme, reptilian placentotrophy is convergent with mammalian placentotrophy. For example, eggs of the African skink Trachylepis ivansii are only about 1 mm in diameter, and the nutrients that sustain the developing embryo are provided entirely through placental transport (Blackburn and Fleming 2012). What is most extraordinary about this species, however, is that the embryo becomes implanted into the tissues of the uterus and a placenta is formed with the embryonic epithelium in direct contact with maternal capillaries.

The evolution of viviparity

Viviparity in reptiles poses three central questions:

- 1. Why are squamates the only viviparous reptiles?
- 2. What is the nature of the transition between oviparity and viviparity?
- What environmental conditions favor the evolution of viviparity?

WHY ARE SQUAMATES THE ONLY VIVIPAROUS REPTILES?

Egg retention in the oviducts is a critical component of the transition between oviparity and viviparity, and crocodylians, birds, turtles, and the tuatara share a common feature that precludes extended egg retention. In these groups, normal embryonic development proceeds only after the eggs are deposited. For crocodylians and birds, development is initiated in the oviduct, but embryogenesis is abnormal if eggs are not laid while embryos are at early developmental stages. For turtles and the tuatara, development is arrested in the oviduct at very early embryonic stages and does not resume until the eggs are laid. In contrast, squamates are predisposed for viviparity because development is initiated at fertilization, and by the time of oviposition embryos have reached limb bud stages (Andrews 2004).

Research by Anthony Rafferty and his colleagues (2013) provides a functional explanation for developmental arrest of turtle embryos in utero. Following observations indicating that developmental arrest is associated with hypoxia (Kennett et al. 1993; Fordham et al. 2006; Parker and Andrews 2006), Rafferty threaded fiber-optic oxygen probes through the cloaca and into the oviducts of four species of turtles and directly measured oxygen partial pressures adjacent to eggs. Oxygen partial pressures ranged from 1.6 to 5.9 mm Hg (0.2 to 0.8 kPa), values substantially lower than those estimated for squamates (Parker and Andrews 2006).

Rafferty et al. (2013) collected oviductal fluids that dripped from the cloaca of sea turtles as they deposited eggs and found that diffusion of oxygen in the fluids is very slow. When exposed to an atmosphere of 100% oxygen, the pressure of oxygen in oviductal secretions increased by only 1.9 mm Hg/min (0.2 kPa/min), while oxygen pressure in a physiological saline solution increased by 14.2 mm Hg/min (1.9 kPa/min) under the same conditions. Thus, the fluids surrounding eggs in the oviduct greatly limited oxygen diffusion into the egg and help explain why turtle oviducts are hypoxic.

While other factors such as eggshell structure and oviductal vascularization may contribute to hypoxia, clearly the composition of oviductal fluids limits how much development can occur before oviposition for turtles, and perhaps for other reptiles as well. This is an intriguing issue because viviparity is not only unevenly distributed among major groups of reptiles, but among squamate taxa as well (Andrews and Mathies 2000).

WHAT IS THE NATURE OF THE TRANSITION BETWEEN OVI-PARITY AND VIVIPARITY? Only a few decades ago, oviparity and viviparity appeared to be discrete reproductive modes: either eggs were deposited when embryos were at limb bud stages of development, or eggs were retained in the female until development was completed. Today, however, several studies comparing closely related oviparous and viviparous taxa support the idea that viviparity evolves through gradual increases in the length of time that eggs are retained in the oviduct. For example, the Mexican phrynosomatid lizard Sceloporus aeneus is oviparous, whereas its sister species S. bicanthalis is viviparous (Guillette 1982; Lambert and Wiens 2013). The European common lizard (Zootoca vivipara) is viviparous throughout most of its wide distribution in Europe and Asia, but some populations in Spain, France, Italy, Austria, Slovenia, and Croatia are oviparous (Surget-Groba et al. 2006). In Australia, some populations of the skinks Lerista bougainvillii (Qualls and Shine 1995) and Saiphos equalis (Smith et al. 2001) are oviparous while others are viviparous. In all three of these examples, the oviparous taxa exhibit transitional characteristics between fully oviparous species and fully viviparous species. The transitional characteristics of the oviparous taxa include:

- 1. Relatively long periods of egg retention
- 2. Relatively short incubation periods
- 3. Relatively thin eggshells
- The ability to extend egg retention without impairing development

WHAT ENVIRONMENTAL CONDITIONS FAVOR THE EVO-LUTION OF VIVIPARITY? The evolution of viviparity is one of the most important and enduring topics in herpetology (Shine 2014). Its conceptual history began when researchers in the early 1900s noted that the proportion of viviparous species increases on both latitudinal and elevational gradients such that all species are viviparous at the highest latitudes and elevations where squamates occur. Moreover, viviparous populations or species are found in colder climates than their oviparous close relatives (Guillette 1982; Qualls and Shine 1995; Smith et al. 2001; Surget-Groba et al. 2006).

Geographic distributions of recent origins of viviparity provide compelling support for the hypothesis that viviparity is not merely associated with cold climates but that it evolves there (Shine and Bull 1979; Lambert and Wiens 2013). In general, the cold climate hypothesis proposes that viviparity is adaptive in cold climates because embryos retained in a thermoregulating female experience warmer and less variable temperatures than embryos developing in a nest at the same location. As a consequence, the rate of development is enhanced and the embryos are protected from the detrimental effects of both high and low temperature extremes (Packard et al. 1977; Tinkle and Gibbons 1977; Shine 1985). A critical component of the cold climate hypothesis is that the initial stages of extended egg retention are adaptive. For example, even small increases in the rate of embryonic development for oviparous females would result in earlier hatching, which would give neonates extra time for growth and fat storage before winter.

Important insights into the evolution of viviparity are derived from the observation that incubation temperature affects a wide diversity of phenotypic characters of hatchlings, including body size and shape, color, physiology, and behavior (Deeming 2004; Rhen and Lang 2004; also see Section 9.6). Richard Shine's maternal manipulation hypothesis proposes that females should select body temperatures while gravid or pregnant that enhance developmental rates or survival of their offspring and their phenotypic quality (Shine 1995, 2014). For example, oviparous female European common lizards select body temperatures that are 2°C lower when they are gravid than those selected when they are not gravid. When gravid females select relatively low body temperature, they increase egg survival and hatchling running performance relative to that of hatchlings from gravid females forced to maintain the relatively high temperature of nongravid females (Rodríguez-Díaz and Braña 2011). Because viviparous females retain embryos until birth, they have an even greater opportunity to enhance the phenotypes of their offspring through their thermoregulatory behavior than do oviparous females.

Viviparity is not restricted to cold climates, however. For example, some viviparous species in the lizard genus *Sceloporus* have ranges that include both cool montane habitats and hot, arid scrub habitats at low elevations in Mexico (Mendez et al. 1998). Similarly, although all xantusiid lizards are viviparous, some species are found in cool montane habitats while others inhabit the arid lowland deserts of Mexico and the American Southwest. This observation suggests that, once evolved, viviparous species can successfully invade a wide range of habitats. The alternative explanation for the presence of viviparous species in warm climates is that viviparity has evolved there. Although little support exists for this alternative hypothesis (Shine 1985), modern phylogenetic approaches have the potential to determine whether in fact viviparity has evolved independently within lineages of exclusively warm-adapted taxa.

9.4 Parental Care

Parental care (in a narrow sense) consists of the behaviors exhibited by parents after egg deposition or birth that enhance the survival of offspring (Shine 1988). Females are typically the caregiver in reptiles, presumably because parental care is most likely to evolve in the sex that is most closely associated with the eggs (Gross and Shine 1981). Because fertilization is internal, and eggs require time in the oviduct for shell deposition, typically only the female is present when the eggs are laid. In general, the evolution and persistence of parental care depend on the balance between its benefits to the eggs or young (increased survival) and its costs to the attending parent (investment of time and energy, reduced survival, and reduced future reproductive output). The potential benefits of parental care should be greatest for species in which reproductive output is already limited for other reasons. If one clutch per season is the norm, for example, then increased investment in that clutch might not reduce reproductive output appreciably.

The occurrence of parental care may also be related to its effectiveness. Consider defense of nests and hatchlings by turtles (which rarely exhibit parental care) and by crocodylians (where parental care may be universal). Turtles are generally small and incapable of inflicting damage on a nest predator. In contrast, adult crocodylians are large and formidable and can effectively defend nests and young.

When nesting *Manouria emys* (a tortoise from Southeast Asia) were confronted with human and simulated animal predators, the females either positioned themselves on top of the nest or pushed the intruder away from the nest. They did not bite, and nest-guarding behavior lasted only 2 or 3 days (McKeown et al. 2013). After nesting communally on sandbars in Brazil's Trombetas River, females of the South American river turtle (*Podocnemis expansa*) remain in the vicinity of the nesting beaches. Hatchlings begin vocalizing just prior to hatching. When the hatchlings enter the water, females are attracted by their vocalizations, and both hatchlings and adults migrate together into seasonally flooded forests. Hatchlings clearly benefit by being guided from nesting beaches to feeding grounds by adults (Ferrara et al. 2013). Parental care by crocodylians is extensive, and although females usually are the caregivers, males can be involved (Lang 1987). Females typically remain near the nest site after oviposition and defend it against potential predators. Vocalization by the young at the end of the incubation period attracts the female or both parents to the nest. Adults open the nest, help the hatchlings escape from the eggshell, and carry them to water (**Figure 9.9**). Young crocodylians remain together for a year or more and are attended by one or both parents during this time. Distress calls by hatchlings stimulate defensive behaviors by adults (Vergne et al. 2011).

The small size and limited defensive options of most squamates explain why only about 3% of oviparous snakes and 1% of oviparous lizards exhibit parental care (Shine 1988). Most snakes that exhibit parent care are large, venomous, or both, and can defend eggs even from vertebrate predators. Attendance of eggs or young is commonly reported for elapids, and may be universal for crotalines and pythonids (Stahlschmidt and DeNardo 2011). Early studies of egg attendance by pythonids documented that female pythons coil

(A)



(C)



Figure 9.9 Parental care by the mugger crocodile (*Crocodylus palustris***).** (A,B) As the eggs begin to hatch, the male parent excavates the nest and assists the juveniles to emerge

tightly around the clutch and warm the eggs by muscular thermogenesis (see Figure 6.27). More recently, comprehensive laboratory and field studies have revealed that muscular thermogenesis is a specialized and derived behavior of only some python species (Stahlschmidt and DeNardo 2011).

Pythons that do not exhibit muscular thermogenesis nonetheless exhibit a diversity of behaviors that regulate the thermal and hydric dynamics of the clutch. Female water pythons (*Liasis fuscus*) in the Northern Territories, Australia, reduce the rate that the clutch cools in the evening by coiling tightly around the clutch, and increase the rate of heating in the morning by exposing the clutch to the air. Females leave the nest to bask in the sun during the day and then transfer heat to the clutch when they return (Stahlschmidt et al. 2012). Female pythons also reduce water loss when relative humidity is low by coiling more tightly around the clutch (Lourdais et al. 2007). These behaviors benefit the young by enhancing development and hatching success. However, the prolonged period of egg attendance has a cost: female pythons do not feed during this time,



(D)



from the egg. (C,D) The male uses his mouth to carry the hatchlings to the water, which is about 9 m away. (Photographs courtesy of Jeffery Lang.)



and the length of clutch attendance is negatively related to reproductive frequency and post-reproductive body condition (Stahlschmidt and DeNardo 2011).

Attendance of young is now well documented for rattlesnakes in temperate North America (**Figure 9.10**). Females remain with their young at the birth site until the young shed and disperse (Greene et al. 2002). Given that females normally feed infrequently, staying with the young for 2 weeks is not a great cost relative to the potential increase in the young's survival.



Figure 9.10 Arizona black rattlesnake (*Crotalus cerberus*) attending offspring. A female and two offspring are basking outside a communal nest site where two females gave birth. (Photograph by Melissa Amarello, SocialSnakes.org.)

The most common type of parental care by lizards is egg attendance. Egg attendance is characteristic of anguids (Greene et al. 2006) and scincids in the genus *Plestiodon* (formerly *Eumeces*) (Shine 1988). Females remain with the eggs in cavities under rocks and bark; parental activities include licking the eggs, removing eggs infected by microbes, regulating water uptake, attacking invertebrate and vertebrate intruders, and reassembling eggs if the nest is disturbed (Somma and Fawcett 1989; Hecnar 1994).

In Morocco, Oudri's fan-footed gecko (*Ptyodactylus oudrii*) nests communally, and adults are associated with eggs year-round; in the laboratory, at least, eggs have higher survival when they are associated with adults than when adults are not present (Mateo and Cuadrado 1998, 2012). Females, males, and subadults attend eggs by rubbing their bodies against them and by licking them, behaviors that could reduce desiccation or remove pathogens.

Varanus rosenbergi and a few other species of large varanids use termites to babysit their eggs. Females dig into termite mounds and lay their eggs inside (King and Greene 1999). When the termites reconstruct their mound, its hard walls protect the eggs, and the interior is a warm and humid site for incubation. Female *V. rosenbergi* defend their nest from other varanids for 1 to 3 weeks after oviposition (Rismiller et al. 2010). While hatchlings of some termite-mound nesters

Figure 9.11 Clutch defense by the skink *Eutropis longicaudata.* (A) Female guarding eggs in drain pipe. (B) Clutch of eggs. (C) An egg-eating snake (*Oligodon formosanus*, on the left) that entered a drain pipe is attacked by the attending female. (Photographs: A, Kevin Messinger; B–C, Wen-San Huang.)





may be able dig themselves out of nests in termite mounds, *Varanus varius* females return to their nests and open the termite mounds so that hatchlings can escape (Carter 1999).

Typically, parental care (or its absence) is a species-specific trait. The long-tailed skink (*Eutropis longicaudata*) is a notable exception (**Figure 9.11**) (Huang et al. 2013). Females on Orchid Island near Taiwan exhibit egg attendance, while females in other populations throughout Southeast Asia abandon their clutch after oviposition. This difference is probably related to the relatively high abundance of the specialized egg-eating snake *Oligodon formosanus* on Orchid Island, combined with the low diversity of lizard-eating snakes in that location. Thus, female skinks on Orchid Island can defend their nests at low risk to their own survival, whereas fe-



males elsewhere cannot. Parental care is facultative: females guard eggs longer when the abundance of *Oligodon* is high than when it is low, and females from other populations exhibit egg-attending behavior if released on Orchid Island as hatchlings. These observations suggest that the expression of egg guarding is a function of the experience of females with egg and lizard predators prior to and during nesting.

9.5 ■ Reproductive Anatomy, Gametes, and Sperm Storage

All reptiles have internal fertilization. The shift from external to internal fertilization must have been associated with the shift from a jelly egg to an amniotic egg; ova of amniotes must be fertilized before the shell is deposited on the egg. Internal fertilization is accomplished with different structures in the major reptilian groups. Male turtles and crocodylians have a penis that lies in the floor of the cloaca.

In contrast, a penis apparently was absent from the lineage leading to extant lepidosaurs. The tuatara (*Sphenodon punctatus*) lacks a distinctive intromittent organ, although possible homologs to the squamate hemipenes are present (see Chapter 4); internal fertilization is accomplished by cloacal apposition, as in birds. Squamates have evolved unique intromittent organs—hemipenes—that develop as paired evaginations from the rear wall of the cloaca (**Figure 9.12A**). When engorged with blood, a hemipenis is everted, turning inside out and exposing a surface ornamented with folds, papillae, or mineralized spines (Dowling and Savage 1960).

as the testes are displaced so they do not overlap. (A, photograph ©

Scott Camazine/Alamy: B after Shine 1991.)





Figure 9.13 Functional regions of a turtle oviduct. Gross morphology of the oviduct of a gopher tortoise (*Gopherus polyphemus*). (After Palmer and Guillette 1992.)

Only one hemipenis is used during copulation. Male green anoles (*Anolis carolinensis*) tend to alternate hemipenes in successive matings (Crews 1980). Because the left and right reproductive tracts of males are independent, alternation of the hemipenes may ensure an adequate number of sperm for each mating. Less explicable, however, is the observation that the male uses his right hemipenis if the ovum ready to be fertilized is on the right side of the female, and vice versa. Which sex controls this behavior is unknown.

The basic internal anatomy of reptiles is typical of vertebrates in general. In snakes and snake-shaped lizards, however, the placement and shape of organs has been reorganized so that they fit within an elongate body (**Figure 9.12B**). The kidneys, testes and ovaries, and oviducts, for example, are elongate and are placed asymmetrically along the body. In some lizards and snakes, the left oviduct is vestigial or absent altogether and in snakes the left lung is greatly reduced in size. As in other vertebrates, spermatogenesis occurs in the testes, and mature sperm are found in the testes and vas deferens. Observations of the lizard *Aspidoscelis sexlineatus* suggest that final structural maturation of sperm occurs in the oviduct (Newton and Trauth 1992). Sperm flushed from males (from the vas def-

erens) had midpieces so strongly bent that the sperm rotated with their midpieces forward. In contrast, sperm flushed from females (from the oviducts) had straight midpieces and rotated normally with their acrosomes forward.

Oogenesis occurs in the ovary, where ova (oocytes) are provided with yolk that is synthesized in the liver (**vitellogenesis**) and transported to the maturing ova by the circulatory system. Yolk is largely composed of lipids and proteins. As in most vertebrates, ova released from follicles enter one of the paired oviducts by way of its anterior opening, the ostium. At the time of ovulation, the ostium envelops the ovary and ensures that the mature ova enter the oviduct. The oviduct consists of four sections: infundibulum, tube, uterus, and vagina (**Figure 9.13**). In turtles and other reptiles with large clutches oviducts are elongate, while in species with a clutch of one egg, the oviducts are highly compact.

Fertilization occurs when ova enter the oviduct and pass through the infundibulum. The inner boundary layer of the eggshell is probably deposited on the ovum in the posterior





and ciliated neck portion (Np). The distal portion of the tubule (Dp), which lacks secretory and ciliated cells, serves as the primary sperm storage area. Note the crowded cluster of sperm aligned together along their long axes (Splu) in the lumen of the Dp. (C) Light micrograph of the distal portion of a sperm storage tubule, illustrating random arrangement of sperm in the lumen. (From Sever and Hamlett 2002.) portion of the infundibulum or in the tube (Guillette et al. 1989). In crocodylians and turtles, a layer of albumen is deposited on the egg in the tube (Palmer and Guillette 1988, 1992); squamate eggs do not contain albumen (Blackburn 1998; Sever and Hamlett 2002). The fibrous shell membrane and the mineral layer of the shell are deposited on eggs in different regions of the oviduct in crocodylians and sequentially in a single region of the uterus in turtles and lepidosaurs (Palmer and Guillette 1992). The uterus also accommodates eggs prior to oviposition and supports gestation in viviparous species. The vagina acts as a sphincter that keeps eggs in the oviduct.

Fertilization may be closely associated in time with copulation. This association is not obligate, however. Female reptiles commonly store sperm in their reproductive tract, and stored sperm are used to fertilize eggs if males are not present or to accommodate disassociated reproductive cycles (see Section 9.7). Sperm are stored at several locations in the oviduct. In turtles and alligators, sperm storage tubules are found in the tube just anterior to the utero-tubal junction and in the uterus just anterior to the utero-vaginal junction (Sever and Hamlett 2002; Gist et al. 2008). In the former location, glands that normally secrete albumen serve as sperm storage tubules. Sperm storage in alligators is limited to the current reproductive season, but female turtles can retain viable sperm for years.

In squamates, the most common (and ancestral) location for sperm storage is in the posterior infundibulum. Iguanian lizards have secondarily evolved sperm storage tubules at the utero-vaginal junction in the posterior oviduct (**Figure 9.14**), and some iguanians have such tubules in both areas (Sever and Hamlett 2002). In cases where sperm are stored in the posterior oviduct, they must move out of storage tubules and up the oviduct to reach unfertilized ova prior to shell deposition. The stimulus that initiates the migration of sperm through the lumen of the oviducts is unknown. The length of sperm storage in squamates is highly variable.

9.6 Embryonic Development

All reptiles have direct development that culminates in the hatching or birth of a small and independent version of the adult. Development involves epigenetic processes, that is, mechanisms that alter the expression of genes, not the genes themselves. Patterns of gene expression thus ultimately determine the sequential unfolding of the phenotype. Numerous environmental factors contribute to the production of a normal phenotype, including temperature, nutrients and water, and hormones deposited in the yolk (Gilbert and Epel 2009). Important facets of evolutionary studies include the assessment of how environmental factors affect the phenotype of individuals and how selection acts to optimize phenotypic outcomes.

Embryos are not simply passive responders to their genetic and physical environment; they exhibit a complex array of physiological and behavioral responses that can enhance development and mitigate stress (see Chapter 6). Turtle embryos exhibit thermoregulatory behavior by moving from the cool to the warm side of the egg (Du et al. 2011), and python eggs exhibit more rapid heating than cooling rates, indicating that embryos have regulatory capabilities (Du et al. 2013).

Differentiation and growth

Development of an embryo from a single diploid cell to a self-sufficient complex multicellular organism is the result of both differentiation of cells and increase in the number of cells. **Table 9.1** presents a general sequence of development for reptiles (and to a large extent, other amniotes as

Diagnostic event introducin Phase phase		Events characterizing phase	
Cleavage	Mitotic cell division	Cell division produces a blastula	
Gastrulation	Epiboly and involution of cells through blastopore	Germ layers (endoderm, ectoderm, mesoderm) form	
Neurulation	Neural plate	Head differentiation, amniotic head fold, somites, blood islands	
Organogenesis (see Figure 9.15)	Torsion initiated, head on left side	Major organ systems established (circulatory, nervous, digestive, respiratory, etc.); amnion, chorion, and yolk sac completed; limb buds formed	
Early growth (see Figure 9.16)	Apical ectodermal ridge forms on limb buds	Chorioallantoic membrane completed; limbs, gonads, and hemipenes differentiated	
Late growth	Lower jaw reaches end of snout	Embryo mass increases substantially; eyelids, scales, pigmentation, and egg tooth form; extraembryonic membranes retracted; yolk absorbed	
Hatching	Pipping	Embryos may rest in opened shell for hours, days, or longer before leaving eggshell	

TABLE 9.1 Major phases in the embryonic development of reptiles

After El Mouden et al. 2000; Andrews 2004.



Figure 9.15 Representative events of lizard development during

organogenesis. Drawings here and in Figure 9.16 are of several species, including Chamaeleo alyptratus, Chondrodactylus turneri, Eublepharus macularis, and Uta stansburiana. Drawings are not to the same scale. Stage numbers are from Defaure and Hubert 1961. (A) The embryo is 2.5 mm long from head to vent. Torsion reaches midtrunk, the large opening in the head region is the neural tube. (B) First appearance of allantois. The heart forms outside body cavity. (C) First appearance of the limb buds. (D) The allantois and limb buds enlarge, and the iris is pigmented. (From Andrews et al. 2013.)

well). Roughly the first half of the developmental period is characterized by differentiation: the commitment of cells to become specific tissues, organs, and structures. By middevelopment (around the beginning of the late-growth stage in Table 9.1), reptile embryos are small but recognizable as turtles, crocodylians, snakes, or lizards. The second half of the developmental period is characterized by a substantial increase in the mass of the embryo, as well as by the maturation of tissues and organs (Andrews 2004).

CLEAVAGE AND GASTRULATION The earliest phases of development are cleavage (mitotic divisions of the diploid cell formed by fertilization to form an undifferentiated multicellar blastula) and gastrulation (organization of cells into the three germ layers—ectoderm, mesoderm, and endoderm). The ectoderm gives rise to neural and epithelial tissues; the endoderm to the gut, liver, pancreas, and lungs; and the mesoderm to the heart, blood, skeleton, muscles, and reproductive system.

NEURULATION The rough outlines of the body plan become apparent during neurulation, with demarcation of the head, neural tube, and somites (blocks of tissue along the embryonic spine) and with separation of the tissues that form the embryo *per se* from those that form three of the four extraembryonic membranes (the amnion, chorion, and definitive yolk sac).

ORGANOGENESIS During early organogenesis, the embryo lies with its ventral surface above the yolk sac. With the onset of torsion, the embryo rotates to its left side. Torsion allows the right and left sides of the embryo to come together to form the gut and close the body wall (Figure 9.15A). The amnion, chorion, and yolk sac are completed during organogenesis. The amnion becomes a fluid-filled sac that surrounds the embryo and buffers it physically and physiologically. The chorion, the outermost membrane, covers the inner surface of the eggshell. The vascular system of the yolk sac transports nutrients from the yolk to the embryo. During mid-organogenesis, the allantois first appears as a small outgrowth of the hindgut and becomes a thin-walled vesicle as it enlarges (Figure 9.15B,C), and limb buds are visible as low ridges (Figure 9.15C). By the end of organogenesis, the iris is pigmented and the limb buds protrude as flattened stumps (Figure 9.15D).

EARLY GROWTH The early growth phase of embryogenesis is characterized by differentiation of the appendages, jaws, gonads, and hemipenes (**Figure 9.16**). The apical ectodermal ridge, a major signaling center for the developing limb, forms on the margin of the limb buds. The allantois expands to lie beneath the chorion and fuses to it, forming the chorioallantoic membrane (see Figure 9.16A). By the end of the early growth phase, this vascularized membrane cov-



Figure 9.16 Representative events of lizard development during early growth. (A) The allantois contacts the chorion to form the chorioallantoic membrane. This is the first appearance of the apical ectodermal ridge (AER). The embryo is 4.3 mm long from head to rump. (B) Differentiation of limb struc-

ers the inner surface of the shell and serves as the embryo's lung. Before oviposition, gas exchange takes place between the chorioallantoic membrane and the vascularized oviduct; after oviposition, gas exchange occurs between the chorioallantoic membrane and the atmosphere of the nest chamber. The allantoic sac itself serves as a storage site for waste products formed from the metabolic breakdown of protein and other materials, as well as a repository for water.

LATE GROWTH During the last half of development the embryo increases dramatically in size. Embryos of the gecko *Phyllodactylus marmoratus*, for example, increase in dry mass by 90% of their hatchling mass during the last 50% of their total developmental time (Thompson and Russell 1999).

Developmental events that prepare the embryo for its departure from the egg include the formation of a mineralized egg tooth and internalization of the extraembryonic membranes. Observations of *Varanus rosenbergi* by Nadav

tures from the apical ectodermal ridge. (C) Mandibular processes fuse to form the incipient jaw. (D) Hemipenal buds form just anterior to the cloaca (vent). The tail has been removed near its base (large white area) to enhance visibility. (From Andrews et al. 2013.)

Pezaro and colleagues (2013) document how the embryo frees itself from the enveloping membranes. When the embryo slits the amnion, elastic forces in the previously stretched membrane pull it down and around the embryo, much as a swimmer peels off a wet swimsuit. Retraction of the amnion detaches the chorioallantois from the surface of the eggshell and pulls it after the amnion (**Figure 9.17A**). As a result, all the extraembryonic membranes are gathered together at one end of the intact egg, with the amnion forming a sleeve over the yolk sac (**Figure 9.17B**).

At this point, the embryo slashes or breaks the shell (pips the egg) with its egg tooth and pushes its head out. Embryos remain in this position over the next few hours; inside the egg, muscular contractions of the amnion push the yolk sac and the inner allantoic membrane into the abdominal cavity. The umbilical opening then closes, leaving part of the chorioallantoic membrane behind. This is all that remains in the shell after the yolk is internalized and hatching occurs.



Figure 9.17 Varanus rosenbergi embryos divesting extraembryonic membranes in preparation for hatching. (A) An egg opened during the early stages of hatching shows the position of the extraembryonic membranes after pipping but before emergence from the eggshell. The chorioallantois has been pulled completely off the surface of the eggshell, and the yolk sac, amnion, and chorioallantoic membranes have accumulated at the abembryonic pole of the egg. (B) The amniotic sleeve during internalization of the residual yolk. The partially internalized yolk sac (yellow ball) is visible through the amnion. The chorioallantoic membrane is situated at the top of the structure and connected to a portion of amniotic sleeve that no longer contains any yolk sac. Also visible is the allantoic vein running from the umbilical opening between the yolk sac and the internal surface of the amniotic sleeve connecting to the chorioallantoic membrane. (Photographs by Nadav Pezaro.)

HATCHING Once embryos are free of the extraembryonic membranes, they are presumably hatching-competent. For some species, disturbance of eggs by a potential predator just prior to hatching provokes premature hatching and allow the neonates to escape. Leaving the egg early, however, is not cost-free. Eggshells of the Australian skink *Lampropholis delicata* that hatched in response to disturbance contained globs of yolk, and hatchlings were relatively small. In contrast, hatchlings from eggs that were not disturbed and hatched normally had completely internalized yolk and were larger in body size (Doody and Paull 2013).

Genetic regulation of development

The reason for the similarities in development among reptiles and other vertebrates is that the basic pattern of development is directed by a common set of **Hox genes** regulatory genes whose products are expressed in specific locations on the long axis of the embryo. Hox genes initiate a cascading expression of other regulatory and structural genes that specify trunk regionalization and limb position during embryonic development. Among other effects, mutations to Hox genes provide the basis for the reduction and loss of limbs in many reptiles (Cohn and Tickle 1999).

Reduction and loss of limbs are typically associated with body elongation and have occurred numerous times among squamates. While the pectoral girdle and forelimbs may be completely absent, some remnants of the pelvic girdle are always present in lizards and amphisbaenians, no matter how reduced the limbs are. In snakes, the pectoral girdle and forelimbs are never present, but some species in basal groups (Aniliidae, Typhlopidae, Leptotyphlopidae, and Boidae) retain rudimentary hindlimbs (Kearney 2002).

Studies by Martin Cohn and Cheryll Tickle (1999) provide a mechanistic explanation for the absence of forelimbs and the extreme reduction in size of the hindlimbs of pythons and other squamates with reduced limbs (**Figure 9.18**). Pythons have more than 300 vertebrae, with ribs on every vertebra anterior to the hindlimbs except the atlas. In essence, the entire trunk resembles an elongated thorax because the Hox genes that specify thorax development (*Hoxc6, Hoxc8,* and *Hoxb5*) are expressed from the most anterior somite to just before the cloaca. The expansion of thoracic identity both anteriorly and posteriorly accounts for the absence of forelimbs and for the elongation of thorax in the axial skeleton.

Hindlimb buds develop at the level of the cloaca just beyond the expression of *Hoxc6*, *Hoxc8*, and *Hoxb5*. The genetic specification of hindlimb position and the initiation of limb bud formation in pythons is normal and similar to that of other tetrapods. What is not normal is that the apical ectodermal ridge of the limb bud, a structure critical for development of a normal tetrapod limb, degenerates early in bud formation (Raynaud 1985). Because of this degeneration, genes responsible for limb development are not expressed, and hindlimbs fail to develop fully. The occurrence of similar gene-expression patterns in other limbless squamates (e.g., *Anguis*; Anguidae) suggests a common basis for the widespread occurrence of limb reduction in squamates and, simultaneously, a mechanism for rapid evolution of this major morphological transformation (Wiens et al. 2006).

Phenotypic plasticity in development

Phenotypic plasticity is the capacity for a genotype to express more than one phenotype depending on environmental conditions. Temperature-dependent sex determination (see Section 9.1) is an example of a phenotypic plasticity. In this case, genetically identical individuals express one of

Figure 9.18 Limb development of

snakes. (A, B) Whole-mount antibody staining showing Hox gene expression (darkly stained cells) in chicken and python embryos. Gene expression is indicated by darkly staining cells. (A) In a stage 25 chick embryo, Hoxc8 expression is restricted to the thoracic region. Arrowheads show the anterior and posterior boundaries of expression. (B) In the python embryo at day 1 of incubation, expression of Hoxc8 (arrowheads) extends throughout the trunk posteriorly as far as the hindlimb bud, at which point there is a sharp posterior boundary of Hoxe8 expression. (C, D) Scanning electron micrographs comparing apical ectoderm in chicken and python embryos at days 5 and 4 of incubation, respectively. (C) The chicken embryo exhibits a distinct apical ectodermal ridge (AER) between the dorsal and ventral surfaces of the limb bud. (D) The python limb bud lacks an AER. (From Cohn and Tickle 1999.)



two phenotypes (male or female) depending on temperature during development. More usual, however, is expression of a continuous range of phenotypes in response to variation in environmental conditions during incubation.

Hatchlings of the skink *Bassiana duperreyi* were subjected to simulated predator attacks 16 times over 4 days (Amiel and Shine 2012). The animals were judged to escape successfully if they entered a refuge within 30 seconds. When eggs were incubated under relatively warm conditions, hatchlings were more likely to escape in the last eight trials than in the first eight trials—that is, they exhibited learning with experience. In contrast, when eggs were incubated under relatively cool conditions, hatchlings did not improve their performance between the first and last sets of eight trials.

The observation that environmental conditions during embryonic development can affect an individual's phenotype later in life raises an important question. Are phenotypic differences produced by variation in environmental factors related to an individual's evolutionary fitness? Brett Goodman and colleagues (2013) asked if phenotypic plasticity could provide a mechanism for adaptation to specific habitat features. Their research subject, the skink Carlia longipes, occupies diverse habitats in northeastern Australia that include both rocky areas where nest sites are relatively cool and forests where nest sites in the litter are relatively warm. The researchers collected females from an area that had both habitats and incubated eggs at nest temperatures corresponding to each habitat. Cool-incubated hatchlings were larger, had longer limbs, and had faster size-adjusted running and climbing speeds than warm-incubated hatchlings. Most important, hatchlings selected the habitat where they had a morphological advantage! The cool-incubated hatchlings selected the rocky habitats where hiding sites are scattered and speed is important to escape predators. Conversely, warm-incubated hatchlings selected the forest habitat where speed is not so important because only short-distance moves are required to escape into the litter. Hatchlings thus exhibited an integrated set of morphological, locomotor, and behavioral phenotypes.

The link between environmental factors such as temperature and individual fitness suggests that gravid or pregnant females can alter their thermal behavior in ways that maximize the fitness of their offspring. This idea, suggested originally as a mechanism associated with the evolution of viviparity (see Section 9.3), has broad general support (Shine 2004, 2014). Nonetheless, females may act selfishly as well (Schwartzkopf and Andrews 2012). Female water pythons (Liasis fuscus), for example, abandon clutches when egg attendance would reduce the female's future reproductive success (DeNardo et al. 2012). Furthermore, environmentally imposed phenotypes are often transitory and disappear within a few weeks or months of life (e.g., Qualls and Shine 2000). Understanding if and how incubation environments affect fitness thus requires longterm observations of the survival and reproductive success of individuals with environmentally modified phenotypes under natural conditions.

Comparative developmental biology

Comparative studies of embryonic development are based on normal tables. The information in a normal table typically includes the chronological sequence of developmental stages, each characterized by the appearance of new morphological features (see Table 9.1), embryo age, and incubation temperature. Comparison of normal tables reveals that the timing and sequence of stages differ among reptile taxa (e.g., Ewert 1985; Ferguson 1985; Miller 1985; Moffat 1985; Tokita and Kuratani 2001; Iungman et al. 2008; Andrews et al. 2013).

Taxon-specific patterns in the sequence of developmental events are evidence of evolutionary change. Such change is evident at the family level among squamates. For example, the allantoic bud of gekkotan embryos emerges relatively late in development compared with other squamates, and torsion by snake embryos is completed relatively early compared with lizards (Andrews et al. 2013). The mechanisms that produce variation in developmental patterns are largely unknown, as are the links between selection on adult features and developmental patterns (Sanger et al. 2012).

Data from normal tables have been used in broadly comparative studies to assess, for example, the validity of Haeckel's assertion that all vertebrate embryos look alike during mid-developmental stages (Richardson 1995), the phylogenetic position of turtles among amniotes (Werneburg and Sánchez-Villagra 2009), and the development of methods to assess phylogenetic information in developmental sequences (Laurin and Germain 2011).

Normal tables of development are also valuable for experimental studies to assess how incubation temperature, for example, affects hatchling phenotypes. Such effects may depend on when during development the temperature treatment is imposed. This is an important consideration for squamates because the stage of development at oviposition (when studies are often initiated) varies among species, populations, and individuals, but is the same for all of the eggs in a clutch (Braña et al. 1991). A normal table provides the information needed to assign a stage to one embryo per clutch, leaving the remainder of the clutch available for experimental treatments. Subsequent use of initial embryonic stage as a covariate in statistical analyses precludes confounding treatment effects with variation in the initial stage of embryos.

9.7 Reproductive Cycles

A **reproductive cycle** consists of the sequence of events that result in the production of offspring. This sequence includes gonadal maturation (spermatogenesis, oogenesis, and vitellogenesis), mating, fertilization, embryogenesis, and hatching or birth. A few species add parental care as the last event (see Section 9.4). A cycle can be repeated multiple times in a year, annually, biennially, or even less frequently. By skipping reproductive years, for example, female rattlesnakes are able to replenish lipid stores before initiating vitellogenesis (Aldridge and Duvall 2002; Diller and Wallace 2002). For female filesnakes (*Acrochordus arafurae*) in tropical Australia, intervals between reproductive events average 7 years and are associated with unusually low rates energy of energy accumulation (Shine 1986).

The length of reproductive events and their seasonal timing vary considerably among species depending on where they live and their phylogenetic and biogeographic history (Goode and Russell 1968; James and Shine 1985; Cadle and Greene 1993; Brown and Shine 2006). Climate provides general constraints on reproductive cycles. Oviparous species, for example require at least several months of continuously suitable environmental conditions for embryonic development. Environmental conditions must also be suitable for the survival and growth of neonates after hatching or birth. In contrast, the seasonal timing of gonadal maturation, mating, and fertilization are flexible because these events do not have to follow each other at fixed intervals.

In most reptiles, both males and females exhibit maximum sex hormone secretion and gametogenesis immediately before mating, and fertilization occurs shortly thereafter. This is called an **associated (prenuptial) gonadal cycle**. Such a cycle characterizes crocodylians and most lizards and is typical of tropical and subtropical latitudes (Lovern 2011; Milnes 2011).

Some species, however, exhibit gonadal cycles in which mating is uncoupled from maximum sex hormone secretion and gametogenesis, and fertilization occurs after a period of sperm storage in the reproductive tract of males, females, or both (Blanvillain et al. 2011; Taylor and DeNardo 2011). This is called a disassociated (postnuptial) gonadal cycle. Disassociated cycles are characteristic of temperate-zone snakes and turtles but occur occasionally in other taxa, and at tropical and subtropical latitudes as well. North American rattlesnakes (Crotalus) have a dissociated gonadal cycle. Spermatogenesis occurs in spring and summer, and sperm are stored in the vas deferens until mating. Mating occurs during vitellogenesis in summer/fall or in spring after winter dormancy, or both depending on the species. Regardless of the time of mating, ova are fertilized in spring, by sperm stored in the oviducts, and birth occurs in the autumn (Aldridge and Duvall 2002).

Disassociated cycles presumably evolve because the temporal separation of the energy and ecological costs of mating and of gamete production allows these events to occur at a time of year when the costs are minimal, and sperm storage allows fertilization to occur at a time that is best for the completion of embryogenesis and for the survival of neonates (Aldridge and Duvall 2002). Because the timing of gametogenesis, mating, and fertilization is so labile, many variants of disassociated gonadal cycles exist.

Reptiles exhibit four basic types of reproductive cycles: aseasonal, and three types of seasonal cycles (**Figure 9.19**). Aseasonal cycles are characterized by reproductive activity year-round and by the lack of synchrony of reproductive events among individuals. Seasonal cycles are characterized by synchrony among individuals and are usually characterized by discrete periods of reproduction and of reproductive quiescence.

REPRODUCTIVE CYCLE

Aseasonal

Anolis trinitatus: oviparous tropical rainforest

Seasonal: discontinuous

Anolis carolinensis: oviparous temperate

Thamnophis sirtalis: viviparous north temperate

Crocodylus johnstoni: oviparous seasonal tropical

> Crotalus viridis: viviparous temperate Iguana iguana: oviparous tropical rainforest

Seasonal: developmental arrest

Chamaeleo chamaeleon: oviparous Mediterranean

> Kinosternon baurii: oviparous warm temperate

Seasonal: continuous

Sceloporus mucronatus: viviparous montane tropical Hoplodactylus maculatus: viviparous south temperate, annual Hoplodactylus maculatus: viviparous south temperate, biennial



Figure 9.19 Reproductive cycles of reptiles. Cycles for representative species are illustrated schematically. Black lines show months when gametogenesis and mating occur, and colored lines show when embryogenesis occurs (i.e., fertilization to hatching or birth). Dashed lines indicate multiple clutches and continuous gametogenesis. Reproductive cycles of Southern Hemisphere species have been shifted by 6 months. For clarity, only one cycle is shown for *Kinosternon baurii* and annual *Hoplodactylus maculatus*; in these species, a single annual cycle extends more than 1 year, such that the events of gametogenesis and embryogenesis overlap.

Aseasonal cycles

Some squamates that live in tropical rain forests, where both temperature and rainfall are relatively constant throughout the year, exhibit aseasonal reproductive cycles. This means that egg and sperm production continue yearround and that individuals progress through the sequence of reproductive events asynchronously. Individuals may exhibit one or many reproductive cycles per year. Species with aseasonal cycles include *Anolis trinitatis* on St. Vincent Island in the West Indies (Licht and Gorman 1970), the gymnophthalmid lizard *Potamites* (formerly *Neusticurus*) *ecpleopus* in Peru (Sherbrooke 1975), and vipers in the genus *Causus* (Ineich et al. 2006; Mathies 2011).

Even in tropical rain forests, however, the intensity of reproduction varies seasonally in accord with subtle variation in rainfall, temperature, day length, and insolation. For example, the island of Espiritu Santo in Venuatu is located near the Equator in the Pacific Ocean. While climatic seasonality appears trivial and gravid skinks in the genus *Emoia* are found year-round, the proportion of gravid females is highest during the wettest part of the year and lowest during the driest (Baker 1947).

Seasonal cycles

Seasonal patterns of reproduction are associated with climatic seasonality, and the greater the magnitude of variation in temperature and rainfall or both during the year, the longer the period of reproductive quiescence.

DISCONTINUOUS CYCLES At temperate latitudes, discontinuous reproductive cycles are imposed by seasonality in temperature. Not only is the activity of adults limited to warm months, but embryonic development must be completed during those months because actively developing embryos cannot survive temperatures cold enough to halt or delay development for more than a few days (Christian et al. 1986; Ewert 1991). The part of the reproductive cycle from fertilization through hatching or birth must thus be completed within one reproductive season.

Green anoles (*Anolis carolinensis*) in the southeastern United States provide a good example of a discontinuous reproductive cycle. Maturation of gametes occurs almost simultaneously in males and females in the spring; mating, the production of multiple single-egg clutches, incubation, and hatching occur during the summer; and the gonads of both sexes regress in the autumn (Jenssen et al. 2001). Similarly, reproduction of the red-eared slider turtle *Trachemys scripta* of the southeastern United States is confined to the summer months and adults are inactive during the winter (Gibbons 1990).

Red-sided garter snakes (*Thamnophis sirtalis*) in Canada have a particularly short reproductive season; they emerge from hibernation in May and return to their dens in September. They are able to complete their reproductive cycle in this brief period because mating is disassociated from gametogenesis and fertilization. Mating occurs upon emergence from the den site where the snakes hibernated. At this time the testes and ovaries are small and the level of sex steroids in the blood is low. After mating, the snakes disperse to foraging areas. During the next 3 months, male testosterone levels increase and sperm are produced in the testes. These sperm are stored in the vas deferens, to be used for mating the following May. Gonadal maturation of females also occurs during summer, eggs are fertilized with stored sperm, and birth occurs (Crews and Garstka 1982).

At tropical and subtropical latitudes, discontinuous reproductive cycles are imposed by seasonality in rainfall. Wet seasons alternate with dry seasons, and the relative lengths of these seasons vary considerably. The season associated with reproduction is taxon-specific. In the Northern Territory of Australia, for example, 5 months of the year receive more than 100 mm of rain; the other 7 months receive substantially less. For the saltwater crocodile (Crocodylus porosus) and some squamates (such as the snake Boiga irregularis), nesting occurs during the wet season (Webb et al. 1983; James and Shine 1985; Shine 1991). In contrast, nesting by the freshwater crocodile (Crocodylus johnstoni) occurs during the dry season (Webb et al. 1983). In Central and South American, courtship and nesting of the large herbivorous lizard Iguana iguana occur during relatively dry months when nesting sites provide the warmest conditions for incubation, and hatching occurs in the early wet season when hatchlings can feast on new leaves and flowers (Rand and Greene 1982).

CYCLES WITH DEVELOPMENTAL ARREST Unlike temperate-zone reptiles that have discontinuous activity because of winter quiescence, tropical and subtropical reptiles that live in seasonal climates are active year-round. Nonetheless, offspring are produced are the time of year most favorable for their growth and survival. Egg production ceases before the end of the favorable season because eggs hatch from 1 to 3 months after oviposition, depending on egg size and incubation temperature. If the unfavorable period is longer than this, hatchlings will emerge at a time of year when they are unlikely to be successful. Egg production, and reproductive activities in general, are therefore temporally constrained to the favorable season.

Some chameleons and turtles bypass this constraint through physiological mechanisms that decouple the time of egg laying from the time of hatching. These mechanisms include forms of developmental arrest. Embryonic diapause is obligate developmental arrest under conditions that would normally promote active development. Reptile embryos enter diapause at the gastrula stage, early in development, and remain in diapause for several months. Development at early stages can also be arrested facultatively by low temperature or by hypoxic conditions (low oxygen). In these cases, development is resumed as soon as conditions become normal.

Embryonic diapause of chameleons and turtles is associated with pronounced wet-dry seasonality and a long period unfavorable to the survival of hatchlings (Ewert 1991; Andrews and Karsten 2010). Embryonic diapause allows eggs laid in one reproductive season to hatch in the reproductive season of the following year (Karsten et al. 2008; Rafferty and Reina 2012). Chamaeleo chamaeleon provides a good example of this reproductive strategy (Figure 9.20) (Andrews et al. 2008). This lizard occurs in regions with Mediterranean climates where summers are hot and dry and winters are rainy and cool. Mating occurs in summer, followed by oviposition in October. Embryos are at the late gastrula stage at oviposition and remain in diapause for several months. This obligate period of diapause ensures that development does not commence when nest temperature is still high in the autumn. When diapause ends in midwinter, embryonic development remains arrested by exposure to environmental temperatures that are below the threshold for active development.

Active development resumes when nest temperature rises above 20°C in the spring, and hatching occurs in August. The incubation period thus spans 10.5 months. Because of developmental arrest, both oviposition and hatching occur during autumn, after the winter rains have commenced.

Not all delays in hatching require some form of developmental arrest; some subtropical and tropical turtles estivate in the egg without pipping the shell during unfavorable dry periods (Ewert 1991; Rafferty and Reina 2012). These individuals have completed development, as indicated by the retraction of the extraembryonic membranes and by internalization of the yolk sac. Freshwater turtles in temperate regions exhibit a similar strategy for controlling the time of emergence or entering water. Hatching occurs during the summer or autumn, but hatchlings remain in the nest or

3.0

2.8

2.6

Figure 9.20 Nest temperature, egg mass, and embryonic development during incubation of *Chamaeleo chamaeleon* eggs in southwestern Spain. Mean bimonthly nest temperatures and mean egg masses are indicated. From oviposition in October through April, embryos overwinter as diapausing gastrulae (marked DG). Development resumes in the spring when the nest temperature rises above 20°C. Embryos reach limb bud stages by May and hatch in August, after 10.5 months of incubation. (After Andrews et al. 2008.) 30

28

26

Nest temperature (°C)

shelter on land over winter and migrate to water the following spring (Gibbons 2013).

CONTINUOUS CYCLES Events of a continuous seasonal reproductive cycle span all or most of a year. Such cycles are characteristic of cool tropical montane and south temperate areas, and the majority of species are viviparous. Embryogenesis during cold months is possible because (1) temperatures are not cold enough to cause death or developmental abnormalities, (2) embryos have physiological adaptations to low temperature, and (3) in viviparous species, maternal thermoregulation is used to enhance embryogenesis.

At Alexandra, New Zealand, mating by the viviparous gecko Hoplodactylus maculatus occurs in summer, at about the time when females initiate vitellogenesis. Vitellogenesis is completed during winter. Fertilization (with stored sperm) in early spring is followed by a 3- to 5-month gestation period, and birth occurs in summer, a year after the cycle was initiated (Cree and Guillette 1995). At another site where environmental temperature is too low to support annual reproduction, female H. maculatus exhibit a biennial reproductive cycle (males continue to exhibit annual cycles of spermatogenesis). While mating, vitellogenesis, fertilization, and early embryogenesis are completed on the same schedule as at the warmer Alexandra site, pregnancy at the cooler site lasts for about 14 months. This prolonged gestation period benefits hatchlings because they are born in the spring (Cree and Guillette 1995).

Events of the reproductive cycle of the viviparous lizard *Sceloporus mucronatus* in the mountains around Mexico City require most of the year to complete. Gametogenesis occurs in summer and autumn, mating and fertilization in autumn, gestation in winter, and birth in the spring (Villagrán-Santa Cruz et al. 2009). For montane *Sceloporus* in Mexico and cool temperate *Hoplodactylus* geckos in New Zealand, a spring birth date gives hatchlings enormous benefits; they begin their independent lives during a period of warming temperatures and increased food availability. Studies of the montane skink *Niveoscincus microlepidotus*



Nest temperature

in Tasmania document the importance of birth season; a shift from fall to spring birth is associated with significantly higher survival of hatchlings (Olsson and Shine 1998).

Female tuatara (*Sphenodon punctatus*) have the longest reproductive cycle known for an oviparous reptile. Vitellogenesis spans 3 years on average, and eggs are in the oviduct for another 6 to 8 months (Cree et al. 1992). Once oviposition occurs, incubation takes about a year (Thompson et al. 1996).

9.8 Life Histories of Reptiles

Life history is the study of how organisms reproduce, grow, mature, and age, and reptilian life histories are extraordinarily diverse. Some lizards, for example, reach sexual maturity within a few months, produce multiple clutches in their lifetimes, and live less than a year. In contrast, some tortoises take decades to reach sexual maturity, produce one clutch a year or less, and live many decades. The basis for this diversity is of great interest to evolutionary biologists.

Patterns of life history variation

Early theoretical studies approached life histories from the perspective of age-specific survival and reproduction (Cole 1954). Both theoretical and empirical studies documented a trade-off between survival and reproduction. Annual adult survival of lizards, for example, decreases as annual reproductive allocation increases (Figure 9.21). Tinkle (1969) additionally noted that high investment in reproduction is associated with traits that should enhance mortality, such as conspicuous sexual dimorphism, elaborate courtship, and aggressive and territorial behavior. These and other observations provide a mechanistic explanation for the trade-off between annual survival rate and reproductive effort (Schwarzkopf 1994).

Another approach to studies of life history variation is to look for (1) similarities of life-history traits (e.g., clutch size,



Figure 9.21 Annual adult survival and annual egg production in lizards. The negative relationship between annual adult survival (the probability of surviving from one reproductive season to the next) and annual egg production (the total number of eggs produced per year) for 14 species of lizards. (After Tinkle 1969.)

clutch frequency, body size at hatching or birth, age and size at maturity, adult body size, relative mass of the clutch, and mode of reproduction) among species and (2) associations between life-history traits and ecological factors such as climate, habitat characteristics, or geographic range.

Multivariate and correlational analyses organize lizard life histories into a multi-branched array, with three major groupings of species (Dunham et al. 1988):

- 1. Species that produce a single clutch per year. Most members of this group exhibit delayed maturity (more than 1 year after hatching) that is offset by high adult survival. Delayed maturity may be related to the time required to grow to large size or to resource limitation. Once mature, however, females of these species produce either large numbers of relatively small eggs (e.g., the green iguana, *Iguana iguana*) or small numbers of relatively large neonates (e.g., the viviparous New Zealand gecko *Hoplodacty-lus maculatus*).
- 2. Species that produce multiple clutches per year and mature within a year of hatching. Early maturity is possible because species in this group are small in size or exhibit rapid growth. For example, gravid females of the Central American lizard *Anolis apletophallus* weigh about 2 g (the mass of a dime) and lay clutches that consist of a single egg every 7–10 days during a reproductive season of at least 6 months. Eggs hatch after about 40 days, and hatchlings grow to reproductive size in about 3 months. The high reproductive potential of this species is offset by high mortality both before and after hatching (Andrews 1988; Andrews and Nichols 1990).

3. Species with multiple clutches per year but with delayed maturity (e.g., the tropical American basilisk lizard *Basiliscus basiliscus*). Delayed maturity in this group is associated with large body size and slow juvenile growth. When females become sexually mature, however, they produce multiple clutches per reproductive season; the total number of eggs is related to body size.

Lizard life histories are also related to ecological factors. A study using life-history data for 551 species of lizards found that reproductive productivity (total mass of offspring produced per year) is higher in warmer than in cooler environments, but is not related to the activity body temperatures of the lizards themselves (Meiri et al. 2012). Viviparous species are less productive than oviparous species, reflecting the former's association with cool climates.

Life histories also differ between island and mainland populations. Lizard communities on islands are denser (have more lizards per unit of area) and less diverse (have fewer species of lizards) than mainland communities. High density and low diversity mean that intraspecific competition is stronger in island than in mainland communities. Large hatchlings are better competitors than small ones, and island species of lizards have smaller clutch sizes and larger hatchlings than their mainland relatives (Novosolov et al. 2013).

Trade-offs and life history evolution

To gain insight into mechanisms of life history evolution, researchers have increasingly focused on experimental studies that examine life history variation among populations of the same species and among individuals within populations. We discuss two life-history trade-offs that have been examined from this perspective. The first is the physiological basis for the trade-off between survival and reproduction. The second is the basis for the trade-off between investment in many small offspring versus a few large offspring per clutch.

TRADE-OFF BETWEEN REPRODUCTION AND SURVIVAL

The negative relationship between annual survival and reproduction is a reflection of body size. That is, species with high survival and low reproductive productivity tend to be large, and species with low survival and high reproductive productivity tend to be small. The continuum of life-history traits illustrated in Figure 9.21 can also be viewed as a paceof-life continuum; species with slow-paced lives (e.g., low mass-specific metabolism, slow growth, low reproduction) fall on the left side of the plot, and species with fast-paced lives (e.g., high mass-specific metabolism, rapid growth, high reproduction) fall on the right.

The pace-of-life hypothesis (also known as the rateof-living and the oxidative stress hypotheses) provides a mechanistic basis for the trade-off between reproduction and survival. This hypothesis proposes that differences in slow versus fast life histories among species are the result of a physiological linkage between metabolism and **senescence** (physiological aging). The biochemical reactions of aerobic metabolism produce reactive oxygen species (ROS), also known as free radicals. These highly reactive molecules cause damage to DNA, proteins, and lipids (Williams et al. 2010). While the effects of ROS can be mitigated to some extent by mechanisms such as DNA repair and synthesis and the acquisition of antioxidant molecules, these processes have high costs of their own, both energetic and nonenergetic (Isaksson et al. 2011).

Size-specific rates of ROS production may partly explain the relationship between body size and longevity among species, but individuals from populations of a single species can differ in longevity and reproductive output as well. The pace-of-life hypothesis predicts that populations with a slower life history should exhibit mechanisms that reduce oxidative damage at the expense of reproduction compared with their relatives with a faster life history.

Studies of the western garter snake (*Thamnophis elegans*), a viviparous colubrid, provide broad support for predictions

of the pace-of-life hypothesis (Table 9.2) (Bronikowski and Vleck 2010; Robert and Bronikowski 2010). Populations that live in mountain meadows near Eagle Lake, California experience low food availability and relatively low predation; they are characterized by slow growth, late maturity, low reproductive output, and a long lifespan. In contrast, snakes from lakeshore habitats experience high food availability and high predation. They are characterized by rapid growth, early maturity, high reproductive output, and a short lifespan. As predicted, the longer-lived individuals from slow-growth populations had low metabolic rates as field-caught adults compared with the shorter-lived individuals from fast-growth populations. Neonates from slowgrowth populations born in the laboratory had higher DNA repair efficiency of ultraviolet light damage, lower ROS production when mothers had been stressed during pregnancy by dermal exposure to corticosterone, and mitochondria that were more efficient at converting ADP to ATP. In short, these observations using natural genetic variation within wild populations support a physiological link between the amount of oxidative stress and life-history traits.

Trait	Long-lived	Short-lived	
Environment			
Habitat, elevation	Meadow, 1630–2055 m	Lakeshore, 1555 m	
Summer daytime temperatures	15–30°C	20–34°C	
Avian predators	Midsized raptors	Large raptors	
Food/water availability	Variable across years	Continuous	
Major prey types	Anurans, leeches	Fish, leeches	
Morphology/life history			
Mean adult body length	538 mm	660 mm	
Female maturation size, age	400 mm, 5–7 years	450 mm, 3 years	
Litter production	Less than annual	Annual	
Mean litter size	4.3 liveborn	8.8 liveborn	
Newborn mass	2.85 g	3.27 g	
Annual adult survival	0.77	0.48	
Median lifespan	8 years	4 years	
Physiology			
Mean metabolic rate (ml O_2 /h) at 28°C at 1 month	0.52 (mean mass = 2.62 g)	Statistically equivalent	
Mean metabolic rate (ml O_2 /h) at 28°C for adult males	2.09 (mean mass = 21.6 g)	3.12 (mean mass = 22.1 g)	
H_2O_2 production under stress	56 pmol/min/mg mitochondria	240 pmol/min/mg mitochondria	
DNA repair efficiency	73%	35%	
Field baseline corticosterone	50 ± 8 ng/ml plasma	7.7 ± 12 ng/ml plasma	
ATP production efficiency	1.18	0.82	

TABLE 9.2 Characteristics of long-lived (slow-growth) and short-lived (fast-growth) populations of the western garter snake (*Thamnophis elegans*)

After Bronikowski and Vleck 2010; Robert and Bronikowski 2010.



The hypothesis that reproduction itself has direct survival costs was tested by researchers who manipulated the amount of reproduction by females of the small iguanid lizard *Anolis sagrei* in the Bahama Islands in the West Indies (Cox and Calsbeek 2010; Cox et al. 2010). They surgically removed the ovaries of one group of females and conducted sham operations on another group. The lizards were returned to their capture site and monitored for the remainder of the reproductive season, and again the following year. The results were clear: females that were rendered non-reproductive had dramatically higher survival than did reproductive females (**Figure 9.22**).

Figure 9.22 Costs of reproduction for Anolis sagrei females. In each of two independent years of study, survival of non-reproductive (ovariectomized) females exceeded that of reproductive (sham ovariectomies) females over three separate intervals. (A) Breeding season (May–September). (B) Over winter (September–May). (C) Interannual (May–May). Averaged results of both years are given in the third pair of data. (After Cox and Calsbeek 2010.)

Survival was enhanced in part because non-reproductive females were more likely to escape from predators: they ran 12% faster and increased their stamina by 9% over their performance prior to surgery. Non-reproductive females also had more surplus energy as measured by their larger fat bodies and faster growth than reproductive females. Finally, immune responses were stronger in non-reproductive females, suggesting that impaired immune function may contribute to the low survival of reproductive females.

Despite the difference in immune status, however, both groups of females had similar infection rates by *Plasmodium* (malaria) parasites, and non-reproductive females had higher parasite loads than reproductive females. Reproductive females grew more slowly as parasite loads increased; apparently the energy they devoted to reproduction reduced their ability to tolerate parasitism. Non-reproductive females, however, were better able to tolerate parasitism. Inexplicably, their growth rates were positively correlated with the number of parasites in their blood. Overall, these observations indicate that reproduction has negative impacts on diverse physiological processes, which in turn reduce survival.

TRADE-OFF BETWEEN NUMBER AND SIZE OF OFFSPRING

Given a fixed amount of energy available for reproduction, a female can produce a clutch consisting of many small offspring or a few large ones. For example, female bluetongued skinks (*Tiliqua scincoides*) with a mass of about 1 kg produce a litter of 11 offspring, each weighing about 30 g. Female Australian sleepy lizards (*Tiliqua rugosa*) of similar size typically produce 2 offspring, each weighing about 100 g (Glenn Shea, unpublished data). The ratio of total offspring mass to adult mass is approximately the same for both species, but *T. scincoides* spreads that mass over many small offspring, whereas *T. rugosa* puts the mass into just two large offspring.

A trade-off between the number of offspring and the size of offspring is fundamental to life-history theory. This trade-off is most explicit when the number of offspring produced per year is adjusted for adult body size: species or populations with fast life histories produce many small offspring; species or populations with slow life histories produce a few large offspring during a breeding season (**Figure 9.23**) (Warne and Charnov 2008).

A negative relationship between clutch size and offspring size is also observed among individuals within popula-





Figure 9.23 The number of eggs produced per year is negatively related to hatchling size in lizards. Variation in the slopes of the regression lines presumably reflects the distinct body plans and foraging modes of six lizards families. For perspective, the data point for the small European common lizard (*Zootoca vivipara;* Lacertidae) would fall at the upper left on the figure (–6.8, 9) and the data point for the large ground iguana (*Cyclura pinguis;* Iguanidae) would fall at the lower right (–10.7, 14). To scale for mass-specific reproductive productivity in this graph, annual egg production is divided by female snout-vent length cubed (to convert length to mass units) and raised to a power of 0.75. Hatchling SVL is also cubed. (After Warne and Charnov 2008.)

tions. For example, female *Lacerta agilis* that produce large clutches produce relatively small offspring, and vice versa (Olsson and Shine 1997). This pattern persisted through the 5 years of the study even though food availability was greater in some years than in others. In good years the size of all hatchlings was larger than in poor years, but the negative relationship between clutch size and offspring size was observed in each year. Similarly, there was a trade-off between clutch size and egg size in each of four populations of the cobra *Naja atra* in southeastern China, despite differences in mean hatchling and clutch size among populations (Ji and Wang 2005).

The way resources are allocated between the size of the clutch and the size of offspring is an adaptive compromise between selection on hatchling viability and selection on females to maximize the number of surviving offspring and minimize the cost to future reproduction (Du et al. 2005). Optimal hatchling size in terms of viability has been the focus of numerous studies (e.g., Ferguson and Fox 1984; Sinervo and Doughty 1996; Warner and Shine 2007; Uller and Olsson 2010; Warner et al. 2010). In general, bigger is better, but larger hatchlings are not favored in all years, and other factors such as the seasonal timing of hatching can complement or override the benefits of hatchling size per se.

Females will not always be selected to produce the most viable hatchlings. For example, if each of two large offspring has a 50% chance of survival, a clutch of two eggs will, on average, produce one surviving hatchling. If each of eight smaller hatchlings has a 20% chance of survival, a clutch of eights eggs will, on average, produce 1.6 surviving hatchlings. In this situation, the optimal solution is for the female to produce a clutch of eight. The optimal solution for a given population will reflect long-term adaptation to particular physical and biotic environments, as well as what solutions are possible given a species' evolutionary history.

Egg size, and thus hatchling size, may be constrained by adult morphology. Experimental studies of the sideblotched lizard (*Uta stansburiana*) provide direct evidence of the negative consequences of producing eggs that are too large (Sinervo and Licht 1991). Side-blotched lizards normally produce clutches of two to nine eggs, and the larger the clutch, the smaller the eggs. When all but one developing follicle were removed surgically, extra yolk was deposited in the remaining follicle and females ovulated one abnormally large egg. In this situation, 36% of the eggs burst while being laid (so the embryo died) or became bound in the oviduct (so both the embryo and female died).

The reason why side-blotched lizards do not normally lay clutches of one large egg is clear. In contrast to sideblotched lizards, the entire genus *Anolis* is characterized by a clutch size of one. An *Anolis* of the same body size as an *Uta* produces an egg that is only slightly smaller than the egg that was produced experimentally in the one-egg clutch of *Uta*. This observation suggests that female *Anolis* produce the largest egg that can safely pass through a female's pelvis. As we discussed in Section 9.7, anoles compensate for a single-egg clutch by producing many eggs during their long reproductive seasons.

Limitation of egg size by the size of the female's pelvis may be widespread. For example, the sizes of eggs of painted turtles (*Chrysemys picta*) from Michigan and of chicken turtles (*Deirochelys reticularia*) from South Carolina are proportional to the width of the female's pelvic opening, and larger females lay larger eggs (Congdon and Gibbons 1987). These observations suggest that these small-bodied turtles (mean plastron lengths of 130 mm and 160 mm, respectively) would lay still larger eggs if females attained larger body sizes.

SUMMARY

Reptiles exhibit diverse mechanisms of sex determination.

Some taxa have genotypic sex determination (GSD), and either males or females can be the heterogametic sex, but sex chromosomes are not always morphologically distinct.

Other taxa have temperature-dependent sex determination (TSD), meaning sex is determined by the temperature that embryos experience during development. The particular sex produced at high and at low temperatures varies among reptiles groups. Theoretically, TSD is adaptive when the match between incubation temperature and fitness differs between males and females.

Reptiles reproduce both sexually and asexually (parthenogenetically).

The great majority of reptiles reproduce sexually.

About 40 species of squamates are all female and reproduce parthenogenetically. Parthenogenesis results from hybridization between closely related species. Parthenogenetic species fill weedy ecological niches relative to their bisexual relatives.

Reptiles exhibit two reproductive modes, oviparity and viviparity.

Oviparity (egg-laying) is the ancestral reproductive mode of reptiles.

Viviparity (live-bearing) has evolved only in squamates, and about 20% of squamate species are viviparous.

The evolution of viviparity is associated with high latitudes and elevations, where cold climates favor both the transition to viviparity as well as viviparity itself. The benefit of viviparity in cold climates is that gravid females retaining eggs can select body temperatures that will optimize the fitness of their offspring.

Parental care consists of the behaviors exhibited by parents after egg deposition or birth that enhance the survival of offspring.

Turtles rarely exhibit parental care, whereas parental care may be universal among crocodylians.

The majority of squamates are small, and very few exhibit parental care.

Snakes that exhibit parental care are large, venomous, or both.

Lizards that attend eggs protect them from relatively small predators and from microbial infection.

The reproductive anatomy and processes of spermatogenesis and oogenesis of reptiles are similar to those of other vertebrates.

The organs directly associated with reproduction are the gonads and associated ducts.

Reptiles have internal fertilization. Male turtles and crocodylians have a penis; male squamates have hemipenes.

Fertilization is typically associated with mating, and occurs as ova enter the oviduct.

Mating and fertilization may be disassociated in time. Sperm stored in the oviduct are used to fertilize eggs if males are not present or if mating occurs prior to ovulation. Sperm are stored in the vas deferens if spermatogenesis occurs prior to mating.

Development is the process by which a single diploid cell is transformed into a self-sufficient multicellular organism.

All reptiles have direct development that culminates in the hatching or birth of a small and independent version of the adult.

Development of an embryo is the result of both differentiation of cells and increase in the number of cells.

Hox genes control basic processes of development. Mutations to Hox genes can have profound effects, such as reducing or eliminating the expression of limbs in snakes.

The temperature that embryos experience during development affects the phenotype of individuals after hatching or birth. Traits affected include sex, morphology, behavior, and cognitive abilities.

The sequence of developmental events (e.g., torsion, limb bud initiation) differs among reptile clades, indicating that developmental processes have evolved.

A reproductive cycle includes the sequence of gonadal maturation, mating, fertilization, embryogenesis, and hatching or birth. Reptiles exhibit four major types of reproductive cycles.

In aseasonal reproductive cycles, individuals reproduce asynchronously and year-round.

In seasonal discontinuous cycles, reproductive events are seasonal and synchronized among individuals. Reproductive activities are suspended for part of the year due to cold or dry conditions.
In seasonal cycles with developmental arrest, a single reproductive cycle includes a period of obligate embryonic diapause or a period of facultative arrest in response to low temperature or hypoxic conditions.

In seasonal continuous cycles, one reproductive cycle requires most of a year to complete.

Life histories are characterized by the birth to death traits of individuals and populations.

A fundamental life-history feature is the trade-off

between reproductive productivity and survival: species that invest heavily in reproduction have high intrinsic mortality, and species that invest heavily in somatic maintenance have low intrinsic mortality.

Investment in reproduction can be divided into many small offspring or a few large offspring.

Determining the physiological and genetic factors that shape trade-offs among traits is a core objective of current studies on life history evolution.

Go to the **Herpetology** Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

10 Body Support and Locomotion

he 17,000-plus extant species of amphibians and reptiles occupy habitats ranging from the open oceans to the crowns of rainforest trees and the depths of desert soils. Such diverse habitats require different modes of locomotion. Feet that gain purchase on a tree limb are very different from those required to propel their owner through a pond. Furthermore, several alternative solutions to the same locomotor challenge may exist, depending on the evolutionary starting points of the lineages involved. Crocodylians and marine iguanas, for example, approach aquatic locomotion with a different anatomy than do sea snakes, leading to the evolution of both different features (e.g., webbed toes for paddling in crocodylians) and of shared attributes (e.g., flattened tails for sculling in all three groups). Some seemingly optimal solutions are unavailable because of anatomical constraints (wheels, for example, are inconsistent with the need for blood vessels to reach spinning tissues), and some features presumably have simply not appeared as variants on which natural selection could act. Despite these limitations, the range of locomotor adaptations among amphibians and reptiles is vast and extends from the elegant (the climbing pads of geckos) to the astonishing (controlled gliding in the paradise tree snake, Chrysopelea paradisi).

This chapter explores the diversity of locomotor modes among amphibians and reptiles from a functional perspective, emphasizing the mechanics of locomotion and examining the underlying similarities observed among diverse taxa that have converged on similar locomotor patterns. First, however, we must consider some physical principles that govern support and locomotion in animals.

10.1 Body Support and Thrust

An understanding of animal locomotion requires a modest appreciation for the fundamental laws of physics, specifically Newtonian mechanics. Newton's first law of motion states that a body at rest will remain at rest, and a body in motion will remain in motion unless acted on by an external force. His second law states that force (*F*) equals mass (*m*) times acceleration (*a*), or $F = m \bullet a$. Finally, Newton's third law states that for every action there must be an equal but opposite reaction. Together, the first and third laws mean that any change in an animal's state of motion must result from an external force acting on it, and that motion results not directly from the actions of an animal's muscles but from the reactive force that the environment exerts on the animal. When the limb of an animal pushes on the ground at an angle, it elicits an equal and opposite **reaction force** on the foot that can be resolved into a **vertical component**, which resists the downward force of gravity, and a forward **propulsive component**, which generates thrust in the direction of motion (**Figure 10.1**).

The problem of body support is very real, and it strongly affects locomotor morphology and behavior. Any object within Earth's gravitational field accelerates toward the center of Earth. That gravitational acceleration times the mass of an object is the object's weight. Gravity acts as if all of an animal's weight were concentrated at a specific point-the center of gravity, or center of mass-the location of which depends on an animal's shape. To keep from falling, an animal must maintain its center of gravity above its base of support, which is the area enclosed by the points of contact (usually the feet) with the ground. Most amphibians and reptiles have a broad, quadrangular base of support when they stand on all four feet (Figure 10.2A), but when one leg is lifted, the base changes to a triangle (Figure 10.2B). When moving at slow to moderate speeds, quadrupedal species such as salamanders, lizards, and crocodylians, bend the vertebral column to maintain their center of gravity over their shifting base of support as they move their feet (Figure 10.2C,D).

In addition to vertebral flexion, the pattern in which the animals' right and left hind- and forefeet respectively are lifted and placed during locomotion—the **footfall pattern**—reflects that need to maintain stability. Most tetra-



pods employ a lateral footfall pattern, in which movement of the forefoot on each side follows movement of the hindfoot on the same side: i.e., RH, RF, LH, LF (see Figure 10.2D). Such a sequence typically produces the largest triangles of support. (A diagonal sequence, in which the forefoot follows the hindfoot of the opposite side, results in a narrower base of support, risking instability if the center of gravity

Figure 10.1 Forces acting on the limb of a tetrapod. Muscular action generates a force that the foot applies to the substrate, eliciting a reaction force that is equal in magnitude but opposite in direction. Components of that reaction force resist gravity and propel the animal.

 ...generates a reaction force (R) that is equal in magnitude and in the opposite direction.

> falls outside the resulting triangle. Keeping the body low to the ground also enhances stability by lowering the center of gravity, making it less likely to lean beyond the base of support. In fact, most amphibians and reptiles do not remain standing for long periods when motionless. Instead, they allow their bodies to rest on the substrate, minimizing the energy required for postural support.

10.2 Lever Systems

Considering musculoskeletal systems as levers provides useful insights into their function. A lever is a simple machine consisting of a rigid bar that pivots around a fulcrum (**Figure 10.3**). Force applied at one end of the lever generates a force at the other end. Bones can be considered levers to which muscles apply force, and the geometry of the lever determines how that muscular force is modified. Every lever consists of two arms: the in-lever and the out-lever. The inlever lies between the point where the in-force is applied



Figure 10.2 Lateral bending and stability. (A) A tetrapod is stable when all four feet are on the ground and the center of gravity lies over the quadrangular base of support. (B) Lifting one foot makes a tetrapod unstable if its center of gravity falls outside the triangular base of support provided by the three feet

in contact with the ground. (C) Bending the vertebral column can shift the center of gravity over the base of support. (D) A salamander bends alternately to the left and right as it walks, keeping the center of gravity over the base provided by three feet on the ground.



Figure 10.3 Levers, limbs, and jaws. Movements of bones around joints are often controlled by first- and third-class levers that have opposite effects. (A,B) In a first-class lever, the in-lever and out-lever are separated by the fulcrum, and the in-force and out-force act in opposite directions. (A) In the hindleg and foot of an alligator, the fulcrum is the ankle joint, between the tibia and foot, and the gastrocnemius muscle provides the in-force. The out-force is exerted against the substrate, as when you are walking. (B) In the lower jaw of a monitor lizard, the quadratomandibular joint is the fulcrum, the depressor mandibulae muscle provides the in-force, and the out-force opens the jaw. (C,D) In a third-class lever, the in- and out-levers overlap in space, and the in-force and out-force act in the same direction. (C) In the alligator hindleg and hindfoot, the fulcrum again is the ankle joint, the in-lever extends along

and the fulcrum; the out-lever lies between the fulcrum and the point where the out-force is produced.

Levers are placed in three classes according to the arrangement of the in-force, out-force, and fulcrum. The sim-



Third class lever:

The fulcrum lies at one end and the

the length of the foot to the point where the tibialis anterior muscle attaches, and the out-lever extends to the tip of the toes. The tibialis anterior muscle provides the in-force, and the out-force lifts the foot upward. (D) In the monitor lizard lower jaw, the quadratomandibular joint again is the fulcrum, the adductor mandibulae muscle provides the in-force, and the out-force closes the jaw. The differences between the out-lever lengths in A and C reflect the different functions of those muscles. The gastrocnemius (A) applies most of its force through the ball of the foot, whereas the tibialis anterior (C) lifts the entire foot, to the tips of the toes. The force exerted by a muscle depends on the size and shape of the muscle and its angle of attachment to the bone. For clarity, we have shown in-forces acting at right angles to the bones.

plest case is a first-class lever (see Figure 10.3A and B), in which the in-force and out-force are applied on opposite sides of the fulcrum, so the in-lever and out-lever are physically distinct (as in a see-saw). In a second-class lever the

fulcrum lies at one end of the rigid bar and the in-force is applied at the other end; the out-force is generated between the two (as in a nutcracker). In a third-class lever (see Figure 10.3C and D), the fulcrum also lies at one end but the out-force is generated at the opposite end, with the in-force being applied between the two (as in a pair of forceps). In both second- and third-class levers, the in- and out-levers physically overlap each other for some distance. Secondclass levers are uncommon in animals, but first- and thirdclass levers are common and often involve the action of antagonistic pairs of muscles that produce opposing motions around the same joint.

Often a lever can be used to amplify the force that powers it. Such a lever has a relatively high mechanical advantage, expressed as the ratio of the out-force to the in-force. One way to increase the out-force is to increase the in-force, simply by applying more muscular force into the lever. Alternatively, the out-force can be increased by adjusting the relative lengths of the two lever arms, because levers are governed by a simple equality: (in-force) • (in-lever length) = (out-force) • (out-lever length). Therefore, as the in-lever gets longer or the out-lever gets shorter, the out-force will increase, even with no change in the in-force. Although this relationship is easiest to visualize with a first-class lever, it applies to second- and third-class levers as well.

If levers can be used to amplify muscular force, why don't all animals converge on the most powerful system possible? The answer lies in a trade-off between force and speed. Although a shorter out-lever results in a higher out-force, a longer out-lever yields greater speed because the end of a longer out-lever swings through a greater arc than a shorter one as the lever rotates around its fulcrum.

10.3 Terrestrial Locomotion with Limbs

Locomotion by means of sprawling limbs is characteristic of most salamanders, lizards, and, to a lesser degree, crocodylians when they move on land. The sprawling posture characteristic of these taxa promotes stability by providing a broad base of support and increases stride length by thrusting the limbs forward as the body bends.

Salamanders

Although vertebral undulation and sprawling limbs are ancestral features, the two work together as a sophisticated system. This can be seen in semiaquatic salamanders, such as the California newt (*Taricha torosa*) (Ashley-Ross and Bechtel 2004). A salamander uses lateral undulations as it swims, and its limbs begin to move as it approaches shore. When it emerges from water onto a sloping bank, the salamander assumes its normal terrestrial gait in which lateral undulations are combined with limb movements. Lateral undulation differs in salamanders during swimming and quadrupedal locomotion, however (Deban and Schilling 2009). When a spotted salamander (*Ambystoma maculatum*) swims, a traveling wave passes down the salamander's trunk; in other words, a bend is initiated at the front of the body and travels posteriorly along the trunk and tail. In contrast, quadrupedal locomotion (both on land and in the water) is characterized by standing waves, which bend the same regions of the body back and forth.

Lizards

The complex mechanics that govern the sprawling limbs of lizards clearly are capable of generating substantial propulsive forces, and some lizards can achieve considerable speeds. An extreme example is the Komodo dragon (*Varanus komodoensis*), the largest living lizard, which reaches a total length of about 3 m. It can briefly attain speeds of up to 18.5 km/h and can sustain a speed of about 14 km/h for more than 0.5 km (Auffenberg 1981).

The stride length of both pairs of limbs is enhanced by substantial lateral bending of the trunk. In addition, the pectoral girdle of lepidosaurs has an unusual sliding joint between the medial sternum and the paired coracoid bones, the ventral bones of the pectoral girdle. This tongue-andgroove joint allows the girdle to slide posteriorly during the propulsive phase, substantially increasing the length of the stride (Jenkins and Goslow 1983).

Locomotion is affected by the substrate on which a lizard runs, and the relationship appears to be more complex that might be expected. Tulli et al. (2012) examined morphology and locomotor performance in 36 species of liolaemid lizards, comparing their speed on sand, simulated stone, and simulated tree bark. The lizards were divided into those with terrestrial, arboreal (tree-climbing), saxicolous (rockdwelling), or arenicolous (sand-dwelling) habits. Surprisingly, none of the groups consistently performed better than the others on the substrate that it typically occupies in nature. Arenicolous lizards ran fastest on the simulated rock surface, whereas the other three groups all ran fastest on sand.

Some species of lizards can run on their hindlegs alone. These species are considered dynamic bipeds, because they are capable of supporting themselves on two legs only while they are running (**Figure 10.4**). Approximately 30% of the strides in trackways left by escaping zebra-tailed lizards (*Callisaurus draconoides*) were bipedal and had longer stride lengths than quadrupedal steps (Irschick and Jayne 1999b). Bipedal locomotion requires no major structural changes for lizards, and some authors have argued that bipedal locomotion in smaller species is simply a by-product of the physical forces acting on a lizard as it accelerates rapidly akin to a motorcycle doing a wheelie (Aerts et al. 2003).

Specialized bipedal lizards, including the Australian frillneck lizard (*Chlamydosaurus kingii*), North American collared lizards (*Crotaphytus*), and Central American *Basiliscus*, are relatively large and have long hindlimbs, short forelimbs, a robust sacral articulation, and a short presacral vertebral column, which results in a posterior shift in



Figure 10. 4 A zebra-tailed lizard (*Callisaurus draconoides*) running bipedally on a treadmill. (A) The right hindfoot is pushing off while the left hindleg is moving forward. (B) The left hindfoot is on the ground while the right hindfoot is near its maximum height. (C) The toes of the right hindfoot make contact with the substrate. In all three images, note that the hip is well above the ground and that the heels never touch the substrate. The belt of the treadmill is moving from right to left. The vertical lines are 10 cm apart and the interval between images (A) and (C) is 0.08 s. (Photographs courtesy of Bruce C. Jayne.)

the center of gravity. *Basiliscus* employ bipedal locomotion when avoiding predators by running across the surface of the water (**Figure 10.5**). These riparian lizards have fringed scales on the posterior edges of their toes that provide resistance as they strike the surface of the water (Luke 1986). Air rushes in behind the foot to form a pocket in the water surface within which the foot can be withdrawn on the

recovery stroke without encountering resistance from the water (Glasheen and McMahon 1996).

Crocodylians

Although a crocodylian at rest appears to have sprawling limbs like those of lizards, these two lineages differ in terms of posture and gait. Indeed, crocodylians may have evolved their sprawling posture secondarily from a more erect ancestral condition. Crocodylians typically use a high walk with the limbs in a semierect position, midway between sprawling (like most lizards) and erect (like most mammals). Muscles attaching to the underside of the femur pull the hindlimb toward the midline, elevating the body (Reilly and Blob 2003). Limb movement of crocodylians is more nearly parasagittal (i.e., the limbs move in a plane that is parallel to the vertebral column) than that of lizards. Crocodylians increase speed by extending their knees and ankles farther, which effectively lengthens the limbs, increasing the stride (Reilly and Elias 1998).

Small crocodylians are capable of rapid terrestrial locomotion, and young crocodiles exhibit a wide range of gaits (Renous et al. 2002). For example, a bounding gait has been described for small saltwater crocodiles (*Crocodylus porosus*) and freshwater crocodiles (*C. johnstoni*) (Webb and Gans 1982). In a bound, both hindfeet contact the ground almost simultaneously, as do both forefeet. Dorsoventral flexion of the vertebral column, an unusual motion for reptiles, extends the stride length of bounding crocodylians. Freshwater crocodiles move about 1.3 times their body length with each bound and attain speeds of 10–15 km/h (Webb and Gans 1982).

Turtles

The vertebrae and ribs of turtles are fused to the shell, so turtles cannot bend the vertebral column to shift their center of gravity. Likewise, their limb girdles are enclosed within the shell, and the humerus and femur can move only within the limits of the openings between the carapace and plastron. Turtles exhibit some obvious modifications that



Figure 10.5 A green basilisk lizard (Basiliscus plumifrons) running bipedally across the surface of a stream. This locomotor habit of Central American Basiliscus species has earned them the local name lagarto Jesucristo ("Jesus Christ lizard"). (Photograph © Bence Mate/Nature Picture Library/Corbis.)



Figure 10.6 Terrestrial locomotion by a turtle. The red dot shows the center of gravity, and the blue lines are drawn between limbs that are in contact with the substrate. The center of gravity falls within the base of support when a turtle is standing on four feet (A) or on three feet (B). During each cycle

circumvent these locomotor constraints. Their limbs are in contact with the substrate for extended periods, and their short, broad bodies and lateral footfall pattern provide wide triangles of support (**Figure 10.6**). Nonetheless, a turtle typically begins to lift its hindfoot before placing its contralateral forefoot on the substrate, allowing the center of gravity to fall forward before the forefoot catches the turtle (Jayes and Alexander 1980).

10.4 Jumping

Jumping (saltation) is characteristic of anuran amphibians. Propulsion is generated by the two hindlimbs acting simultaneously, rather than alternately as in most other tetrapod locomotor modes. Anurans have a short and relatively rigid vertebral column and greatly elongated hindlimbs (Figure 10.7). A frog's hindlimb has a long femur, a long lower leg formed by the fused tibiofibula, and a long hindfoot. In addition there are two more functionally distinct segments: (1) the astragalus and calcaneum of the ankle are elongate and move independently relative to the more distal tarsals, and (2) the pelvic girdle is movably articulated with the vertebral column via the diapophyses (enlarged transverse processes) of the single sacral vertebra, rather than being rigidly attached to the sacrum as in most tetrapods. (The conspicuously hunched posture of some resting frogs is the result of the moveable articulation between the pelvic girdle and the vertebral column.) The pelvic girdle is shaped like an elongate U, with very long ilia (the pelvic elements that articulate with the sacral vertebra). The overall result is a pair of very long, multiply jointed hindlimbs that launch the frog into the air.

A jumping frog (**Figure 10.8**) is subject to the laws of **ballistic**, or **projectile**, **motion**—that is, once a frog is fully airborne its flight path is influenced only by the forces of gravity and of air resistance (which is small and can be disregarded). The height and distance of a frog's jump depend on two variables, the takeoff angle and takeoff velocity. Jump height is maximized when the takeoff angle is 90° from the horizontal (that is, when the frog jumps straight

of limb movements, a turtle lifts its hind foot before placing its contralateral forefoot on the substrate (C), leaving the center of gravity anterior to the line connecting the two feet that are in contact with the ground. As a result, a turtle falls forward until its forefoot reaches the ground. (After Walker 1971.)

up), and jump distance is greatest when the takeoff angle is 45°. Takeoff velocity is the product of the acceleration generated by contraction of the animal's muscles and the time over which that acceleration acts ($V = a \bullet t$). Acceleration is increased by powerful leg muscles, and the amount of time acceleration acts is increased by long legs because the feet remain in contact with the substrate longer.

Although the contributions of individual muscles change in a complex fashion as the hindlimbs straighten, the primary propulsive muscles include a series that retract the femur (semimembranosus, semitendinosus, and gracilis major), a pair that straighten the knee (gluteus maximus and cruralis), and one that extends from the tibiofibula around the ankle to the tarsals and straightens the ankle joint (plantaris longus) (see Figure 10.7B). Together these muscles comprise 60% of the muscle mass of the hindlimbs.

Elastic tendons make an important contribution to acceleration (Astley and Roberts 2012). In the leopard frog (*Rana pipiens*) the plantaris longus muscle, which straightens the ankle joint during jumping, begins to contract well before any bone movement can be detected, storing energy in the tendon until suddenly the ankle joint opens in a burst of acceleration. The catch mechanism, which locks the limb during tendon loading, has not yet been identified, but it may be as simple as the resistance that results from the resting frog's mass, a so-called inertial catch (Roberts and Marsh 2003). Elastic recoil also contributes to retraction of the hindlimbs while the frog is in the air (Schnyer et al. 2014).

Not all frogs are strong jumpers, and the morphological distinctions underlying different locomotor modes in frogs were explored by Sharon Emerson (1982, 1983, 1985). Several features of the pelvic girdle and sacrum tend to vary in concert and constitute a functional unit.

- Strong jumpers such as *Rana* have relatively short ilia, and the sacral diapophyses are round in cross section, allowing the ilia to rotate around them as the trunk is straightened during takeoff.
- Most hopping and walking anurans, such as *Bufo*, have iliosacral joints that permit the ilia to swing laterally.



Figure 10.7 Anatomy of a frog's jump. (A) Long, multiply jointed hindlimbs and the iliosacral articulation (the junction of the vertebral column with the pelvic girdle, clearly visible on many species; *Rana temporaria* is shown here) contribute to a frog's ability to launch itself off the substrate. (B) Four groups of powerful muscles contract during the jump. (1) Muscles that extend across the iliosacral articulation (including the longissimus dorsi and the iliolumbaris) raise the frog's trunk. (2) Muscles that extend from the rear of the pelvic girdle to the

femur (primarily the semimembranosus, semitendinosus, and gracilis major) retract the femur, initiating the jump. (3) Muscles that extend from the pelvic girdle across the front of the knee to the tibiofibula (including the gluteus maximus and cruralis) straighten the knee. (4) The plantaris longus extends from the tibiofibula around the ankle to the tarsals and straightens the ankle joint. Several groups of muscles act around the limb joints simultaneously, and the propulsive forces they generate are additive. (Photograph © CreativeNature/R. Zwerver/Shutterstock.)

Figure 10.8 A European common frog (*Rana temporaria*) illustrates the characteristics that maximize jump distance. The very long hindlimbs and feet extend the time through which force can be applied, increasing the acceleration. A 45° takeoff angle maximizes the distance jumped. Midair flexion of the hindlimbs positions them for the next jump. (Photograph © Stephen Dalton/ Minden Pictures/Corbis.)



A third sacral condition consists of broadly expanded sacral diapophyses enveloped by a wide ligament that permits the ilia to slide anteroposteriorly. This condition is found in a range of specialized taxa, including some branch-walking species such as *Agalychnis* (Hylidae), fossorial species such as *Scaphiopus* and *Spea* (Scaphiopodidae), and specialized swimmers including *Xenopus* and *Pipa* (Pipidae). In all of these taxa, pelvic sliding contributes to thrust.

Analysis of these skeletal features and locomotor behaviors in a phylogenetic context reveals that moderately expanded sacral diapophyses and lateral bending at the pelvic joint characterize basal frog lineages and their extinct precursors (Reilly and Jorgensen 2011; Jorgensen and Reilly 2013). This conclusion suggests that the earliest frogs were hoppers rather than leapers.

Frogs land on their forelimbs, which are extended while the frog is in the air (see Figures 10.7 and 10.8) until the elbow is nearly straight. The elbow flexes on landing, absorbing some of the shock of impact and transmitting it to the pectoral girdle (Gillis et al. 2014). Toads are unusual; instead of stopping after each jump, they rotate on their extended forelimbs, land on their hindfeet, and jump again. This bounding gait maintains velocity and increases the distance moved with each hop (Reilly et al. 2015).

10.5 Terrestrial Limbless Locomotion

Reduction or loss of limbs has been a recurrent evolutionary theme among amphibians and reptiles (see Chapters 3 and 4). Caecilians (except for one extinct species), pygopodids, amphisbaenians (with the exception of one genus), and snakes (except for a few extinct species) are functionally limbless from the standpoint of locomotion. In addition, many lizard families (notably Scincidae and Anguidae) include species that exhibit partial or complete reduction of limbs, often with numerous intermediate conditions represented among living forms. Indeed, functional limblessness, in which the limbs are no longer used effectively for locomotion, has evolved at least 25 times in Squamata (Weins et al. 2006; Sites et al. 2011). Limb reduction also occurs in several genera in the plethodontid subfamily Hemidactyliinae, including Batrachoseps, Lineatriton, and Oedipina. Many species of terrestrial salamanders fold their legs against the body and move with snakelike undulations when they are escaping from a predator (Edwards 1985). Limb reduction generally is associated with elongation of the body. In snakes such elongation appears to have evolved by speeding up the rate at which somites, the embryonic precursors of vertebrae, form during early embryogenesis (Gomez et al. 2008).

Terrestrial limbless locomotion has been studied most extensively in snakes, which exhibit the greatest diversity of movement patterns among limbless taxa. The modes of locomotion used by snakes have inspired engineers to create robotic snakes for tasks as diverse as urban search and rescue and exploration of extraterrestrial bodies (Bogue 2014; Lou et al. 2014; Marvi et al. 2014). The anatomical basis for the locomotor system of snakes consists of large numbers of vertebrae and multisegmental muscle chains, some of which span more than 40 vertebrae (**Figure 10.9**) (Gasc 1981).

Lateral undulation is the most widely used and familiar locomotor mode of snakes. Horizontal waves travel down alternate sides of the body axis and generate force at fixed points in the animal's physical environment. During lateral undulation, segmental units of the three primary lateral muscle masses (the spinalis-semispinalis, longissimus dorsi, and iliocostalis) on one side of the body contract almost synchronously at any one point along the body (Jayne 1988a,b).

Initially studies of undulatory locomotion emphasized the role of major surface irregularities—rocks, sticks, and the like—which have usually been referred to by the French



Figure 10.9 The axial muscles of snakes are complex.

(A) A dissection of the Sahara sand viper (*Cerastes vipera*) shows the overlapping segmental units of each muscle mass. (B) A view of single segmental units of the major axial muscles of the banded water snake (*Nerodia fasciata*) shows that several of the muscles are linked through their tendons into chains that span many vertebrae. For example, a single segmental unit of the lon-

term *points d'appuis* ("points of application" of force; also called pivot points). The body pushes posterolaterally on each point, eliciting a reaction force that has both lateral and anterior components (**Figure 10.10**). The lateral components of the reaction forces at the *points d'appuis* cancel each other, leaving a net forward reaction force for propulsion.

Recent studies have revealed an important role for friction in generating propulsive force. Snakes lift portions of their body slightly in regions where friction opposes forward motion, increasing speed by 35% and locomotor efficiency by 50% (Goldman and Hu 2010).

Concertina locomotion is employed on low-friction surfaces, in climbing tree trunks, and in confined spaces such as rodent burrows, where lateral undulations are not possible. A portion of the body is anchored against the walls of the burrow while another portion is moved (**Figure 10.11**). For example, the anterior region of the body may remain stationary while the posterior end is drawn up behind it in a series of tight curves. Next, with the posterior end anchored, the anterior region is extended forward and the se-

gissimus dorsi is connected by a tendon to a single, more anterior unit of the semispinalis and by another tendon to a unit of the iliocostalis. These segmental units are stacked against the vertebral column, as seen in (A). Contraction of these muscle chains causes the lateral bending that is the basis for locomotion. (A, after Cundall 1987; B, after Jayne 1985, 1988a.)

quence is repeated. Some snakes may rotate their ventral scales to dig into the substrate (Marvi and Hu 2012), and arboreal snakes may use a prehensile tail to grasp a branch.

Concertina locomotion is relatively slow. The banded water snake (*Nerodia fasciata*) can travel 1.88 times its length per second using lateral undulation, but only 0.05 times its length using concertina locomotion, and speed decreases on inclines. Concertina locomotion also is energetically costly, requiring seven times more energy than lateral undulation for the black racer (*Coluber constrictor*) (Walton et al. 1990).

Sidewinding is associated with low-friction or shifting substrates, generally sand dunes and mud. Most snakes appear to be capable of sidewinding, and some, such as *Cerberus*, Australasian colubrids that inhabit mudflats, use that mode when frictional resistance is insufficient for lateral undulation. The most specialized sidewinders, however, are inhabitants of shifting sand dunes, such as the sidewinder rattlesnake (*Crotalus cerastes*) of the American Southwest, and several desert-dwelling Asian and African viperines, including Peringuey's adder (*Bitis peringueyi*).



d'appuis. (B) The magnitude and direction of forces acting against the body at a single point. The thrust of the snake's body against an object (F_i) elicits an equal and opposite reaction force (R), which can be resolved into lateral (F_i) and forward (F_i) components. The lateral components of the reaction forces from each point, directed to the right and left, cancel each other, while the forward components are additive and contribute to forward movement. (C) Tracings of a rat snake (*Pantherophis*) passing through a field of vertical pegs. The interval between each tracing is 0.17 s. Arrows show the direction of the forces applied by the snake to the pegs. Note that the snake continues to push against the same pegs with progressively more posterior parts of its body as it moves. (A,B, after Hildebrand 1995; C, after Gans 1974.)

Figure 10.11 Concertina locomotion by a corn snake (*Pantherophis guttatus*).

(A) When a corn snake crawls through a narrow tube, it presses a portion of its body against the sides of the tube (shaded areas) and extends the unanchored portion forward. By alternating the static and unanchored points, the snake advances through the tube. (B) The same snake crawling along the top of a branch also uses concertina locomotion, but in this situation it grasps the branch to anchor one or more portions of its body (shaded areas) while it advances the unanchored portion. The times of successive images are given on the left side of each tracing. (After Astley and Jayne 2009.)





Figure 10.12 Sidewinding on loose sand. Because sidewinding exerts force downward rather than horizontally, it is an effective mode of locomotion on loose sand. (A) A North American sidewinder rattlesnake (*Crotalus cerastes*) showing five successive positions. (B) The track left by a Peringuey's adder (*Bitis peringueyi*) crossing windblown sand in the Namib Desert of Africa. (A, after Gans 1974; B, photograph © Theo Allofs/Corbis.)

Watching a sidewinder can be a bewildering experience because loops of the body appear to be thrown in all directions. However, sidewinding is a highly ordered process in which virtually all forces directed against the substrate act vertically, avoiding the slipping that would result if the body pushed against loose sand at an angle. Sections of the body are alternately lifted, moved forward, and then set back down (**Figure 10.12**), producing a series of separate, parallel tracks, each oriented at an angle to the direction of travel. The snake itself usually is in contact with the ground at two points. Using this extraordinary locomotor pattern, *Crotalus cerastes* can probably attain forward velocities of twice its body length per second.

Rectilinear locomotion does not rely on alternating contraction of the lateral muscle masses of the trunk. Instead, muscles on both sides of the body act synchronously, sequentially contracting and relaxing to draw the body



forward in a more or less straight line (hence the name) (Figure 10.13). Generally, several waves of such symmetrical contractions pass down the body simultaneously, establishing several points of static contact with the substrate and presenting an appearance that the ventrolateral skin is crawling on its own while the dorsal skin moves at a nearly even rate. Although most snakes can employ rectilinear locomotion, it is most commonly used by heavy-bodied snakes such as large boas, pythons, and vipers (Edwards 1985; Marvi et al. 2013).

10.6 Aquatic Locomotion

Aquatic locomotion differs in two important respects from locomotion on land, and both reflect the physical properties of water. Water is both dense and viscous, features that simultaneously enhance and detract from locomotor efficiency. Water provides greater support against the force of gravity than does air, and its density makes it possible to elicit substantial reaction forces for propulsion. However, it is also heavy to move and difficult to push through, requiring considerable power for locomotion.

All animals that swim encounter resistance due to the viscosity of water. That resistance is known as drag, which



Figure 10.13 Rectilinear locomotion by the boa constrictor (*Boa constrictor*). The body wall has been cut away to reveal the ribs. The superior costocutaneous muscles (blue) angle up and forward, and the inferior costocutaneous muscles (red) angle up and back. Only every tenth rib, muscle, and ventral scale are shown. The superior costocutaneous pulls the skin anteriorly, after which the inferior costocutaneous pulls on the ribs, drawing the body forward. Waves of bilateral contraction of the costocutaneous muscles pass posteriorly, alternately stretching, fixing, contracting, and moving the skin. (After Gans 1974.)

arises from several sources. The most important for amphibians and reptiles is surface drag, which results from layers of water sliding past the body. A thin layer of water, known as the boundary layer, adheres to the surface of the animal and moves with it. Beyond the boundary layer, the water is pulled along at a velocity that decreases with increasing distance from the moving body.

Lift is a component of the hydrodynamic force that is generated when certain shapes pass through water. A relatively thin, curved (cambered) structure passing at an angle through the water separates the fluid so that water passes more quickly around one side than the other (**Figure 10.14**). The result is a pressure differential that moves the structure toward the convex surface. The component of that motion that acts at right angles to the surface drag is defined as lift. Importantly, the direction of lift is defined in reference to the direction of drag, which in turn is determined by the direction in which the hydrofoil moves.



Figure 10.14 Generation of lift by a cambered hydrofoil passing downward through water. A thin, curved (cambered) structure moving through the water acts as a hydrofoil, eliciting a hydrodynamic reaction force that can be resolved into drag (a component acting in the direction opposite to the motion) and lift (a force at right angles to drag). In the situation shown lift is inclined forward, indicating that there is a forward propulsive component to its action.

Undulatory swimmers

Undulatory swimmers, which include many aquatic amphibians and reptiles, generate waves of movement along their bodies. Aquatic salamanders, including larvae, propel themselves primarily by axial undulation. Some species, such as *Necturus*, have a laterally compressed tail that displaces a large water mass with each stroke. Elongate aquatic salamanders such as *Amphiuma* and *Siren* often have a laterally compressed cross section in the rear of the body, as do typhlonectid caecilians.

Aquatic locomotion by snakes resembles terrestrial locomotion, but there are important differences. When swimming, snakes produce regular axial waves that increase in amplitude (lateral extent) posteriorly (**Figure 10.15**) (Jayne 1985), whereas terrestrial locomotion involves the application of force at fixed points and a tendency for waves to dampen posteriorly. Many aquatic snakes have modifications that increase their lateral surface area. *Acrochordus* have loose skin that hangs down when an animal swims, forming a compressed ventral keel. Marine snakes such as *Laticauda* and *Hydrophis* have strongly compressed tails that may generate lift. Even the water snake *Nerodia sipedon* alters its body shape during swimming by actively rotating its ribs so as to deepen and compress its body (Pattishall and Cundall 2008).

tory propulsion involves the paired appendages rather than the axial skeleton, it is employed by two lineages that have limited lateral flexion of the vertebral column: frogs and turtles.

ANURANS Frogs usually swim with synchronous extension of their hindlimbs, and aquatic species typically have large, webbed hindfeet. Their movement in water has been described as a kick and glide system in which the power stroke is followed by a period when the body continues to move forward under its own momentum (Richards 2010). Only about the first half of leg extension provides useful forward thrust, but the legs continue to be held in the extended position behind the body to maintain streamlining and reduce drag.

The unusual sacral articulation of the fully aquatic pipid frogs permits anteroposterior sliding of the ilia relative to the sacral diapophyses. The African clawed frog (*Xenopus laevis*) can extend its body nearly 20% beyond its contracted length (**Figure 10.16**), with the extra extension contributing to propulsion in the same manner as the sliding seat of a rowing shell (Videler and Jorna 1985). The contribution of the sliding pelvis to power production is unclear (Robovska-Havelkova et al. 2014).

Oscillatory swimmers

Oscillatory swimmers use limbs that move forward and backward like a human swimmer's arms. Because oscilla-



Figure 10.15 Undulatory swimming by a banded water snake (Nerodia fasciata). The lines on the grid are 5 cm apart. Successive tracings at intervals of 0.021 s have been displaced to the right by one square of the grid. Note the increase in amplitude (lateral extent) of waves of the body posteriorly. Compare this figure, in which smooth waves move continuously along the length of the body, with Figure 10.10, in which the body forms irregular curves that remain fixed relative to the environment. (After Jayne 1985.)



Figure 10.16 The sliding pelvis of the African clawed frog (*Xenopus laevis*). The relationship of the pelvic girdle to the sacrum is shown during contraction (left) and extension (right). The extended length of the body can be nearly 20% greater than the contracted length. (After Videler and Jorna 1985.)



TURTLES Most aquatic turtles use their webbed feet to produce forward thrust (Rivera et al. 2006, 2011). Typically the forelimb on one side and the hindlimb on the other side move synchronously, a pattern that minimizes side-to-side movement and provides stability. Aquatic turtles are highly maneuverable, generally extending one of their forelimbs just as a rower extends an oar to generate drag and turn sharply.

The greatest morphological specialization for oscillatory propulsion is seen in the marine turtles of the families Cheloniidae and Dermochelvidae. Sea turtles generate lift-based propulsion with their forelimbs, which are modified into elongate, winglike paddles, with the forearm and forefoot fully bound together into a blade borne on a short humerus. Rapid movement in open water involves synchro-



Figure 10.17 Oscillatory swimming by a young green sea turtle (Chelonia mydas). (A) The axis of the body pitches up and down through the forelimb cycle. (Traced from a video recording; the interval between frames is about 2 s.) (B) The tip of the forelimb describes a figure 8 around the horizontal plane of the body. By twisting the limb to change its angle of attack (i.e., the angle it cuts through the water), the forelimb provides

nous movement of the forelimbs, combining retraction with

Adjustment in the angle of the forelimbs during protraction and retraction generates a forward component of lift on both the downstroke and the upstroke (Davenport et al. 1984). (Birds also are capable of generating lift during both phases of the wing cycle, and marine turtles can be thought of as flying through the water.)

10.7 Burrowing

Fossorial amphibians and reptiles dig in substrates of varying consistency. Frogs in several families burrow, and most species use a modification of the hindlimb motion employed in jumping to dig themselves into the ground backward. An enlarged metatarsal tubercle forms a sharp digging blade on the underside of the hindfoot of many burrowing anurans (Figure 10.18), and the legs are extended alternately, turning the foot upward to expose the tubercle (Emerson 1976). The forelimbs brace the frog against forward displacement during digging. The hindlegs of burrowing frogs are relatively short, increasing the force exerted by the leg muscles during digging, but sacrificing jumping ability.

Hemisus, which are among the few frogs that dig headfirst, bend their head downward, bringing the snout into contact with the ground to serve as a brace while the forelimbs alternately scoop soil out and back. Major musculoskeletal modifications are associated with both flexion of

Figure 10.18 The spade on the hindfoot of an eastern spadefoot toad (Scaphiopus holbrookii). This enlarged metatarsal tubercule (arrow) is used in burrowing. (Photograph by R. D. Bartlett.)

the head and retraction of the forelimbs, including a threefold increase in the size of the retractor muscles (Emerson 1976). *Hemisus* also have an enlarged metatarsal tubercle and sometimes use the hindlimbs to initiate digging before switching to forelimb excavation. The Australian turtle frog (*Myobatrachus gouldii*) uses its forelimbs to dig in search of termites and its large hindlimbs to consolidate the soil.

Many fossorial species occur among limbless lineages of amphibians and reptiles, including caecilians, amphisbaenians, and snakes. Specializations of burrowing squamates often include smooth skin, a reduced number of scales, and secondary contacts between bones that impart rigidity to the normally highly flexible skull (Savitzky 1983).

Some burrowers, including caecilians and uropeltid snakes, use internal concertina flexion of the vertebral column to anchor themselves as they burrow (Figure 10.19). The skin is only loosely connected to the axial muscles, so vertebral flexion presses the sides of the body against the walls of the tunnel, both widening the tunnel and providing a static platform for further penetration.

Uropeltids have evolved a remarkable division of labor between the anterior and posterior ends of the body (Gans et al. 1978). The powerful anterior axial muscles draw the anterior end of the vertebral column into a series of concertina flexions from which the pointed skull is thrust forward through the soil. The posterior end of the body, which has weak axial muscles, serves mainly as a passive vessel for the viscera. The muscles at the anterior end of the body have high oxidative metabolic capacity, whereas those at the posterior end are primarily glycolytic. This condition has been likened to the design of a freight train, in which an engine pulls a load of cargo behind it.



Figure 10.19 Internal concertina locomotion during burrowing. The skin of some burrowing squamates is loosely attached to the trunk muscles and ribs. These species can anchor themselves in a tunnel by flexing the vertebral column to increase the diameter of a portion of the body. (A) The sharply pointed head of Schneider's shield-tail snake (*Rhinophis axyrhynchus*) is used for burrowing. (B) A cycle of movement begins (i) as the anterior portion of the vertebral column bends, anchoring the body against the burrow wall. (ii) The anterior portion of that bend straightens, pushing the pointed skull forward to lengthen the tunnel while the posterior portion remains bent and continues to anchor the snake. (iii) Finally, the entire anterior portion of the vertebral column bends, allowing the snake to draw the posterior portion of its body forward. (C) The small-headed worm lizard (*Amphisbaena microcephalum*) has a shovel-shaped snout that it uses for burrowing. (D) The lizard bends its vertebral column to press its body against the walls of the tunnel, anchoring itself as it moves backward following excavation. (Photographs: A, by Anselm de Silva; C, by Leandro dos Santos Lima Hohl; D, from Hohl et al. 2014.) (A)



Most amphisbaenian species have rounded heads that they use as a battering ram. These species thrust the head forward to first loosen the soil and then compact it into the tunnel walls.

(C)



Trogonophiids have a short skull covered with heavy scales that form a ridge around the snout. These species drill tunnels, using a twisting movement of the head to shave soil from the end of the tunnel, then compacting the loose soil into the tunnel walls with the sides of the head.

Figure 10.20 The snouts of amphisbaenians reveal their methods of burrowing. These images, created by highresolution X-ray computed tomography, show four skull shapes that are characteristic of amphisbaenians. (A) Rounded head,

Most amphisbaenians use their heads for burrowing (Figure 10.20) Round-headed species use their blunt head to loosen soil from the face of the tunnel. Shovel-snouted forms force their sharp snout into the soil, then lift the head to pack the loosened soil against the ceiling of the tunnel. Keel-headed amphisbaenians ram their snout into the soil and then flex the neck sideward to widen the opening. Many trogonophiids have a heavy scale on the snout and employ a rotary (drilling) motion to shave soil away from the face of the tunnel. *Bipes*, the only amphisbaenians with limbs, have a blunt snout and use their short forelimbs for scratch-digging, as well as for moving the front end of the body during surface activity.

Although caecilians move by lateral undulation while on the surface, swimming, or moving through loose soil, they employ internal concertina locomotion when burrowing in harder, more tightly compacted soils (Gaymer 1971; Summers and O'Reilly 1997). The axial musculature is separated (B)

Some amphisbaenians have a shovel-headed morphology with a sloping, dorsoventrally flattened snout. These species burrow by thrusting the head forward and slightly downward, then lifting the head and compressing soil into the roof of the tunnel with their snouts.

(D)



The laterally compressed skulls of keel-headed species have bladelike snouts that are driven into the end of the tunnel. The head is then bent left and right, pressing the loosened soil into the walls of the tunnel with the sides of the head.

exemplified here by *Amphisbaena alba*. (B) Shovel-shaped head, as in *Amphisbanea microcephalum*, (C) A drilling head is seen in species such as *Diplometopon zarudnyi*. (D) Keel-headed morphology in *Anops kingii*. (Photographs © DigiMorph.org.)

from the skin and lateral muscles of the body wall. Thus, as in uropeltid snakes and some amphisbaenians, concertina flexion of the vertebral column increases the diameter of the body, anchoring it during tunnel extension. The force produced during such locomotion is further enhanced by a novel arrangement of the muscles and connective tissues of the body wall. Some of those muscles attach to sheets of connective tissue containing crossed helical arrays of fibers (O'Reilly et al. 1997). As vertical muscles in the body wall contract, hydrostatic pressure within the body cavity increases, rendering the body rigid. Meanwhile, oblique muscles contract and pull on the helical sheets, shifting the angle of the fibers and propelling the body wall forward. The combination of the rigid body and the forward-moving body wall adds to the anteriorly directed force of the skull against the soil. Measurements show that caecilians using this system can generate about twice as much force as fossorial snakes of similar size.



Figure 10.21 Sand-swimming squamates have wedgeshaped snouts, countersunk lower jaws, and smooth scales. (A) An Arabian sandfish (*Scincus mitranus*). (B) A banded sand snake (*Chilomeniscus stramineus*). (Photographs: A, R. D. Bartlett; B, Wayne Van Devender.)

Loose sand presents unique challenges to fossorial species. Some lizards, such as the North American fringe-footed lizards (Uma) and the African dune lizards (Meroles) are sand-divers. These species bury themselves shallowly in sand to escape from predators, but move only a couple of body lengths after they enter the sand. Burrowing through sand presents a challenge because is not possible to create open tunnels in loose sand; the sand collapses behind an animal as it progresses. Furthermore, sand generates substantial friction around the body surface of a moving animal. Sand-swimmers, the most specialized sand-dwelling squamates, have wedge-shaped heads that penetrate sand, countersunk lower jaws that prevent sand grains from being forced into the mouth, and smooth scales that minimize friction (Figure 10.21). Sandfish (Scincus) can bury themselves completely in less than 1 s, submerging to a depth of 2-4 cm (Maladen et al. 2009; Goldman and Hu 2010). The limbs are tucked close to the body, and the lizards rely on strong flexion of the vertebral column to generate propulsion, achieving speeds of nearly two body lengths per second. Curiously, these lizards move more rapidly when sand grains are packed tightly. Mathematical modeling of their locomotion revealed that, even as resistance increased with tighter packing, so did the thrust that the lizards could generate.

Ventilation of the lungs poses a unique problem under sand. In most squamates, expiration involves compression of the ribs, which reduces the diameter of the body. In sand-swimmers, however, sand would immediately fill the surrounding space, preventing subsequent inspiration. Instead, sand-divers and sand-swimmers raise and lower their ventral surface when breathing. The ribs prevent sand from entering the void created beneath the animal during expiration, leaving an open space for subsequent ventilatory movements (Pough 1969).



10.8 Climbing

Many amphibians and reptiles are climbers. Grasping climbers use their tail, feet, or toes to hold the object they are climbing, whereas adhering climbers use specialized areas of skin on the feet and tail to fasten themselves to surfaces.

Grasping

Many amphibians and reptiles can climb stems, twigs, and branches by grasping them with their fingers and toes, and lizards can gain purchase on larger surfaces, such as tree trunks and rocks, by using claws to cling to irregularities (**Figure 10.22A**). Chameleons are well known for having feet that are specialized for climbing. Their fused zygodactylous toes form opposing pincers that can grasp a twig and provide such stable support that a chameleon can simultaneously disengage one forefoot and the hindfoot on the opposite side, maintaining its balance with the remaining two feet as it steps forward.

Keeping the center of gravity directly above the twig is important to this balancing act, and a chameleon's locomotion is unlike that of any other lizard. Chameleons keep their vertebral column nearly straight as they walk, rather than creating lateral bends as other lizards do, and the feet are placed directly beneath the body so that the limbs move in the parasagittal plane (**Figure 10.22B–E**). X-ray films of chameleons show that some bending occurs in the posterior portion of the vertebral column, and that horizontal movement of the pelvic girdle contributes to the stride length (Fischer et al. 2010; Higham and Anderson 2014).

Prehensile tails, another method of grasping during climbing, are phylogenetically widespread, being found among salamanders (*Bolitoglossa*), skinks (*Corucia zebrata* and *Prasinohaema prehensicauda*), and geckos (some species of *Diplodactylus*, *Gehyra*, *Oedura*, *Pseudothecodactylus*, and *Rhacodactylus*), as well as among large-bodied species of chameleons. Many arboreal snakes grasp with their posterior body and tail.

Some arboreal snakes move by gap-bridging, extending their body forward as a cantilever, unsupported against



Figure 10.22 Chameleons have a specialized form of locomotion. (A) The limbs of most lizards project horizontally, and lateral undulation of the vertebral column increases stride length, as shown by these tracings of a walking rainbow lizard (Agama agama). (B) In contrast, the limbs of chameleons are held close to the body and lateral undulation is greatly reduced, keeping the center of gravity directly above the narrow base of support while gripping a branch. (C-E) Frames from a computer animation of the skeleton of a veiled chameleon (Chamaeleo calyptratus) illustrate its locomotion. (C) Dorsal and lateral views show the extensive parasagittal motion of the limbs. In the lateral view, the left forefoot and right hind foot are grasping a twig, and the right forefoot and left hindfoot are about to release their grasp and move forward. (D,E) Cross sections at the levels of the pectoral girdle (D) and pelvic girdle (E) show that the feet are directly beneath the body. (A,B after Peterson 1984; C-E from Fischer et al. 2010, courtesy of Martin Fischer.)

the force of gravity until it reaches another branch (**Figure 10.23**). Snakes that regularly travel by gap-bridging often have a laterally compressed body and broad vertebral scales that may stiffen the body in the dorsoventral plane. Julie Ray (2012) studied gap-bridging in a community of arboreal snakes in Panama and found that the cantilever ratio (the percentage of the snake's total length that could be extended without support) ranged from 36% to 51%. Small individuals of the brown tree snake (*Boiga irregularis*) of Indonesia and Australia are able to cantilever 64% of their SVL (Jayne and Riley 2007).





Adhesion

Adhesion is an alternative to grasping, and many climbing salamanders, frogs, and lizards have modifications of the feet, toes, and even tails that allow them to adhere to surfaces. Amphibians rely on wet adhesion, whereas reptiles use dry adhesion.

Bolitoglossine salamanders have two different methods of adhering: stickiness and suction, both of which involve fully webbed feet (Alberch 1981; Alberch and Alberch 1981). Capillary adhesion, which relies on surface tension in a lubricating fluid, is sufficient to support a small salamander. Larger arboreal species such as the giant palm salamander, *Bolitoglossa dofleini*, are too heavy to be supported by capillary adhesion. Those species create a suction cup by lifting the center of the foot, which has a reinforced periphery that remains in contact with the substrate.

Many arboreal and rock-dwelling frogs, including hylids, hyperoliids, rhacophorids, and some ranids, have specialized toe pads beneath the tip of each digit, as do plethodontine



Figure 10.23 Gap-bridging by the brown tree snake (Boiga irregularis).

This arboreal species can bridge gaps greater than half of its SVL by crawling or by lunging. The white marks on the body are at intervals of 10% of the snake's SVL, and the times on each panel indicate seconds before contacting the destination perch on the right side of the gap. (A) During crawling, the extended portion of the snake's body is nearly horizontal and straight as the snake moves forward with a rather slow but nearly constant speed (often <10% SVL/s). (B) Snakes can bridge still longer gaps by lunging. The forward progress of the snake often momentarily ceases (-1.73 s to 0.30 s) as it slowly lifts its body in preparation for a lunge that has rapid movement forward along the supporting perch (>60% SVL/s from -0.13 s to contact) and downward movement of the head toward the destination perch. (Photographs by Bruce C. Jayne.)

salamanders in the genus *Aneides*. These pads consist of polygonal epithelial cells with very flat exposed surfaces separated by deep crevices (**Figure 10.24**). Mucus glands that open between the cells secrete mucus. The viscosity of mucus contributes to adhesion, and the adhesive force increases in proportion to the concentration of the mucus solution (Barnes et al. 2006). A dead frog has roughly the same adhesive strength as a live one, but adhesion is lost when a detergent is applied to the substrate (Green 1981).

Toe pad size increases roughly as the square of linear dimensions, whereas body weight increases roughly as the cube of linear dimensions. Because of that relationship, larger species of frogs should be unable to support themselves by capillary adhesion unless their toe pads are modified in some way. A comparison of seven species of hylid frogs from Trinidad revealed that larger species had larger individual cells and a lower density of channels between the cells, disproportionately increasing the area of surface contact with the substrate (Smith et al. 2006). Some frogs have patches of similar tissue on their subarticular tubercles that increase the area of capillary adhesion (see Figure 10.24A).

A frog releases its toe pads by lifting them from the base of the toe toward the tip as the foot is raised (Hanna and Barnes 1991). Frogs are unable to adhere when their toes point straight down because gravity peels the toe pads from the substrate. Treefrogs keep their toes pointing upward even when their body is at an angle to the ground, and they descend trees backward.

Members of some anuran families, such as Hylidae and Centrolenidae, have **intercalary cartilages**, small elements located between the last two phalanges of each toe. The purpose of those structures is unknown, but they may influence the forces acting on the toe pad.

A very different mechanism, called **dry adhesion**, has arisen independently in three lineages of lizards, including many geckoes, the New World genus *Anolis*, and the green tree skink *Prasinohaema virens* from Papua New Guinea. These lizards have **scansors**—pads with

(A) Subarticular tubercule

(C)

Toe pad

(B)

Mucus pore



Circumferential groove



tips. Each seta of the large Asian tokay gecko (*Gekko gecko*) is $30-130 \ \mu\text{m}$ long and branches into about 500 tips, or spatulae, only 0.2–0.5 μm (200–500 nm) wide. (A page of this textbook is about 100,000 nm thick.) A single foot has almost 500,000 setae and is capable of producing about 10 N of force through dry adhesion (Autumn et al. 2000). The epidermis of the scansors is tightly bound to deeper layers of the skin and to the lateral tendons, coupling them to the skeletal and muscular system of the limb.

After placing its foot on the substrate, the lizard draws its limbs slightly toward the body, generating shear forces as the curved setae straighten and their angle relative to the substrate decreases (Autumn et al. 2006). This movement brings the spatulate tips into intimate contact with the substrate (Autumn et al. 2014). However, the setae lose their adhesive force when the setal angle exceeds 30° to the substrate, which occurs as the toes curl up from the surface. This phenomenon allows rapid and coordinated detachment. Like the toe pads of frogs, the scansors of geckos peel off if gravity lifts them from the base of the toe, and therefore geckos keep their toes pointing upward when they descend (Birn-Jeffery and Higham 2014).

Although the adhesive forces are generated by the setae themselves, the scansor system is controlled by tendons and blood vessels (Russell 1975, 1979a, 1981, 1986; Russell and Bauer 1990; Lauff et al. 1993). In the tokay gecko, paired lateral tendons send branches to each lamella. The tendons are assisted in their control of the scansors by a complex hydraulic system that includes a network of blood vessels deep within each lamella and a central venous sinus that may be a fluid reservoir. Together those vascular mechanisms probably facilitate close contact between the scansors and the substrate, and perhaps contribute to control of the scansors' release and reattachment.

Geckos with scansors can climb glass windows and cross ceilings with remarkable agility, sometimes clinging by a single foot. As you might expect, the ability to climb

Figure 10.24 Scanning electron micrographs of the toe pads of a frog. (A) The ventral side of the forefoot of a footflagging frog (*Staurois parvus*) shows the toe pads and the subarticular tubercles. (B) The second digit of the forefoot. The toe pad is defined by a circumferential groove. (C) Polygonal epithelial cells surrounded by deep channels form the surface of the pad. A mucus pore is visible in the center of the image. (From Drotlef et al. 2014; photographs courtesy of Jon Barnes.)

transversely expanded, platelike scales (**lamellae**)—beneath their toe tips (**Figure 10.25**). Each lamella is covered with microscopic **setae** composed of keratin (Autumn et al. 2014). The details of setal morphology differ among lineages, but each seta bears at least one spatulate ending. The setae of geckos and *Anolis* are probably derived from the minute spines that cover most of the body scales in those taxa (Williams and Peterson 1982). Clinging ability increases with increasing area of the digital scansors (Irschick et al. 1996). The system is enhanced in some geckos by scansors beneath the tail.

Attachment by dry adhesion results from van der Waals forces, the attraction between closely associated surfaces produced by transient changes in the distribution of electrons (Autumn et al. 2002). This mechanism requires intimate contact between the surfaces, which is accomplished because the setae possess minute branches with flattened





Figure 10.25 Scansors of the tokay gecko (Gekko gecko). These images demonstrate the structural hierarchy from the whole animal to the individual adhesive surfaces (note the different scale in each photo). (A) A gecko adhering to a glass surface with both forelimbs. (B) Ventral view of a foot, showing the scansors (pads) made up of lamellae (transversely expanded, platelike scales). (C) Electron micrograph of a cross section through an isolated array of setae (bristles). Note the curvature and branching tips of the setae. (D) Tips of a series of setae, which are arranged in groups of four. (E) Branches at the end of a single seta, showing the hundreds of spatular tips. (F) Detail of the minute spatular tips that comprise the adhesive surfaces. (G) Two spatular tips shown in intimate contact with the substrate. (From Autumn et al. 2014, courtesy of Keller Autumn.)

vertical surfaces has attracted the attention of engineers. Climbing devices based on synthetic gecko-foot technology are being developed by the Z-Man program of the Defense Advanced Research Projects Agency (DARPA) and by private industry; two hand-size pads allow a 70 kg human to scale a vertical glass wall (Defense Advanced Research Projects Agency 2014; Hawkes et al. 2015).

(B)

(D)





1 cm



4 um





500 nm

10 µm

100 nm

10.9 Aerial Locomotion

A few amphibians and reptiles have gone beyond simple arboreality to aerial movement, leaping from a tree and traveling horizontally as they drop. Animals that fall at an angle steeper than 45° are considered to parachute, whereas those that fall at an angle flatter than 45° are said to glide.

Unlike the complex aerodynamics of powered flight, the physics of parachuting and gliding are relatively simple, combining the principles of gravitational forces and fluid dynamics (Figure 10.26). Although the distinction between parachuting and gliding is arbitrary, it reflects differences in the relative contributions of lift and drag and has some practical consequences. A parachuting animal's vertical drop exceeds its horizontal travel, whereas a gliding animal travels horizontally farther than it drops. An animal that glides can also parachute, but an animal that parachutes cannot necessarily glide.

Two related variables, body weight and surface area, are frequently modified in parachuting and gliding species.



Figure 10.26 Falling, parachuting, and gliding. Gravity pulls an object toward the center of Earth, and its weight is a force equal to body mass times acceleration due to gravity ($W = m \cdot g$). Aerodynamic resistance (R) is equal in magnitude but opposite in direction to weight. Drag (D) acts opposite to the direction of motion. When an object simply falls straight down (A), drag from air resistance acts straight up, and D = R. In both parachuting (B) and gliding (C), airfoils slow the descent, and the animal travels forward as well as downward. In that case, R can be resolved into two components: drag (D), which again acts opposite to the direction of motion, and lift (L), which acts

at a right angle to drag. Note that as the contribution of lift increases, the angle of descent becomes shallower, and therefore the horizontal distance traveled increases. The magnitude of *L* is inversely related to the wing loading, which is the body weight divided by the area of the airfoil. (D) Relatively small airfoils, like the webbed feet of Wallace's flying frog (*Rhacophorus nigropalmatus*), allow an animal to parachute. (E) Larger airfoils, such as those that Blandford's flying lizard (*Draco blanfordii*) deploys by spreading its ribs, allow gliding. (B,C modified from Norberg 1985; D © Stephen Dalton/Minden Pictures/Corbis; E © John Downer/Nature Picture Library/Corbis.) Lighter animals parachute and glide better than heavy ones. Increasing the surface area exposed to the air increases lift. Thus, specialized parachuting and gliding species have structures such as greater toe webbing or folds of lateral skin that increase their surface area.

Several lineages of extant amphibians and reptiles include species that can parachute and a few that can glide. Some arboreal frogs, including the Mexican fringe-limbed treefrog (*Ecnomiohyla miliaria*), the Central American leaf frog (*Agalychnis spurrelli*), and several species of the Southeast Asian genus *Rhacophorus*, have large feet with extensive webbing between their fingers and toes, and sometimes fringes of skin on their limbs. By spreading their digits and holding their limbs in a bent position at their sides, some of these species can glide at angles as flat as 18° (Emerson and Koehl 1990). Some species of *Rhacophorus* exhibit considerable maneuverability, turning as much as 180° while descending (McCay 2001).

The Puerto Rican coquí (*Eleutherodactylus coqui*) parachutes in the morning from nocturnal foraging sites in trees to diurnal retreats on the forest floor (Stewart 1985). This species has no special morphological features associated with aerial locomotion, but individuals spread their limbs in a manner similar to that of other parachuting frogs and thereby slow their rate of descent. The coquís are so abundant and the behavior so common that for a brief period at dawn, frogs can be heard raining from the trees.

The forests of tropical Asia are home to many other aerial taxa, including several lineages of squamates (Brown et al. 2012). Among lizards, some geckos of the genus Luperosaurus have flaps of skin on their toes and legs, which increase drag and slow descent when the animals fall (Brown et al. 2011). Members of another southeast Asian gekkonid genus, Ptychozoon, have strongly webbed digits and broad flaps of skin, known as patagia, on either side of the body that spread passively when an animal falls, as well as small flaps of skin behind the head and along the tail. Although the webbing and skin flaps may have evolved from smaller cutaneous appendages associated with crypsis, the scales and dermal layers of the flaps are modified in most species of *Ptychozoon* to enhance their stiffness and maintain a cambered profile. Ptychozoon can achieve glide angles as flat as 40° from horizontal, although their total glide path is usually steeper (Russell 1979b; Russell et al. 2001).

The most specialized aerial lizards belong to the more than 40 species of arboreal agamids in the genus *Draco*, known as flying dragons (see Figure 10.26E). Unlike the skin-flap patagia of *Ptychozoon*, the much larger patagia of *Draco* are supported by five to seven elongate ribs and are actively deployed when a lizard jumps. The iliocostalis muscle pulls the first two ribs forward, and the remaining ribs are attached to the first two by ligaments, so this muscular action spreads the entire airfoil. The aerial path can be divided into three phases (Rayner 1981). First, the lizard enters a rapid fall at an angle as steep as 80°, during which time the long tail is raised behind the body. When enough kinetic energy has been accumulated, the tail is lowered to raise the front of the body and the leading edges of the patagia are raised to increase the angle of attack. The lizard enters the horizontal phase of its glide, which can achieve an angle as shallow as 15°. In about half of recorded glides, *Draco* attain an equilibrium condition, in which speed and angle of attack (the angle at which the patagium cuts through the air) remain constant. Just before landing, the tail is again raised and the animal sweeps sharply up before landing gently, usually on a tree trunk. Lizards jumping from a height of 10 m can glide as far as 60 m and land less than 2 m below their launch height.

Interestingly, species of Draco span an order of magnitude in body mass from about 3 g to 35 g. Without a proportional increase in the size of the patagia, projected area increases as the square of body length, whereas mass increases as its cube. However, patagium size appears to be constrained (the ribs must fold to the sides of the body, between the fore- and hindlimbs), and therefore larger species of Draco have higher wing loading (weight divided by the area of the patagium). Consequently, larger species descend more rapidly than their smaller congeners and must achieve higher speeds during the dive before they enter a level glide (McGuire and Dudley 2005). As many as seven species of Draco occur sympatrically, and the larger species typically occupy higher strata of the forest, from which they can safely descend far enough to gain the speed necessary to generate adequate lift (McGuire and Dudley 2005).

Gliding by squamates is not limited to lizards. Like *Draco*, Asian colubrid snakes of the genus *Chrysopelea* glide by spreading their ribs as they fall, achieving an angle of descent as flat as 13°. At least one species, the paradise tree snake (*C. paradisi;* **Figure 10.27**), also exhibits a remarkable degree of control, maneuvering to avoid obstacles while airborne (Socha 2002).

A recent series of studies of this remarkable glider has begun to explain how the slender body of a snake can be transformed into an undulating wing (summarized in Socha 2011). In about three-quarters of the observed takeoffs, the snake hangs from a branch by its tail, with its head elevated, a so-called anchored J-loop takeoff. The snake then rapidly raises its body to or above the horizontal plane and, sending a traveling wave backward along the body axis, pushes itself from the perch. The initial propulsive force probably helps increase speed, and therefore lift, at the start of the glide. As the snake launches itself, the entire body flattens dramatically as the ribs extend dorsolaterally; the midbody roughly doubles in width from its rounded resting shape.

The snake's body undulates conspicuously as it glides. Recent experiments using models of the snake's cross section have shown that the concave body shape generates considerable lift within a broad range of angles of attack (20–60°, peaking at 35°) (Holden et al. 2014). The head and anterior body remain nearly stable as the snake descends (Socha et al. 2010). How *Chrysopelea paradisi* maneuvers while airborne, dramatically changing its trajectory to alter its landing site or avoid obstacles, remains unknown. One possibility is that changes in body shape, mediated by the ribs, play a role (Socha 2011). As with *Draco*, smaller individuals appear to be better gliders (Socha and LaBarbera 2005). The remarkable ability of a slender, wingless reptile to glide so effectively, in a manner still not completely understood, emphasizes how much remains to be learned about the diverse locomotor modes of reptiles and amphibians.

(B)





Figure 10.27 Gliding by the paradise tree snake (*Chrysopelea paradisi*). (A) Body shape as the snake rests on a perch. (B) As the snake launches itself into a glide, the body flattens dramatically as the snake undulates the body. (C) The snake's body assumes a broadly rounded triangular shape that is concave ventrally. (Photographs by Jake Socha.)

SUMMARY

Amphibians and reptiles occupy a wide range of habitats and exhibit an equally diverse array of locomotor modes and associated morphologies and behaviors.

Several alternative solutions to the same locomotor challenge may exist, often depending on the evolutionary starting points of the lineages involved.

Body support and locomotion in amphibians and reptiles are governed by the laws of Newtonian mechanics.

- Motion results from the reaction force that the environment exerts on the animal, in response to the animal's muscular activity.
- Animals must be supported against the force of gravity. In limbed terrestrial species, the center of gravity must remain over the base of support provided by the limbs.
- Most quadrupeds have a lateral footfall pattern that generates broad triangles of support as the animal lifts and places its feet.

Bones and muscles form lever systems that can amplify the power or speed of movement.

Every lever consists of an in-lever, an out-lever, and a fulcrum.

- First-class and third-class levers are common in vertebrate musculoskeletal systems.
- Lever systems often involve antagonistic pairs of muscles that produce opposing motions around the same joint.

■ Locomotion by means of sprawling limbs and lateral undulation of the vertebral column is characteristic of most salamanders, lizards, and to a lesser degree, crocodylians when they move on land.

- Some lizards can run bipedally on their hindlimbs, and a few larger species are specialized for extended bipedal locomotion.
- The quadrupedal locomotion of extant crocodylians may have evolved from a bipedal ancestral stance. Crocodylians often employ a high walk, and young crocodylians of some species can use a bounding gait.

Turtles are unable to use lateral undulation, and despite their broad base of support, turtles often exhibit brief periods of instability as they walk.

Jumping anurans use synchronous hindlimb movements to launch themselves into the air, and they cushion their landing with their forelimbs.

- Jumping involves rapid extension of the hindlimbs and is governed by the laws of ballistic motion. Long hindlimbs increase the time that force can be applied to the substrate and allow higher takeoff velocities.
- Elastic tendons store muscular energy before takeoff and rapidly release that energy during a jump.
- The structure of the pelvic girdle and its articulation with the sacral vertebra are related to locomotor modes in anurans.

Limb reduction or loss has occurred in many lineages of amphibians and reptiles.

Snakes exhibit the most varied modes of limbless locomotion. Some modes are associated most frequently with specific habitats or with large body size, and many species are capable of using more than one locomotor mode.

The most common mode of locomotion in snakes is lateral undulation, in which points along the body push against surface irregularities or generate points of friction against the substrate.

Concertina locomotion is employed in confined spaces such as rodent burrows, where lateral undulation is not effective. A portion of the body is anchored against the walls of the burrow while another portion is moved. It is relatively slow and energetically costly.

Sidewinding is used on low-friction surfaces, such as loose sand and mud, and applies force vertically rather than horizontally.

Rectilinear locomotion is produced by waves of contraction that sequentially raise, protract, and lower regions of the ventral skin. It is used most commonly by heavy-bodied snakes.

Aquatic locomotion may involve either undulatory or oscillatory movements.

The principles of fluid dynamics, especially lift and drag, govern both aquatic and aerial locomotion, although the different densities of water and air result in many different locomotor solutions.

Many aquatic amphibians and reptiles, especially elongate species, are undulatory swimmers, generating waves of movement along their body.

Oscillatory swimmers use limbs that move forward and backward, as in a human swimmer. Because oscillatory propulsion involves the paired appendages rather than the axial skeleton, it is employed by two lineages that have limited lateral flexion of the vertebral column, frogs and turtles.

Oscillatory locomotion can be lift-based (sea turtles) or drag-based (frogs and freshwater turtles).

Many amphibians and reptiles are burrowers, employing diverse mechanisms for traveling through soil or sand.

Some burrowing frogs dig with the hindfoot, which features an enlarged, bladelike metatarsal tubercle.

Many burrowing amphibians and reptiles are limbless and possess strongly reinforced skulls used to penetrate the soil. Several groups of limbless burrowers employ internal concertina locomotion, in which the vertebral column flexes independently of the skin.

Many lizards are sand-divers, propelling themselves headfirst into loose sand to escape from predators.

Some lizards and snakes are sand-swimmers, moving by lateral undulation beneath the surface of loose sand.

Many amphibians and reptiles are climbers and may rely on either grasping or adhesion.

Climbers may grasp branches with fingers, toes, and/ or claws. Prehensile tails also occur in many amphibian and reptilian climbers.

Chameleons possess zygodactylous feet with opposable digits that effectively grasp branches.

Among adhering climbers, amphibians rely on wet adhesion and reptiles rely on dry adhesion.

The toe pads of arboreal frogs have flat surfaces moistened by mucus to provide wet adhesion between the foot and the substrate.

Many geckos, anoles, and a few skinks have scansors that provide dry adhesion. This system relies on an intimate association between the substrate and keratinous setae on the digits, which generate forces at the molecular level.

A few species have evolved specializations for aerial locomotion, leaping from a perch and traveling horizontally as they drop.

Animals that fall at an angle steeper than 45° are said to parachute. Those that fall at an angle flatter than 45° are said to glide.

Some arboreal frogs and lizards are capable of parachuting, and a smaller number possess airfoils that generate sufficient lift to sustain gliding.

The most specialized gliding lizards are in the agamid genus *Draco* and have expanded ribs that support extensive skin flaps called patagia.

One genus of colubrid snakes, *Chrysopelea*, is capable of gliding, generating lift by greatly flattening the body.

Go to the *Herpetology* Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

11 Feeding

A mphibians and reptiles exhibit an extraordinary diversity of feeding modes, mirroring their range of habitats and the wide variety of foods consumed in water or on land. Most species are carnivorous (including many that eat arthropods), and prey capture is enhanced in several groups by the use of a projectile tongue, which is fired from the mouth to ensnare the prey. Other species engulf prey with mobile cranial bones organized into complex linkages and controlled by a remarkable array of muscles. Venom-delivering systems have evolved independently in several lineages of snakes and lizards, apparently based on a shared genomic heritage, and the specializations associated with venom delivery can be spectacular.

This chapter takes a functional perspective, grouping organisms that exhibit similar feeding modes. This organization requires the simultaneous consideration of independently evolved lineages, emphasizing the pattern in which different evolutionary lines converge on similar solutions to shared functional problems.

11.1 ■ Suction and Suspension Feeding

The dynamics of feeding are different for animals that feed in water and those that feed on land. The density of water supports food items, and swallowing does not require saliva for lubrication. Suction feeding relies on generating negative pressure by expanding the volume of the buccopharyngeal cavity. The negative pressure must be great enough to draw the prey into the mouth, and it must be achieved rapidly to capture elusive prey. In addition, the opening of the mouth must be small if directional suction is required.

A snapping turtle (*Chelydra serpentina*) darts its head forward, opening its mouth and expanding the buccopharyngeal cavity as the head advances and the jaws snap over the prey. The increased volume of the buccopharyngeal cavity compensates for the forward movement of the head—a phenomenon called **compensatory suction**, which prevents the predator's attack from creating a pressure wave that pushes the prey away. In contrast, expansion of the long neck of the Australian snake-necked turtle (*Chelodina longicollis*) not only accommodates all of the water the turtle displaces, but also creates an inward flow of water, or **inertial suction**, which pulls prey into its mouth. Inertial suction is employed by aquatic salamanders (both larvae and paedomorphic adults), larval caecilians, aquatic frogs, tadpoles, and some turtles.

Salamanders and caecilians

Larval salamanders and some paedomorphic adults can create a one-way flow of water-in through the mouth and out through the branchial slits (Figure 11.1A). As the jaws open, the hyoid apparatus (which supports the floor of the mouth) drops and the buccopharyngeal cavity expands from front to back, imparting a rearward motion to the water. A robust hyoid apparatus is key to this system. Early in the feeding sequence, the depressor mandibulae muscle, which runs from the rear of the braincase to the retroarticular process at the posterior tip of the mandible, contracts and causes the mandible to drop (Figure 11.1B). Simultaneously, the hyoid apparatus is retracted by ventral muscles and the skull is lifted by dorsal muscles. Retraction of the hyoid arch causes a rapid drop in the floor of the mouth, expanding the buccopharyngeal cavity. This expansive phase can be very quick, as little as 25 ms in larval axolotls (Ambystoma mexicanum) (Lauder and Shaffer 1985).

The compressive phase of the feeding cycle follows, releasing the water that had carried the prey into the mouth. During this phase the mandible is rapidly elevated by the large adductor mandibulae muscles, and the hyoid is elevated and protracted by several other muscles. Toward the end of the compressive phase the branchial abductor muscles expand the branchial arches, and water is ejected through the opened branchial slits as the buccal cavity is compressed



Figure 11.1 Inertial suction feeding. Larval and paedomorphic adult tiger salamanders (*Ambystoma tigrinum*) create a one-way flow of water. (A) Rapid expansion of the buccal cavity creates an inward rush of water through the mouth. The water is expelled though the branchial slits, which are visible when the first two gills are moved aside. (B) Contraction of the epaxial muscles lifts the head while the buccal cavity is expanded by contraction of the rectus cervicis. The mandible is lowered by the depressor mandibulae and by the genioglossus muscle, which forms a linkage between the mandibles and the hyoid. The mouth is closed by contraction of the adductor mandibulae muscles. The entire sequence of opening and closing takes only 60 ms.



by the rising floor of the mouth (Lauder 1985; Lauder and Shaffer 1985). The mouth serves as an intake valve that opens during expansion and closes during compression, whereas the branchial slits constitute the outflow valve, closing during expansion and opening during compression.

Fleshy modifications of the lips, known as **labial lobes**, occur in several aquatic salamanders, such as the paedomorphic North American salamanders *Amphiuma*, *Necturus*, and *Siren*. Labial lobes seal the sides of the mouth and prevent water and prey from escaping during suction feeding.

Suction feeding has been demonstrated in the larvae of the caecilian *Epicrionops*, and anatomical evidence suggests that other caecilian larvae are also suction feeders (O'Reilly 2000). The pattern of suction feeding by caecilian larvae resembles that of larval salamanders, including the use of rapid hyobranchial depression to expand the pharynx. The branchial slits of larval caecilians presumably allow water to exit the pharynx.

Tadpoles

Most anuran larvae—tadpoles—are filter feeders that use suction to produce a flow of water across surfaces that trap suspended particles, either in a strainer or in sticky mucus

Figure 11.2 Tadpoles create a flow of water to gather food particles. (A) Overview of the flow of water through the buccal and pharyngeal cavities of a representative tadpole. (B, C) Water enters the mouth, passes over the ventral velum into the pharyngeal cavity, is ejected through the branchial filters (on the dorsal surface of the branchial arches) into the atrial cavity, and exits through the spiracle. Upward and downward movements of the floor of the buccal cavity alternately draw water in through the mouth and force it back and out past the branchial filters. The mouth and nares are open when water is being drawn into the mouth. The ventral velum prevents water from being sucked back into the buccal cavity from the pharyngeal cavity. The mouth and nares close and the valve created by the ventral velum opens when water is being forced into the pharyngeal cavity. Water movement is created by movements of the ceratohyal cartilages, which lie beneath the floor of the mouth. (D) The medial ends of the ceratohyal cartilages are rotated downward when the orbitohyal muscles pull their lateral tips upward. This action lowers the floor of the buccal cavity and draws water in through the mouth and nares. (E) Contraction of the interhyoid muscles pulls the lateral tips of the ceratohyal cartilages downward, rotating their medial ends upward. This action raises the floor of the buccal cavity and decreases its volume. The mouth and nares are closed, and the increased pressure in the buccal cavity forces water from the buccal cavity past the ventral velum into the pharyngeal cavity and through the branchial filters into the atrial cavity. Suspended food particles are trapped in mucus on the branchial filters and ventral velum (see Figure 11.3). Water exits the atrial cavity through the spiracle, and a stream of mucus carries the trapped food particles to the esophagus. (A-C after Gradwell 1972; D,E after Ryerson and Deban 2010.)

(**Figure 11.2**). Some tadpoles feed on particles that are already in suspension, such as phytoplankton floating in the water column, whereas others use keratinized mouthparts to scrape plant material from surfaces.

The suction pump of tadpoles is unlike that of other amphibians and is based on a morphology radically different from that of adult frogs (Figure 11.3). The cartilaginous skeletal support for the mouthparts of the typical tadpole includes a greatly elongated palatoquadrate cartilage. The hyobranchial skeleton includes a series of branchial arches fused to form a basket and a pair of transversely oriented ceratohyals. Each ceratohyal articulates with the corresponding palatoquadrate, which bears a tall orbital process from which a large muscle, the orbitohyal muscle, arises. Each orbitohyal muscle inserts onto the lateral tip of the ceratohyal, providing power to a first-class lever (see Figure 11.2D). By lifting the lateral tips of the ceratohyals, the paired orbitohyal muscles drop the floor of the mouth, increasing the buccal volume (Wassersug and Hoff 1979). A pair of transverse ventral muscles, the interhyoid muscles, act as a unit to lower the lateral tips of both ceratohyals, raising the floor of the mouth and decreasing buccal volume (see Figure 11.2E). The alternating contraction of the orbitohyal and interhyoid muscles controls the fall and rise of the buccal floor. Their action first draws water in through the mouth and external nares and then, with the mouth and internal narial valves closed, forces the water back into the pharyngeal cavity, which lies above the gill arches. A large flap of soft tissue on the floor of the mouth, the ventral velum, allows water to pass back to the gills and prevents backflow from the pharynx to the buccal cavity.

Food particles as small as $0.126 \,\mu\text{m}$ are captured by entrapment in mucus on the ventral velum (see Figure 11.3D) and by sieving through the branchial filters, which consist of branching ridges on the dorsal surface of the branchial arches (see Figure 11.3E). Strands of mucus break loose and are carried by the feeding current to the esophagus (Sanderson and Kupferberg 1999).

In addition to cornified jaw sheaths, most tadpoles have several rows of small keratinized structures known as labial teeth, or denticles, on the oral disc that surrounds the mouth. High-speed videography of American bullfrog (*Rana catesbeiana*) tadpoles shows that the labial teeth anchor the tadpole's mouth to the substrate while the upper and lower beaks scrape algae. As the tadpole releases its grip, the labial teeth rasp across the substrate, placing even more algae into suspension for the next suction cycle. The jaws themselves are remarkably flexible. They can attain a gape angle of 180°, allowing both jaws to scrape the substrate simultaneously (Wassersug and Yamashita 2001).

The mouths of tadpoles are related to their diets and feeding habitats (**Figure 11.4**). Generalized pond-dwelling tadpoles spend most of their time on or near the bottom. They scrape algae and bacteria from surfaces, but they can also feed on decaying animal matter or sieve suspended







branchiai basket

Figure 11.3 The skull of a tadpole supports suction feeding. (A) The mouthparts of a typical tadpole are supported by the cartilaginous chondrocranium (larval braincase) and hyobranchial skeleton. The palatoquadrate cartilages lie along the sides of the buccal cavity, and the ceratohyals form its floor. (B) The orbitohyal muscles originate on the palatoquadrates and insert dorsally on lateral tips of the ceratohyals. (C) The transverse interhyoid muscle inserts ventrally on the (D)



(E)



lateral tips of the ceratohyals. (D) The most extensive branchial food traps are found on the undersurface of the ventral velum (see Figure 11.2) where, in the larvae of more derived families of frogs, ridges capped with mucus-secreting cells form a regular array. These cells release strands of mucus that capture food particles. (E) The branchial filters form a sieve with a pore size of about 5 μ m. (A–C after De Jongh 1968; D,E from Wassersug and Pyburn 1987, photographs courtesy of Richard Wassersug.)

Figure 11.4 Tadpoles' mouths match their trophic niches The feeding

phic niches. The feeding specializations of tadpoles extend from collecting particles floating on the water surface (neuston) to rasping algae from rocks in fast-flowing streams. Most tadpoles are herbivorous, but there are carnivorous species that consume frog eggs or other tadpoles. (A,C after Duellman and Trueb 1986; B,D–G after Wells 2007.)



The surface-feeding tadpole of the Asian horned frog (*Megophrys montana*) collects small particles (neuston) floating on the water's surface.



palmipes) is a generalized pond dweller that uses a hard, keratinous beak to scrape algae from solid surfaces.

(D)

The mouth of the stream-dwelling tadpole of the variegated treefrog (*Megastomohyla mixomaculata*) forms a suction disk that anchors the tadpole in the current as it scrapes algae from rocks.



The egg-eating tadpole of Zetek's treefrog (*Isthmohyla zeteki*) live in small pools that collect in the leaf axils of bromeliads and feeds on eggs deposited by female frogs (including those of its own species).



The carnivorous tadpole of the Brazilian horned frog (*Ceratophrys aurita*) rasps flesh from the bodies of other tadpoles with coarse labial denticles. It also has a large, powerful beak.

particles from the water column. These tadpoles usually have a terminal mouth (i.e., it faces forward). Midwater suspension feeders hover in the water column, where they are potentially conspicuous to predators. Some of these tadpoles are nearly transparent, and many have an elongated tail tip, which is the only part of the body that moves continuously. Surface-feeding tadpoles have a mouth with an oral disc shaped like a funnel. Surface tension holds the tadpole in place, while currents produced by buccal pumping carry floating material on the water surface (neuston) into the feeding apparatus. Many tadpoles are arboreal, living in tree cavities or the axils of epiphytic plants, and these species eat organic debris that falls into the water, mosquito larvae, or frog eggs of their own or other species.

Macrophagous larvae—those that feed on large food items—have a long lever arm of the ceratohyals (with a high mechanical advantage) and pump a large buccal volume with short movements of the broad floor of the mouth (Wassersug and Hoff 1979). In contrast, microphagous tadpoles, such as midwater suspension feeders, have a low mechanical advantage and a small buccal floor. Nonetheless, they can still pump a large buccal volume by moving the floor through a considerable vertical distance.

A few tadpoles are fossorial. Tadpoles of the pancake frog (Otophyne pyburni), a microhylid from northern Amazonia, have large keratinized toothlike projections on the upper and lower jaws and an asymmetrical spiracle that is drawn out into an enormous tube (Figure 11.5). Their fierce appearance suggests a predatory diet, but examination of their gut contents revealed only small items such as bacteria and algae. The clue to the feeding habits of these tadpoles is their behavior. The tadpoles burrow in the sandy substrates of streams, leaving their long spiracle projecting into the water column. Water flowing past the opening of the spiracle apparently creates negative pressure by means of the Bernoulli effect, drawing water from the interstitial spaces in the sand into the mouth, across the filters, and out through the spiracle, while the large projections keep sand grains from entering the mouth (Wassersug and Pyburn 1987).

Only pipid frogs continue to use suction feeding as adults (Deban et al. 2001). All pipids are aquatic, but they are fully metamorphosed and do not retain gill slits. As a result, water both enters and leaves the buccopharynx via the mouth, creating an outward current that might carry the prey with it. *Xenopus* and *Pipa* augment buccal suction by stuffing prey into their mouths with their forelimbs.

(A)



(B)



Figure 11.5 A fossorial tadpole. (A) Scanning electron micrograph of the front of the lower jaw of the tadpole of a pancake frog (*Otophryne pyburni*), showing the sharp labial teeth that block sand grains from entering the mouth. (B) The long spiracle is believed to project into the water current when the tadpole is buried. The Bernoulli effect draws water into the mouth, across the branchial basket, and out through the spiracle (arrows). (After Wassersug and Pyburn 1987; photograph courtesy of Richard Wassersug.)

11.2 Terrestrial Feeding Mechanisms

Many terrestrial amphibians and reptiles simply open their jaws and move their head forward to seize and engulf food. Others have evolved mechanisms of tongue projection, ranging from slight protrusion of a fleshy tongue to the rapid firing of a lengthy projectile. Many squamate reptiles have a skull that permits **cranial kinesis**—movement of the bones of the skull—as prey is seized and swallowed. As we examine this range of diversity, we will again take a functional approach rather than a phylogenetic one.

Akinetic, nonprojectile feeding

The simplest tetrapod feeding system, although not necessarily the ancestral one, consists of an **akinetic** (rigid) skull to which the lower jaw is hinged. Most caecilians, amphisbaenians, turtles, and crocodylians feed in this manner, and we will focus on those groups.

CAECILIANS The modifications of the skulls of caecilians for burrowing (described in Chapter 3) have placed constraints on their feeding (Bemis et al. 1983; Nussbaum 1983). The overlying skull roof and the narrow head limit the size of the adductor mandibulae muscles, which are the primary jaw-closing muscles of tetrapods. However, caecilians have an unusual condition of the mandible, a very long retroarticular process, so named because it extends behind the joint that connects the mandible and the skull (Figure 11.6). An enormously enlarged interhyoid muscle extends beyond its ancestral position below the throat and continues far back along the sides of the neck, attaching to the retroarticular process from below. This arrangement powers a first-class lever that pulls down on the retroarticular process, thereby raising the mandible, a function normally served by the adductor mandibulae muscles alone. Thus, hypertrophy of the retroarticular process and the interhyoid muscle shifts much of the jaw-closing power from muscles on the side of the skull, where space is at a premium, to muscles on the sides and floor of the neck. The two muscles exert their strongest forces at different points in the jawclosing cycle: the interhyoid has the greatest mechanical advantage when the jaw is wide open, whereas the adductor mandibulae exerts the most force when the mouth is nearly closed (Kleinteich et al. 2008).

Combined with large teeth, this system provides a strong grip on slippery prey, such as earthworms. Some caecilians use rotational feeding (i.e., spinning around their long axis) to reduce large prey to smaller pieces. However, even small prey may be subjected to spinning, suggesting an alternative function, perhaps using the prey's inertia to determine its mass in an underground environment in which other sensory cues to prey size are limited (Measey and Herrell 2006).

TURTLES Extant turtles lack teeth and instead have a keratinous sheath that covers the margins of the upper and lower jaws and usually has sharp cutting edges. Many prey items, especially larger ones, are forcefully bitten after capture and are sometimes also torn apart with the forelimbs. Turtles have some of the most heavily built skulls among reptiles. As with caecilians, however, that condition appears to represent a secondary loss of cranial kinesis early in the history of the testudine lineage. Apart from aquatic suction, the feeding mechanics of turtles are fairly simple. As in caecilians, the adductor mandibulae muscles mainly lie in a space between the braincase and the complete dermal skull roof (referred to in reptiles as the anapsid condition).

The head size of turtles is not limited by the demands of burrowing, and the adductor muscles are relatively massive and, in combination with a rather short mandible (resulting in a short out-lever), are capable of generating substantial bite force. Nonetheless, two limitations on the dimensions

et al. 1983.)



long retroarticular process on the mandible of the Mexican caecilian (*Dermophis mexicanus*) provides the interhyoid muscle with a long in-lever, for powerful closing of the jaws (A). This supplements the weaker force produced by the adductor mandibulae muscles, which are limited in extent by constraints on head width (B). Some caecilians also exhibit streptostyly (kinesis of the quadrate bone), which further enhances jaw-closing force. (After Bemis

Figure 11.6 Jaw muscles of a caecilian. The

of the head in turtles do exist. First, the middle ear is greatly expanded in extant turtles, occupying some of the space that might otherwise be filled by adductor muscles. Second, the demands imposed by retraction of the head into the shell limit head size. In most turtles, therefore, there is a posterior emargination of the skull roof known as a temporal notch, which is coupled with displacement of the adductor musculature toward the rear of the skull. That shift in muscle position aids in limiting head width, but it also creates a mechanical problem. A muscle transmits its force most effectively when it inserts perpendicular to a bone. How, then, can turtles pull vertically on the lower jaw when the adductor muscles run horizontally forward from the rear of the skull?

Turtles have solved that problem twice, in ingenious fashion. Extant turtles have a trochlear process in the skull, which acts as a pulley to change the direction of the muscle with minimal loss of force. Each of the two major lineages of turtles has a different position for the trochlear process (**Figure 11.7**). In pleurodires the pulley is formed by the pterygoid bone of the palate, whereas in cryptodires it is formed by the quadrate and/or prootic bones, in front of the inner ear. In both lineages the adductor muscle curves around the trochlear process to insert at a steep angle on the mandible, providing maximum force transmission. The



Figure 11.7 Trochlear processes of turtles. The trochlear process allows the adductor mandibulae muscle to pull vertically on the mandible. This pulley system arose independently in the pleurodire (A) and cryptodire (B) lineages. (After Gaffney and Meylan 1988.)

different locations indicate that each group evolved a pulley system independently, presumably in response to the demands of cervical retraction (Gaffney 1975).

Many terrestrial tortoises feed on vegetation and exhibit adaptations for grinding food. An extreme example is seen in the gopher tortoises (*Gopherus*), which occupy semiarid to arid environments in North America and feed on tough, xeric-adapted plants (Bramble 1974). The adductor mandibulae muscles are divided in a complex fashion. Several divisions pull upward on the mandible, whereas others pull back on the lower jaw. The lower jaw slips backward as it closes, grinding fibrous food between the ridged surfaces of the jaws. The amount of rearward movement of the mandible roughly correlates with the toughness of the vegetation in the diet of the four species of *Gopherus*.

CROCODYLIANS Crocodylians, like turtles, have an akinetic skull. Unlike turtles, however, crocodylians open their mouth by lifting their head, not by lowering their jaw. A short but stout depressor mandibulae muscle extends from the rear of the skull to the large retroarticular process on the lower jaw. Contraction of this muscle, assisted by the dorsal neck muscles, elevates the skull and opens the mouth. These jaw-opening muscles have very little mechanical advantage, which is why it is not difficult to keep a crocodylian's mouth closed by holding its snout. Biting down is a different story. A complex but relatively small adductor mandibulae muscle is augmented by two massive pairs of pterygoideus muscles that arise from the roof of the mouth to insert on the mandible via a complex system of tendons shared with the external adductors (Schumacher 1973). These muscles can produce a strong crushing force when a crocodylian bites.

The relatively elongate snout of crocodylians and the insertion of adductor muscles close to the mandibular articulation produce rapid closure of the jaws. Species that feed predominantly on fish, such as the African slender-snouted crocodile (*Mecistops cataphractus*) and the gharial (*Gavialis gangeticus*), have long, narrow jaws that close especially rapidly (Cleuren and De Vree 2000). In contrast, species with more varied diets, such as the American alligator (*Alligator mississippiensis*), have a shorter, broader snout that generates great force at the expense of speed. Alligators can crush the shells of large turtles, a feat that requires considerable bite force.

Although the cranial mechanics of crocodylians are relatively simple, their feeding behavior is remarkably complex and varied. Like certain caecilians, some adult crocodylians employ rotational feeding when consuming large prey items in the water. They bite the prey and spin rapidly around their own longitudinal axis, tearing pieces from the carcass (Helfman and Clark 1986). The limbs are folded against the body to increase the speed of rotation, just as ice skaters do while executing a spin. As a result of a property of motion known as the conservation of angular momentum, rotating the head, trunk, and tail in one direction causes the crocodylian's entire body to rotate in the opposite direction, just as a tightrope walker rotates a pole to the right in order to shift their body to the left (Fish et al. 2007). Crocodylians may also wait to eat large prey until decomposition makes it easier to tear the carcass apart. Morelet's crocodile (*Crocodylus moreletii*) allows large prey to rot for a day or more before feeding on the bloated carcass (Pérez-Higareda et al. 1989). Smaller prey may be crushed by the thick tongue, which presses food up toward the roof of the mouth.

Both the American alligator and the mugger crocodile (*Crocodylus palustris*) of Asia have been observed resting in the water below egret rookeries during the birds' nesting season, with sticks resting on their snouts. This appears to represent luring behavior, as the birds use the sticks to build their nests, and such nesting material is in short supply. Birds seeking to collect sticks for their nests may fall victim to crocodylian predation (Dinets et al. 2013). Crocodylians may also hunt cooperatively, employing group members to herd fish or direct prey to ambushing individuals, although the observations of such behavior are open to other interpretations (Dinets 2014).

TUATARA The tuatara (Sphenodon punctatus), the sole surviving rhynchocephalian, eats a variety of vertebrate and invertebrate prey. The skull of Sphenodon is structured more lightly than that of turtles or crocodylians, with two large temporal fenestrae defining a pair of slender temporal arches. These arches appear to brace the skull so that kinesis does not occur in adult tuatara. The acrodont dentition of Sphenodon includes a pair of large, incisor-like teeth at the front of the upper jaw, a pair of caninelike teeth near the front of the lower jaw, and a row of smaller marginal teeth extending posteriorly along the maxilla and dentary bones. Like many lepidosaurs, Sphenodon also has teeth on the palate, in this case on the palatine bone. The palatal teeth form a row parallel to the maxillary teeth, leaving a groove between the two rows. The mandibular teeth fit into this groove when the mouth is closed. It is believed that as the jaws close, the mandible slides forward and rotates slightly about its long axis, allowing the lower teeth to shear the food against the maxillary teeth first and then the palatal teeth (Jones et al. 2012).

AMPHISBAENIANS Amphisbaenians, like caecilians, are fossorial and have a reinforced and secondarily akinetic cranial structure associated with burrowing. Unlike the skulls of caecilians, however, those of amphisbaenians are reinforced medial to the adductor muscles rather than lateral to them. Thus, there is space for large jaw muscles, especially posteriorly (Daza et al. 2010). In some species the mandible bears a dorsal extension to which the adductor muscles from the rear of the skull attach at a favorable angle. Thus, both amphisbaenians and turtles have displaced the adductor muscles posteriorly, and both have evolved a solution to retaining a favorable angle of muscle insertion. However, in amphisbaenians that solution involves elevat-



Median tooth

Figure 11.8 Amphisbaenians have a unique tooth.

A single median tooth on the premaxilla is a unique character of amphisbaenians such as the speckled worm lizard (*Amphisbaena fuliginosa*) shown here. (Photograph © DigiMorph.org.)

ing the insertion point on the mandible, whereas in turtles it involves altering the path of the muscle.

Amphisbaenians feed on a variety of prey, including both invertebrates and vertebrates. Their teeth generally are strong and sharp, and those of trogonophiids are acrodont. Amphisbaenians have a median tooth in the upper jaw, a feature seen in no other adult tetrapod (Figure 11.8). When the jaws close, that median tooth lies between the anteriormost teeth of the mandibles, providing an interlocking grip. Smaller prey, such as ants and spiders, are quickly consumed whole, whereas prey that are larger than the amphisbaenian's gape are reduced by twisting or repeatedly shearing off chunks (Gans 1974; López et al. 2013). Some larger and relatively hard-bodied arthropods are consumed by scraping the more nutritious contents from within the exoskeleton. One species, Amphisbaena ridleyi, has enlarged, blunt rear teeth that it may use to crush terrestrial snails.

Projectile feeding

The ability to project the tongue has evolved independently in several lineages of amphibians and reptiles, including many frogs, several clades of salamanders, and the lizard family Chamaeleonidae. As might be expected from the diversity of lineages, striking differences characterize the mechanisms involved in tongue projection, but elastic energy storage plays a large role in many of them. Substantial power is required to launch the high-speed projectile tongues of amphibians and reptiles with the velocity required to capture insects: 11,392 Watts per kg of muscle for the dwarf chameleon *Rieppeleon brevicaudatus* and 18,128 W/kg for the plethodontid salamander *Bolitoglossa dofleini* (Deban et al. 2007, Higham and Anderson 2014). (On a per kg basis, those power outputs are at least equivalent to, and possibly greater than, the power in a boxer's jab.) Power is a function of the work done per unit time, so both force and speed factor into power production. The storage and release of elastic energy is an effective way to generate high power, because it releases a great deal of force in a short amount of time. The system works the same way as a bow and arrow: An archer pulls slowly back on the bowstring, storing muscular energy in the deformation of the bow. When the archer releases the bowstring, the energy stored in the bow is released more rapidly (i.e., with much greater power) than if the archer had thrown the arrow like a spear.

In the case of the projectile tongues of salamanders, some frogs, and chameleons, the muscle that powers the tongue stores energy while it contracts. In frogs the elastic energy is stored in the muscle fibers themselves, but salamanders and chameleons store much of the energy in sheets of connective tissue that are deformed by contraction of the muscle that powers the tongue. When the tongue is released, the sheets recoil elastically to fire the tongue at high speed (Herrel et al. 2009).

An additional advantage of elastic storage is that the Q_{10} value for release of elastic energy is low, so temperature has a negligible effect on tongue projection. Whereas most muscles have a Q_{10} of approximately 2 (i.e., their rate of contraction decreases by half with a 10°C drop in temperature), the release of elastic energy by the projectile tongues of salamanders has Q_{10} values of only 1 (i.e., no change with temperature) to 1.4 (about a 30% decrease) (Deban and Lappin 2011; Anderson and Deban 2012). As a result, firing the tongue is effective across a wide range of activity temperatures, although both the muscular loading of the elastic system and the subsequent transport of captured prey to and within the mouth is much slower at colder temperatures.

SALAMANDERS Although a few terrestrial salamanders use the jaws to seize prey, most use only their tongue (Wake and Deban 2000). Species of *Ambystoma* typically feed by slapping their prey with a large, moist, fleshy tongue. Advanced tongue-projection systems have evolved in several lineages of salamanders, including two genera of salamandrids and several plethodontids (Figure 11.9).

Wake (1982) has argued convincingly that the evolution of a projectile tongue is facilitated by a shift in the mode of respiration, which in turn reflects the environment in which those salamander lineages evolved. The salamandrids *Chioglossa* and *Salamandrina* are lungless, as are all of the Plethodontidae. In the absence of lungs, the buccal floor is no longer involved in pumping air, and the hyobranchial apparatus is freed from its role in respiration. Absence of lungs is critical to the evolution of tongue projection, because the hyobranchial cartilages must be slender



Figure 11.9 Tongue extension by plethodontid salamanders. (A) The tongue of the seal salamander (*Desmognathus monticola*) is attached to the floor of the mouth and is capable of only minimal protrusion. (B) Although the tongue of the ensatina salamander (*Ensatina escholtzii*) is also attached, it can be protruded farther. (C) The tongue of the red salamander (*Pseu-*

for tongue projection to occur, but slender hyobranchials are incompatible with pumping air into the lungs.

The most extreme tongue-projection systems in salamanders, as well as the best studied, occur in the family Plethodontidae. Fully developed tongue projection appears to have evolved three times within the Plethodontidae: in the genus Hydromantes (Hydromantini), in the Spelerpini, and in the large tribe Bolitoglossini (Vieites et al. 2011). Several functionally and anatomically distinct variations on the theme of tongue projection have been recognized in plethodontids (Lombard and Wake 1986). Tongue projection occurs when the specialized subarcualis rectus (tongue projector) muscles contract around the arms of a Y-shaped hyobranchial skeleton (hyobranchium). This muscular contraction propels the hyobranchium rapidly forward, firing the tongue pad out of the mouth (Figure **11.10**). The projectile tongue of the giant palm salamander (Bolitoglossa dofleini) accelerates at a rate of 4,492 m/sec² (Deban et al. 2007). A delay between onset of contraction of the tongue projector muscles and tongue projection indicates that the muscle loads an elastic system (Anderson et al. 2014).

The most extreme ability to project the tongue is observed in the plethodontid genus *Hydromantes* and in the Bolitoglossini, and the ability seems to have arisen as a consequence of another, seemingly unrelated, adaptation. In aquatic larvae, the large first ceratobranchials depress *dotriton ruber*) is free and can be projected from the mouth. (D) Bell's false brook salamander (*Pseudoeurycea bellii*) has a free tongue and extreme projection. The tongues of (A) and (B) are shown at maximum protrusion, whereas those of (C) and (D) are shown partway through projection. (After Lombard and Wake 1977.)

the buccal region during suction feeding and respiration. Ceratobranchial I remains larger than ceratobranchial II after metamorphosis, however, and binds against ceratobranchial II during tongue protrusion (**Figure 11.11A**). Bolitoglossines have direct development, and, apparently freed from the constraint of larval suction feeding and pumping water across the gills, members of this group have greatly reduced the width of the ceratobranchial I. As a result the arms of the hyobranchium are projected farther before the basibranchials bind (**Figure 11.11B**). A similar reduction of the first ceratobranchials evolved independently in *Hydromantes*, which also has direct development.

Figure 11.10 Ballistic tongue projection by the Italian ► cave salamander (*Hydromantes supramontis*). This plethodontid launches the tongue with its internal skeleton (the hyobranchial skeleton, or hyobranchium) out of the mouth ballistically. (A) The tongue projector muscles originate on the ceratohyal cartilages and wind spirally around the epibranchial cartilages. The tongue retractor muscles extend from the pelvic girdle to the tongue tip. (B) When the projector muscles contract, they force the entire hyobranchial skeleton forward with great force. The retractor muscles are stretched when the tongue is projected, and their contraction pulls the tongue and prey back into the mouth. (After Deban et al. 1997; photograph by Stephan M. Deban.)


Figure 11.11 Modifications of the hyobranchial skeleton of pletho-

dontids. Hyobranchia of two plethodontids are seen from below at nearly full projection. (A) The larvae of *Eurycea* are aquatic, and the large first ceratobranchials retained in adults limit tongue projection. (B) Species of *Pseudoeurycea* have direct development. Their smaller first ceratobranchials allow greater folding, and therefore greater tongue projection. (After Lombard and Wake 1977.)

Large first ceratobranchials bind when hyobranchium collapses, limiting tongue projection.

Once the tongue has been projected and the sticky tongue pad has made contact with the prey, it must be retracted. That action involves contraction of the rectus cervicis profundus, a straplike muscle that is continuous with the rectus abdominis profundus; together they extend from the pelvic girdle to the inside of the tongue tip (Deban and Dicke 1999).

Apart from the kinematic aspects of launching the tongue toward the prey, there are other consequences of tongue projection in plethodontids. For example, the nerves that run to the tissues of the tongue must lengthen greatly as projection occurs. The nerves serving the projectile tongue are tightly coiled and often looped, allowing them to stretch during prey capture (Wake et al. 1983). Another consequence of advanced tongue projection is the requirement for special visual processing. A range-finding system is needed to determine prey distance, and plethodontids apparently use stereoscopic vision to judge distance. Stereoscopic vision involves transmission of visual information from each eye to both sides of the brain, which estimates distance based on the slight differences in the visual image from the vantage point of either eye. Bolitoglossine salamanders have such stereoscopic vision, which involves neural organization roughly comparable to that of mammals (Wiggers et al. 1995).

FROGS Tongue projection by frogs involves an entirely different mechanism from that of salamanders, and basal clades of frogs differ from more highly derived taxa in their degree of tongue projection. Basal frogs such as tailed frogs (*Ascaphus*) and painted frogs (*Discoglossus*), as well as most hylids and some other groups, contract the genioglossus muscles, which attach to the front of the mandible, causing the tongue to project slightly beyond the tip of the lower jaw during prey capture. These frogs exhibit relatively slow projection speeds (up to 40 cm/sec) and modest accelerations (15 m/sec²). These frogs often feed on prey that is relatively large in relation to their own body size. Tongue projection often is accompanied by lunging at the prey and using the forearms to assist in stuffing it into the mouth (Peters and Nishikawa 1999).

At least six derived clades of frogs have independently evolved inertial elongation, in which the tongue is flipped



from the mouth by a mechanism resembling a catapult (Figure 11.12). The tongue is flung forward and downward, stretching inertially to as much as 180% of the jaw length and landing upside down on the prey. Frogs with inertial elongation have projection speeds of more than 270 cm/sec and accelerations of 310 m/sec². These frogs typically feed on small arthropods and rely almost solely on the tongue for prey capture (Peters and Nishikawa 1999).

Again, elastic recoil is required to provide the high level of power required for such acceleration. The depressor mandibulae muscle, which lowers the mandible, is greatly hypertrophied in toads and provides the force needed to load the elastic system. The mass of the paired depressor muscles of the Colorado River toad (*Incilius alvarius*) exceeds the combined mass of all the jaw-closing muscles, which in most animals are much larger than the depressor (Lappin et al. 2006). That muscle begins to contract well before the mouth opens. The rapid depression of the lower jaw (<20 ms) then converts that elastic strain energy into kinetic energy, which is transferred from the mandible to the genioglossus muscle, flinging the tongue forward (Deban and Lappin 2011).

Hydrostatic tongue protrusion has evolved in several lineages of anurans that feed on ants and termites, including the shovel-nosed frogs (*Hemisus*) and several genera of microhylids. The tongue has a fixed volume, but muscles can act to make it longer and narrower or shorter and wider. Opposing longitudinal and vertical muscles in the tongue of *Hemisus* allow a frog to double the length of its cylindrical tongue (Nishikawa et al. 1999; Nishikawa 2000). This method is slower but more accurate than the inertial elon-



Figure 11.12 Inertial elongation of an anuran tongue.

(A) The tongue in its resting position. (B,C) As the jaw is lowered, contraction causes the short, thick submentalis muscle at the front of the jaw to bulge as the genioglossus muscles contract, pivoting the tongue over the submentalis. (D) That rotation, combined with jaw depression, propels the soft tissues of the tongue forward so that the sticky tongue pad lands on the prey, seen here as a smooth-sided toad (*Rhaebo guttatus*) captures a mouse. The hyoglossus muscle will draw the tongue and prey back into the mouth. (A–C after Gans and Gorniak 1982; D, photograph © Danita Delimont/Alamy.)

gation of most frogs, and fine control further permits the tongue to flex dorsally and laterally as it captures termites.

The Mexican burrowing frog (*Rhinophrynus dorsalis*) also feeds on social insects. The base of its tongue is attached to a highly mobile hyobranchial apparatus. Apparently *Rhinophrynus* feeds by protruding just the tip of its glandular tongue, sliding it straight out of the arched mouth while the lips remain closed laterally. Presumably, *Rhinophrynus* digs into a colony of termites or ants, pushes its narrow snout into a tunnel, and uses its tongue tip to snare its tiny prey (Trueb and Gans 1983). The highly carnivorous South American horned frogs (*Ceratophrys*) feed at the opposite end of the spectrum of prey sizes. Species of *Ceratophrys* have large, bony skulls, wide mouths, and daggerlike teeth. They feed on a variety of prey, including vertebrates similar to their own body size, which are swallowed whole. The large, ballistic tongue returns large prey to the strong jaws, and the mucus-covered tongue generates an adhesive force as much as 6.5 times the frog's weight (Kleinteich and Gorb 2014).

CHAMELEONS The most extreme tongue projection, in terms of distance covered relative to body length, has arisen among lizards of the family Chamaeleonidae, the Old World chameleons. The ballistic tongue of chameleons works on a principle similar to that of plethodontid salamanders, with muscle fibers wrapped around an elongated portion of the hyobranchium (Figure 11.13). In chameleons, however, the muscle itself, rather than the hyobranchium, is the projectile. The chameleon tongue contains a powerful circular accelerator muscle and bears a sticky pad at its tip. At rest the accelerator muscle is wrapped around the end of the entoglossal process, a long forward extension of the hyobranchium. The entoglossal process is tapered only at its tip, with the remainder of its length being parallel-sided. Two longitudinal hyoglossus muscles lie loosely pleated behind the accelerator muscle.

When a prey item is sighted, the lower jaw is depressed and the hyobranchial apparatus is drawn up and forward, slowly at first (see Figure 11.13B) and then protracted rapidly in a burst of muscular activity (see Figure 11.13D) (Wainwright et al. 1991; Wainwright and Bennett 1992a,b). The helical fibers of the accelerator muscle begin to contract long before the tongue is projected, building pressure against the parallel sides of the rod. As it contracts the accelerator muscle stores energy in the muscular tissue and in nested lavers of collagen sheets that line the inside of the tubular muscle (de Groot and van Leeuwen 2004). As the accelerator muscle contracts, it becomes narrower but longer, and the collagen sheets slip past each other and extend like sections of a telescope, their helical fibers stretching like the coils of a spring. As the muscle reaches peak power, it extends over the rod's tapered tip. The accelerator muscle closes on its now-empty central cavity, squeezing itself off the rod and rapidly launching the tongue tip from the mouth as the stretched sheets of collagen recoil. An acceleration of 486 m/sec2 and maximum velocity of 5.8 m/ sec have been recorded.

Smaller prey simply adhere to the sticky tongue tip, but a pouch retractor muscle, which pulls the tip of the tongue pad inward to form a deep pocket, allows chameleons to capture prey up to 15% of their body mass, and even to tear such prey from their perches. The lips of the pocket actively grasp the prey on contact, while suction is created by muscular enlargement of the pocket (Herrel et al. 2000).

As the tongue leaves the mouth, the hyoglossus muscles are stretched behind it. A sheet of elastic connective tissue





Anterior end of entoglossal process



Figure 11.13 Tongue projection by a chameleon. (A) The hyobranchium and the muscles that project the tongue are shown in the resting condition. (B) Contraction of the sternothyroid and associated muscles moves the hyobranchium forward until the tongue protrudes from the mouth. (C,D) The accelerator muscle is wound around the tip of the entoglossal process (blue) of the hyobranchium. Contraction of the accelerator muscle squeezes the tongue off the entoglossal process and propels it from the mouth. The hyoglossus muscle retracts the tongue, carrying the prey with it. (A-C after Wainwright et al. 1991; photograph © Svoboda Pavel Shutterstock.)



attaches the tongue to the hyobranchial skeleton, perhaps serving as a shock absorber when the tongue reaches its maximum extension. Following contact with the prey, the hyoglossus muscles contract to return the tongue tip and prey to the mouth. These muscles are specialized to allow them to contract strongly even when greatly stretched. Once the tongue is returned to the mouth, a system of elastic fibers may help fold the hyoglossus muscles into their resting position (Herrel et al. 2001a, 2002).

Chameleons are able to measure the distance to prev rather precisely, with the timing of contraction of the hyoglossus muscles determining how far the tongue travels. The evolution of tongue projection in chameleons has been accompanied by the evolution of specialized distance perception. The eyes of chameleons are unique among vertebrates in their degree of mobility and independence (Figure 11.14). Located on movable turrets, the right and left eyes of chameleons can scan the environment independently. When a prey item is observed, both eyes are trained on the object. Although it seems reasonable that binocular vision would be used for range finding, experiments have shown that chameleons need only a single eye to determine prey distance, which is measured by accommodation (focusing) rather than binocularity (Harkness 1977). The lens in a chameleon's eye focuses very rapidly and, uniquely among vertebrates, enlarges the visual image, acting like a telephoto lens to magnify a small region of the visual world (Ott and Schaeffel 1995).

Kinetic feeding

Cranial kinesis is widespread among vertebrates, and its absence often reflects secondary loss. Mammals are unique among tetrapods in having no degree of kinesis. It is hard for us to appreciate how unusual our rigid akinetic skull is. Cranial kinesis is present in only a few amphibians (notably **Figure 11.14 The eyes of chameleons operate independently.** The right eye of this panther chameleon (*Furcifer pardalis*) is looking up while the left eye is looking down. (Photograph by David McIntyre.)

some caecilians), but it is widespread among squamates and reaches its highest expression in snakes.

LIZARDS Lizards are a diverse group, and their feeding habits are correspondingly varied. The vast majority of lizards prey on arthropods, including insects, although the diversity of feeding habits is greater than generally believed (Schwenk 2000). Some lizards, such as varanids, often eat vertebrates, and a few are herbivorous. The diapsid skulls of lizards have lost the lower temporal arch, which immobilized the ventral end of the quadrate bone in the ancestral condition. As a result, the quadrate is streptostylic-that is, the bone is free to move forward and back around its dorsal articulation with the squamosal and supratemporal bones (Schwenk 2000; Evans 2008). Two additional points of potential flexibility occur in the skulls of lizards, which are said to be amphikinetic (Figure 11.15). The extent of cranial kinesis varies among lineages of lizards, and the mesokinetic and metakinetic joints allow little or no movement in some lineages. Both mesokinesis and metakinesis have been lost in chameleons, although streptostyly remains, at least to a limited degree.

Kinetic movements of the skull are part of the feeding mechanisms of at least some lizards. Streptostyly may increase biting force by adding the quadrate to the in-lever

Mesokinetic Metakinetic



Streptostylic

Figure 11.15 The skulls of many lizards have three poten-tially kinetic points. The skull of a water monitor (*Varanus salvator*) illustrates the amphikinetic condition of lizard skulls, in which the mesokinetic joint lies between the frontal and parietal bones and the metakinetic joint allows movement between the parietal and supraoccipital bones. In addition, the streptostylic quadrate bones can rotate around their articulations to the squamosals. (Photograph © DigiMorph.org.)

of the mandible (Smith 1982). The magnitude and significance of mesokinesis and metakinesis during natural feeding may vary among lizard taxa. Flexibility at either of these articulations could increase gape by elevating the snout as the mouth is opened. A mesokinetic joint could also allow the snout to flex downward during jaw closing, and the simultaneous depression of the snout and elevation of the lower jaw could reduce the time required to close the mouth around an active prey item (Schwenk 2000).

Secondary reduction of kinesis occurs in some herbivorous lizards and in lizards that are **durophagous**—that is, they eat hard-coated foods, such as seeds, beetles, crustaceans, or molluscs. Durophagous lizards include the South American caiman lizard (*Dracaena guianensis*), the Australian blue-tongued skinks (*Tiliqua*), and some species of monitor lizards (*Varanus*). These species all have large, blunt teeth at the rear of the jaws (**Figure 11.16**). *Dracaena* is the most specialized, preying on molluscs that it crushes in its jaws. *Dracaena* differs from the related teiid *Tupinambis* in having very large molar-shaped teeth, a stronger palatal skeleton, and slower and more precise prey handling behaviors that improve prey retention and crushing (Schaer-

(A)



Figure 11.16 Durophagous lizards have large, blunt teeth. A comparison of two large teiid lizards from South America shows modification of the teeth in relation to diet. (A) The tegu lizard (*Tupinambis teguixin*) preys on invertebrates and small vertebrates and has relatively pointed teeth. (B) The caiman lizard (*Dracaena guianensis*) crushes snails with blunt teeth. (Photographs by Karen E. Petersen.)

laeken et al. 2012). Varanus olivaceus, an unusual monitor lizard from the Philippines, eats both fruits and animals, especially land snails. Crushing dentition develops late in its life, and it is primarily the adults that prey on snails (Auffenberg 1988). In contrast to these taxa, mesokinesis seems to have been enhanced in several lineages of crevicedwelling lizards, in which it contributes to flattening of the head when the lizards enter narrow refuges (Arnold 1998).

Most lizards use their jaws for capturing prey, which is often processed by puncture crushing (McBrayer and Reilly 2002). The tongue is the primary mechanism of prey prehension among iguanian lizards (Schwenk 2000). The surface of the tongue captures prey by wet adhesion, and perhaps by interlocking with the folded lingual surface. Many iguanians also employ palatal crushing, in which the food is compressed between the tongue and the palate. At least some lizards show the capacity to modulate their feeding kinematics, using feedback from their tongue, and perhaps other sensory systems, to adjust the feeding cycle to suit different prey (Herrel et al. 2001b).

A few lizards, notably *Tupinambis* and monitors (*Varanus*), resemble snakes in possessing a deeply forked tongue that is primarily involved in chemoreception, including chemosensory trailing (Schwenk 1994). Therefore, tegus and monitors employ an alternative mechanism, inertial feeding, for the initial transport of large prey. The food is held aloft in the jaws, the head is drawn back, and the prey is momentarily released while the head is rapidly thrust forward and the grip reestablished.

SNAKES The body form of snakes presents a dilemma. The substantial body mass of a snake must be sustained by food that passes through a relatively small mouth (Gans 1961). Two fundamentally different solutions to this problem evolved among snakes, one in the Scolecophidia and the other in the Alethinophidia (see Figure 4.44). Most scolecophidians feed on very large numbers of very small prey, whereas althinophidians evolved the capacity to consume fewer but much larger prey.

Most members of the Scolecophidia are small snakes with short jaws, few teeth, and a very small gape (**Figure 11.17**). Scolecophidians compensate for the small size of their prey by rapidly consuming enormous numbers of ants and termites, which the snakes locate by following their pheromone trails. The guts of four species of the Australian typhlopid genus *Anilios* contained primarily ant larvae and pupae, with pupae accounting for as much as 93% of the prey items of one species. Many of the snakes contained an astonishing 1,431 items (Shine and Webb 1990). Similarly, specimens of the African *Leptotyphlops scutifrons*, only 10– 15 cm long, were found to contain as many as 350 ant larvae or pupae (Webb et al. 2000).

Typhlopids have teeth only on the maxillary bones of their upper jaw, which they use to rake ant larvae and pupae into the mouth (Kley 2001). The maxillae of *Afrotyphlops*





Prokinetic joint

Supratemporal does Short not move relative quadrate to the cranium

Rhinokinesis



Supratemporal moves relative to the cranium

quadrate

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Figure 11.17 Skulls of scolecophidian snakes. (A) *Afrotyphlops punctatus* (Typhlopidae), (B) *Trilepida microlepis* (Leptotyphlopidae). Note that typhlopid snakes have a transverse maxilla that bears teeth (arrows), but no teeth on the lower jaw. Leptotyphlopids have teeth on the dentary of the lower jaw, but none on the maxilla. The proportions of the quadrate and compound bones also differ greatly between these two families of scolecophidians. (After Parker and Grandison 1977.)

lineolatus and *A. schlegelii* swing forward and back three to five times per second, while the toothless mandibles do little more than prevent the prey from slipping back out of the mouth. In contrast, leptotyphlopids have teeth on the dentary bones and rake in prey with their lower jaw. Mobile articulations in the middle of the mandibles of *Rena dulcis* permit the toothed dentary bones to swing forward and back, again as often as three times per second (Kley and Brainerd 1999).

The gape of snakes is enlarged by the evolutionary loss of the mandibular symphysis, the bony articulation between the paired mandibular rami. In alethinophidians this feature allows the mouth to accommodate disproportionately large prey. Most alethinophidian snakes swallow prey whole with alternating movements of the right and left upper and lower jaws. The combination of independent movement of the two sides of the lower jaw, an intramandibular hinge that allows each mandible to flex in the middle, and a loosely articulated streptostylic quadrate that allows the jaws to be moved sideways permits large items to pass through the mouth.

Many basal alethinophidians have short quadrates, whereas more derived taxa have longer quadrates, increasing the gape (**Figure 11.18**). These derived taxa are generally referred to as macrostomates (*macro*, "large," + *stoma*, "mouth"). In many, the cranial element that links the quadrate to the braincase, the supratemporal bone, also is elongate and mobile, contributing even further to the gape. Recent phylogenies indicate that the macrostomate condition has evolved independently in several lineages of snakes.

Because there is no bony mandibular symphysis nor, in most snakes, is there a rigid articulation at the front of the

Figure 11.18 The quadrates and supratemporal bones of alethinophidian snakes form a flexible connection between the cranium and the lower jaw. (A) The pipe snake (*Cylindrophis ruffus*) illustrates the basal alethinophidian condition: the quadrates are short and the supratemporals are immoveably attached to the cranium. (B) Derived alethinophidians, such as the checkered garter snake (*Thamnophis marcianus*), have long quadrates, and the supratemporals can move relative to the cranium, adding an additional joint between the lower jaw and the braincase. Derived alethinophidians also exhibit movement among the bones of the snout (rhinokinesis). (Photographs © DigiMorph.org.) (A)



Figure 11.19 An alethinophidian snake swallows its prey by advancing its jaws and pulling the rest of the skull forward. As it swallows a mouse, a western diamondback rattlesnake (*Crotalus atrox*) turns its head to the right (A) as it protracts its left maxilla, then starts to turn to the left (B) in preparation for protracting its right maxilla. Turning the head increases the reach of each jaw protraction. (Photographs by Wayne Van Devender.)



upper jaw, the right and left sides of the upper and lower jaws typically operate independently during swallowing, driven by the palatal muscles and the streptostylic quadrate. The braincase of snakes is heavily ossified, and the frontal and parietal bones surround the brain laterally as well as dorsally, articulating rigidly with the floor of the skull. This condition obliterates the ancestral mesokinetic articulation. The metakinetic articulation also is lost, and the result is a rigid braincase from which the powerful palatal muscles can pull on the bones of the upper jaw, driving the unilateral feeding sequence. A new point of flexion, the prokinetic articulation, arises between the bones of the snout (the premaxilla, nasals, septomaxillae, and vomers) and the frontal bones of the braincase (see Figure 11.18), and some snakes also have flexible connections among the bones of the snout, a condition known as rhinokinesis (Cundall and Shardo 1995). Those new articulations allow the snout to move as the bones of the upper jaw draw prey into the mouth.

Most alethinophidians have teeth on the palatal bones (palatine and pterygoid), as well as on the maxillae. The mandibular teeth are often the first to contact the prey. The teeth of the upper jaw become embedded as the head continues forward, pivoting on the mandibles that are snagged on the prey item (Cundall and Deufel 1999).

As it swallows, the snake moves over the prey rather than pulling the prev into its mouth (Figure 11.19). The tooth-bearing palatal bones on one side of the head are lifted and protracted to gain a more forward grip on the prey. Once the palatal teeth are embedded in the prey, muscles attached to the palatal bones pull forward on the braincase, drawing the snake's head over the prey item. Those actions are then repeated by the bones of the opposite side. That sequence repeats itself until the prev item is sufficiently far down the esophagus to be moved by concertina-like flexion and extension of the vertebral column, which pushes the head forward over the prey (Moon 2000; Kley and Brainerd 2002). Axial movement then shifts to undulatory bending, in which curves in the body push the prev back toward the stomach.

Accommodating large prey requires that tissues stretch far beyond their resting dimensions. The mandibles can be stretched up to ten times their resting distance without damaging the skin, which has numerous folds and a deep layer of elastin; the mucosa of the lower jaw is highly pleated, with fine folds oriented anteroposteriorly (Cundall et al. 2012; Close and Cundall 2013). The muscles between the mandibular tips stretch to more than twice their resting length, as does the skin of the neck (Rivera et al. 2005; Close et al. 2014).

Most snakes swallow soft prey whole, without crushing or chewing it, but a few genera of colubrids eat hardbodied prey (Figure 11.20). The teeth of several lineages of snakes that feed on hard-bodied prey, such as skinks, are attached to the jaws by a connective tissue hinge rather than being firmly fused to the bone. These teeth fold back as a prey item passes into the mouth, but lock in a vertical position if the prey tries to escape (Savitzky 1981, 1983; Jackson et al. 1999). The Asian crab-eating snake *Fordonia leucobalia* eats hard-shelled crabs and mud-burrowing shrimp, twisting the legs off prey too large to be eaten intact (Shine 1991). A related homolopsid, Gerard's water snake (*Gerarda prevostiana*) of southern Asia, limits its





Figure 11.20 Only a few species of snakes eat hard-bodied prey. This black-headed snake (*Tantilla cucullata*) is swallowing a centipede. (Photograph by Wayne Van Devender.)

prey to freshly molted crabs, often feeding on prey much larger than it can ingest intact. After a large crab is struck, *G. prevostiana* presses a loop of its body over the soft crab and pulls the prey through the loop, tearing the crab apart. The legs are then consumed as separate morsels (Jayne et al. 2002). These two species are a significant exception to the general rule that snakes consume their prey intact.

Two independent lineages, the slug snakes (Pareatidae) of Southeast Asia and the Neotropical snail snakes (Colubridae: Dipsadinae, Dipsadini), specialize on shelled and unshelled molluscs. They extract the body of a snail from its shell with long excursions of the mandibles, which are laterally compressed and bear a comblike array of teeth (Figure 11.21) (Savitzky 1983). In Asia, most species of pareatids have asymmetrical mandibles, in contrast to other snakes. The asymmetry of the snakes' mandibles apparently relates to the asymmetrical twist of their molluscan prey (Hoso et al. 2007). The direction a snail shell twists is under genetic control. Most snails are dextral, meaning the twist to their shell is clockwise, but a few are sinistral (with a counterclockwise twist). In feeding studies, Pareas successfully consumed dextral snails in every trial but were successful in only 12.5% of attacks on sinistral snails. The proportion of snail species with sinistral shells is elevated in regions where pareatid snakes occur (Hoso et al. 2007, 2010).

Although many snakes eat bird eggs, a few genera of colubrids specialize on that food source, notably the African egg-eating snakes (*Dasypeltis*) (Figure 11.22). Several species of colubrid snakes are specialized for feeding on squamate eggs, which differ from bird eggs in having flexible shells. These snakes typically have a pair of flattened, saberlike posterior maxillary teeth that slice the leathery eggshells. Among the genera known to feed in this manner are the scarlet snake (*Cemophora coccinea*) and the leafnosed snakes (*Phyllorhynchus*) of North America, as well as the kukri snakes (*Oligodon*) of Asia, which receive their common name from the fancied resemblance of their rear teeth to a Gurkha knife.

Figure 11.21 Some snakes can extract snails from their shells. (A) Iwaski's snail eater (*Pareas iwasakii*) braces its blunt snout against a snail's shell and uses alternate movements of its long mandibles to extract the snail's body. After being attacked by the snake, the snail lost its grip on the branch; the snake is dangling with its head down as it extracts the snail. (B) The mandibles of *P. iwasakii* are asymmetric, with 16 teeth on the left mandible and 24 on the right. (Photographs by Masaki Hoso.)



Figure 11.22 Egg-eating snakes swallow eggs intact.

(A) The 12 species of African egg-eating snakes, *Dasypeltis*, can swallow hard-shelled eggs up to four times the diameter of their head, although most of the eggs they eat are smaller. The teeth are reduced to a few small vestiges, and the jaws, which are covered by soft mucosal tissue, are pushed over the egg. (B) The skin of the neck and tissues of the lower jaw are extraor-dinarily elastic. (C) The shell is not cracked until the egg has moved a short distance down the throat, where it encounters specially modified ventral processes of the vertebrae (D) dur-

11.3 Capturing and Subduing Prey

Most amphibians and reptiles capture prey that is small relative to the size of the predator. Repeated biting is sufficient to subdue their prey. Macrostomate snakes are the exception to this generalization, and many of them eat prey that is large in relation to the predator. A prey item can be large relative to a snake in two ways: the weight ratio (prey weight/ snake weight) or the ingestion ratio (diameter of the prey divided by the diameter of the head of the snake) (Greene 1983, 1997). Elongate prey such as earthworms, eels, caecilians, and other snakes can have a high weight ratio but low ingestion ratio, whereas bulky prey such as birds can have a low weight ratio and a high ingestion ratio (**Figure 11.23**).

Aniliids and cylindrophiids, the extant taxa believed most closely to resemble the earliest alethinophidians, feed on elongate prey, and the challenge they face is subduing a struggling prey item. The well-established hypothesis that the earliest alethinophidians fed on heavy prey of modest diameter (Greene 1983, 1997) received support from a recent study, which mapped various characteristics of snakes on a phylogeny that includes many fossil taxa (Hsiang et al. ing its passage through the esophagus. Rounded hypapophyses appear to crush the eggshell, and behind them are a series of long, anteriorly directed hypapophyses that protrude into the esophagus. These projections apparently slit the shell membrane of the egg, freeing its liquid contents and preventing the shell from passing farther back into the gut. The liquid contents are swallowed, and the eggshell is compressed by the lateral body muscles and is regurgitated. (Photographs © Kim Taylor/Nature Picture Library/Corbis.)

2015). Although this is not a novel insight, it does support the hypothesis that basal snakes (before the split between extant Scolecophidia and Alethinophidia) fed on elongate prey. Following the split, Scolecophidia and Alethinophidia became specialized for fundamentally different prey types: very small for Scolecophidia and very large for Alethinophidia. Among alethinophidians, macrostomate snakes further specialized on prey that have both high weight and high ingestion ratios. Some, such as boas and pythons, employ constriction to subdue their prey, whereas many Colubroidea employ venom. In general, constriction and venom delivery appear to be alternative strategies for prey immobilization.

Constriction

Many macrostomate snakes swallow living prey items, and these species may restrain struggling prey by using a loop of their body to press it against the substrate (**Figure 11.24A**). This behavior may have been the precursor of constriction, a prey-handling method that consists of passing loops of a snake's body around a prey item (**Figure 11.24B**). Death of the endothermal prey is rapid, suggesting that restriction of blood flow and cardiac function is the proximate cause

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Figure 11.23 Weight ratios and ingestion ratios describe different functional categories of prey. (A) Elongate prey have a low ingestion ratio and a high weight ratio. This ringneck snake (*Diadophis punctatus*) easily swallows a Texas night snake (*Hypsiglena jani*) that is about 50% of the weight of the ringneck snake. (B) Bulky prey have high ingestion ratios and variable weight ratios. Birds have high ingestion ratios because their feathers make them bulky, and low weight ratios because their feathers and hollow bones make them light. This gray rat snake (*Pantherophis alleghaniensis*) is stretching to swallow an American robin (*Turdus migratorius*) that is only 5% of the snake's weight. (Photographs: A, Wayne Van Devender; B, Harvey Pough.)

(Hardy 1994). Constriction is widespread among snakes; among basal ophidian lineages it is characteristic of at least the Tropidophiidae, Cylindrophiidae, Xenopeltidae, and Loxocemidae, as well as boas and pythons (Greene and Burghardt 1978).

Although constriction seems to have arisen to handle the elongate (low ingestion ratio) prey of basal snakes, it proved well suited to bulky (high ingestion ratio) prey such as mammals. Boas and pythons retain constriction as a means of dispatching their prey, which often are large relative to the snake's body size. Although constriction and envenomation are generally regarded as alternative ways to reduce the risk of injury during prey handling, some Aus-



Figure 11.24 Subduing prey. (A) Many snakes use loops of the body to hold prey against the substrate, as this smooth snake (*Coronella austriaca*) is doing as it consumes a European common lizard (*Zootoca vivipara*). (B) Constriction consists of seizing prey in the jaws and coiling the body around the prey, as this olive whip snake (*Psammophis mossambicus*) is doing with a Cape skink (*Trachylepis capensis*). (Photographs: A, © Joe Blossom/Alamy; B, © Philippe-Alexandre Chevallier/Biosphoto/ Corbis.)

tralian elapids use constriction to restrain prey after they have envenomated it (Shine and Schwaner 1985).

Envenomation

Although venom is not nearly as widespread among reptiles as most people imagine, complex and potent venoms have evolved several times, often accompanied by extraordinary mechanisms for their hypodermic injection. To understand the evolution of such systems, it is important to recognize that venom delivery is fundamentally a strategy for prey capture and that its use in defense is only a secondary function, although sometimes an important one.

(A)



Figure 11.25 Duvernoy's gland of a colubrid snake. Duvernoy's gland lies posterior to the eye. The gland and the grooved fang that injects venom are large in the African boomslang (*Dispholidus typus*), one of the species of rear-fanged snakes that can deliver a bite that is lethal to humans. (After Parker and Grandison 1977.)

As we discussed in Section 4.3, the origin of venom among reptiles is a topic of debate. One view maintains that venom evolved in the common ancestor of the Iguania, Anguimorpha, and Serpentes, whereas a different interpretation identifies two origins of venom (once in the common ancestor of advanced snakes and independently in helodermatid lizards), with a possible third occurrence in varanid lizards. The most elegant mechanisms for delivery of venom are seen in advanced snakes and helodermatid lizards, and we will focus our discussion on those taxa.

VENOM DELIVERY The highly kinetic skulls of colubroid snakes have provided a rich substrate for the evolution of diverse venom-delivery strategies. Enlarged and/or grooved fangs at the rear of the maxilla have evolved multiple times among colubroids, and tubular fangs at the front of the maxilla have evolved three times.

Duvernoy's gland is present in most colubroid snakes (Figure 11.25). It arises from the embryonic tissue that also gives rise to the posterior pair of maxillary teeth (Vonk et al. 2008). Grooves on the fangs conduct secretions from Duvernoy's gland into the prey. The widespread occurrence of Duvernoy's gland and grooved rear teeth among colubroid snakes suggests that this venom-delivery system evolved early in that group and that its absence in members of some colubroid families is a secondary loss. Some colubrid snakes that have secondarily evolved constriction, such as the North American ratsnakes (*Pantherophis*) and king snakes (*Lampropeltis*), have a reduced Duvernoy's gland.

The secretions of Duvernoy's gland appear to immobilize prey and aid digestion. For example, North American lyre snakes (*Trimorphodon*) prey at night on lizards that sleep in rock crevices and defend themselves by inflating their lungs to wedge their body in place. A lyre snake will bite a lizard and hold on, sometimes for hours, until the slowacting toxins in their venom immobilize the prey, which eventually deflates and can be withdrawn from the crevice and swallowed (Greene 1989).

Several rear-fanged snakes are capable of inflicting significant bites on humans. Life-threatening bites are uncommon, but symptoms ranging from local swelling to death have been reported following bites by more than 30 genera and 40 species of colubrids (Gans 1978; Minton 1990; Weinstein et al. 2014). The most notorious example is the death in 1957 of Karl P. Schmidt, a prominent herpetologist, as the result of a bite by a boomslang (*Dispholidus typus*). The story of his death, based largely on Schmidt's own notes, makes riveting reading (Pope 1958).

Front-fanged venom-delivery systems, in which the anteriormost maxillary teeth conduct the venom, have evolved in Viperidae, Elapidae, and Atractaspidinae (Figure 11.26). The demonstration that the venom glands, like Duvernoy's gland, arise embryonically from the dental lamina of the fangs suggests that front fangs represent rear maxillary teeth that have been shifted forward by reduction of the anterior part of the



Figure 11.26 Venom apparatus of elapid and viperid

snakes. (A) Elapids, such as the Indian cobra (*Naja naja*), have a relatively short fang at the anterior end of a long maxilla. Some have a one or more small teeth behind the fangs, in this case one such tooth (arrow). (B) Vipers, such as the cottonmouth moccasin (*Agkistrodon piscivorus*), have a long fang that is the only tooth on the short maxilla. The muscle that compresses the venom gland differs in the two lineages. In elapids it is the adductor mandibulae externus superficialis, whereas in viperids it is the compressor glandulae. (After Kochva 1978.)





maxilla (McDowell 1968). This hypothesis was supported by a subsequent study demonstrating that the fang-bearing maxilla of front-fanged snakes represents the rear portion of the ancestral colubroid maxilla (Vonk et al. 2008). The fangs of front-fanged snakes have an enclosed tube for conduction of the venom that presumably evolved by complete enclosure of the ancestral groove (Jackson 2002).

The venom glands of all front-fanged snakes are relatively large and have a lumen lined with secretory epithelium. The lumen is filled with venom that is expelled under pressure exerted by a muscle that compresses the gland. The muscle is not homologous among all groups of front-fanged snakes, and that lack of homology supports the hypotheses of multiple independent origins of the front-fanged condition. The front-fanged venomous snakes include two large and diverse families, Elapidae (cobras, coral snakes, and sea **Figure 11.27 Fang erection by a viper.** (A) When the mouth of an African puff adder (*Bitis arietans*) is closed, the fang lies parallel to the palate. (B) Contraction of two palatal muscles (the protractor pterygoidei and levator pterygoidei) pulls the palatal bones forward, rotating the maxilla and prefrontal bones and erecting the fang. The retractor pterygoidei returns the fang to the resting position. (After Parker and Grandison 1977.)

snakes) and Viperidae (true vipers and pit vipers). Two unusual front-fanged African genera, the mole vipers (*Atractaspis*) and dwarf garter snakes (*Homoroselaps*), have long been considered independently derived from each other, but recent molecular phylogenies suggest they are sister taxa, now placed in the lamprophiid subfamily Atractaspidinae (see Figure 4.44).

Differences in the mechanics of venom delivery by elapids and vipers reflect differences in the nature of their venoms and in their prey-handling behaviors. Most elapids have relatively short fangs compared with the size of their heads, and the fangs remain in a vertical position when the mouth is closed. The maxilla is long, and many elapids have a few solid teeth posterior to the fang on the maxilla. Elapid venoms are rich in short-chain polypeptides that interfere with neuromuscular transmission and immobilize prey relatively rapidly as it is held in the jaws. Viperids, in contrast, have relatively long fangs that are the only teeth on the highly mobile maxillary bones. The fangs lie against the roof of the mouth at rest, and protraction of the palatomaxillary arches causes the fangs to rotate through an angle of about 120° (Figure 11.27). The venom, which generally is rich in proteolytic enzymes that break down capillaries and destroy local tissues, is injected deep into the prey, which is then released. The strike itself is very rapid. The time from initiation of a strike by a rattlesnake to contact with the prey is about 30 ms, and the entire strike sequence lasts only about 200 ms (Kardong and Bels 1998). Remarkably, even in that short period of time vipers can reposition their fangs if one fails to penetrate the prev due to the strike angle or contact with a bone, as happens in nearly half of all strikes (Cundall 2009).

During the strike, the snake must launch its head and neck while retaining a stable position on the ground. Terrestrial vipers typically have a narrow neck, while the more robust posterior region of the body provides greater inertia to resist displacement during the strike (Cundall 2002). Terrestrial vipers typically accumulate a substantial fecal mass in the large intestine and retain it for weeks or months, and this mass further anchors the posterior body during the strike (Lillywhite et al. 2002). After releasing the prey, the snake trails it as it succumbs and swallows it after it has become immobilized (Chiszar et al. 1992). Two venom components, crotatroxin 1 and 2, give a distinctive odor to envenomated prey (Saviola et al. 2013).

Although the description of elapid fangs as fixed, and viperid fangs as movable, is generally true, exceptions exist. Among elapids, for example, a modest degree of rotation of the maxillary bone occurs in the so-called spitting cobras, a polyphyletic group of cobras that spray venom as a defensive mechanism. Rotation of the fangs, together with a backward tilt of the elevated head, directs twin jets of venom upward toward the eyes of the predator. Maxillary rotation by elapids is especially pronounced in Acanthophis, the death adders of Australia, which exhibit convergence on viperid foraging ecology, among other traits (Shine 1980). The independently evolved mole vipers, Atractaspis, have a relatively rigid skull, consistent with their fossorial habits. However, they also have relatively long fangs that rotate out of the side of the mouth, allowing them to strike with their mouth closed (Deufel and Cundall 2003). This unusual behavior appears to be an adaptation to feeding in burrows, where these snakes stab and envenomate entire broods of nestling rodents before consuming them.

The two species of dangerously venomous lizards—the Gila monster (*Heloderma suspectum*) and Mexican beaded lizard (*H. horridum*)—have a large venom gland that extends along the lateral surface of each mandible (**Figure 11.28**). This gland secretes its product through one or more ducts to the labial side of the mandibular tooth row. The large mandibular teeth associated with the ducts of the helodermatid venom glands bear deep grooves on their anterior and posterior surfaces. Venom is conducted into the







bite wound as the lizard tenaciously holds its prey, which consists of a variety of small animals, including nestling birds. Helodermatid venom is about as toxic as cobra venom and, in mammals, causes a drop in blood pressure, irregular heartbeat, internal hemorrhage, swelling, and difficulty breathing (Mebs 1978; Beck 2005). The venom gland of helodermatids appears to be homologous to the mandibular gland of varanids, which produces pharmacologically active compounds related to other squamate toxins (Fry et al. 2009, 2012). The hypothesis that Komodo dragons (*Varanus komodoensis*) employ venom as part of their predatory repertoire has not been tested in the field.

ACTIONS OF VENOM Snake venoms consist of a complex blend of ingredients with diverse effects (**Table 11.1**). Peptides and small proteins include a variety of toxins, many of which attack neuromuscular junctions. Although it is likely that many venoms immobilize prey simply by causing massive and nonspecific physiological damage, increasing evidence suggests that some components of venoms are under selective control. Much of that evidence comes from geographic variation in venom within a species, as in the Malayan pit viper (*Calloselasma rhodostoma*). Individuals from different regions have different proportions of amphibians, reptiles, and mammals in their diets, and variation in venom composition among populations correlates with diet, but not with geographic proximity or phylogenetic relatedness of the populations (Daltry et al. 1996).

Interspecific differences in venoms show similar adaptive features. A study of the composition and toxicity of venoms of coral snakes (*Micrurus*) showed substantial variation in toxicity to different kinds of prey. The venom of each species is more toxic to that species' natural prey than to non-prey species tested (Jorge da Silva and Aird 2001). The most distinctive venom composition was found in *Micrurus surinamensis*, an aquatic coral snake that feeds on fish. Its venom is up to 25 times more toxic to fish than to snakes, the preferred prey of many other coral snakes.

EVOLUTION OF VENOM Recent genomic and proteomic studies have altered our view of venom evolution significantly and have revealed that advanced venom-delivery systems are built on an ancient genetic and physiological foundation. The genomic signature of incipient venom systems goes back to the origin of the Toxicofera, the lineage that includes monitors, snakes, and even iguanian lizards (see Figure 4.12). However, recent genomic and proteomic studies have spawned a controversy over what constitutes "venom" and the property of being "venomous."

Figure 11.28 Venom gland and venom-conducting teeth of a Gila monster (Heloderma suspectum). (A) The venom gland lies along the lateral surface of the mandible. (B) A lingual view of the right mandible. The grooves in the teeth (arrows) conduct venom into the wound. (A after Kochva 1978; photograph courtesy of Harvey Pough.)

Class of compounds	Occurrence	Function	Biological activity in venom					
Acetylcholinesterase	Colubroids, Elapidae	Hydrolysis of acetylcholine	Depletion of neurotransmitter, possibly induction of paralysis					
Cystein-rich secretory proteins (CRiSPs)	<i>Heloderma</i> , colubroids, Elapidae, Viperidae	May block cyclic nucleotide-gated potassium channels	Induce hypothermia, may induce paralysis					
Dinstegrins	Viperidae	Inhibit binding of integrins to receptors	Inhibit aggregation of platelets, promoting hemorrhage					
Hyaluronidase	Heloderma; Elapidae; Viperidae	Hydrolysis of hyaluronan, a major constituent of connective tissues	Decrease viscosity of interstitial tissue, promoting diffusion of venom					
Kallikrein-like serine proteases	Heloderma, Viperidae	Release of bradykinin; hydrolysis of angiotensin	Induce rapid hypotension, immobilizing prey					
L-amino acid oxidase	Elapidae, Viperidae	Deamination of L-amino acids	Induce cell damage and cell death					
Myotoxins	Viperidae	Modify voltage-gated sodium channels, affect lipid membranes	Destroy muscle and induce pain, causing immobilization of prey					
Nerve growth factors	<i>Heloderma</i> , Elapidae, Viperidae	Promote nerve growth	Unknown					
Phosphodiesterase	Colubroids, Elapidae, Viperidae	Hydrolysis of nucleic acids and nucleotides	May induce hypotension					
Phospholipase A ₂	Heloderma, colubroids, Elapidae, Viperidae	Hydrolysis of 2-acyl groups of phosphoglycerides	Damage lipid membranes, destroy muscle					
PLA ₂ -based presynaptic neurotoxins	Elapidae, Viperidae	Block release of acetylcholine from axons	Neurotoxicity, prey immobilization					
Prothrombin activators	Elapidae	Activate clotting factors	Induce small blood clots that can disrupt blood flow to tissues					
Snake venom metalloproteinases	Colubroids, Elapidae	Hydrolysis of structural proteins, disruption of epithelia, some hydrolyze fibrinogen	Induce hemorrhage, damage muscles, pre-digestion of prey					
Three-finger toxins	Colubroids, Elapidae	Inhibit neuromuscular transmission, some affect cardiac function	Rapid immobilization of prey, death					
Thrombin-like serine proteases	Viperidae	Catalyze hydrolysis of fibrinogen	Rapid depletion of fibrinogen and disruption of hemostasis					

	TABLE 11.1	Some of t	the major co	omponents of	reptilian ve	noms
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Source: After Mackessy 2010b.

Note: Under "Occurrence," not all members of the listed families necessarily have such compounds. "Colubroids" refers to members of the Colubroidea other than Viperidae and Elapidae. Note that some classes are limited to one or two taxa, but many others are widespread among these groups. Most classes of compounds contain many different forms of these molecules.

Some authors consider that the presence of any pharmacologically active compounds that are homologous to the toxins of dangerously venomous species is sufficient to designate a taxon as venomous (Fry et al. 2006). An alternative view maintains that these compounds are simply widespread proteins expressed in many tissues (Hargreaves et al. 2014; Reyes-Velasco et al. 2015). At the base of this controversy is the manner in which individual toxins, the chemical components of venoms, arise during evolution. That process appears to begin most often with gene duplication. When multiple copies of a gene arise, some are free to mutate into sequences that encode for a different protein. Those new genes, which are known as paralogues, become the raw genetic material for the evolution of diverse new toxins, which are said to belong to the same gene family (Casewell et al. 2011). Study of both the amino acid sequences of venom proteins and the DNA sequences that encode them can reveal which compounds gave rise to others, as well as the sequence in which they arose. Such studies are now an active area of molecular biology and have revealed that some classes of venom proteins have diversified rapidly within the Toxicofera, especially among advanced snakes, and in some cases have acquired new and very different functions.

A toxin known as trocarin D, found in the rough-scaled snake (*Trophidechis carinatus*) of Australia, is an example. This protein exerts its effect by activating prothrombin, a compound produced in the liver and involved in normal blood clotting. By promoting many small clots, the toxin depletes the supply of prothrombin and increases leakage of fluid from the capillaries. Trocarin D is a paralogue of TrFX, a normal blood factor that aids in the clotting response. However, the gene for trocarin D is expressed about 30 times more highly in the venom gland than its paralogue TrFX is in the liver. Although the two genes are very similar, one difference lies in a small insertion of 264 base pairs in the promotor region, which regulates expression of the gene. Kwong et al. (2009) labeled that insertion and then transfected cultured venom gland cells from a related Australian elapid and cultured mammalian liver cells with the promotor. They found that the high level of gene expression was indeed due to the insertion in the promotor of trocarin D. However, both the venom gland and liver cells expressed the promotor region equally, so some other factor must be responsible for limiting transcription of the full trocarin D gene to the venom glands alone.

Digestion

Consuming infrequent large meals requires physiological as well as morphological specializations. The digestive systems of snakes that feed frequently on small prey are continually in an active state, whereas those of snakes that feed infrequently on large prey are in an inactive state until a prey item has been swallowed (Secor and Diamond 1998). Within 6 hours of a meal, changes have occurred in the expression of more than 2,000 genes in the small intestine (Andrew et al. 2015). Within 24 h, the small intestine of a Burmese python (*Python molurus*) has increased in mass by 70%, and the length of the microvilli (the fingerlike cellular projections where nutrient absorption takes place) has increased four-fold. Two or three days after ingestion, the pancreas, liver, and kidneys have doubled in mass (Secor 2008). The mass of the heart increases by 40%, the volume of blood pumped with each contraction increases by 50%, and the heart rate by 300–400% (Jensen et al. 2011).

All vertebrates increase their metabolic rate in response to feeding; for humans and many other mammals, this increase is about 25%, whereas for pythons it can be as high as 687% (Secor 2009). The increased metabolic rate accompanying digestion appears to reflect the cost of upregulating the tissues of the gut, as well as increasing the secretion of hydrochloric acid and digestive enzymes. Although this burst of metabolic activity is indeed energetically costly, infrequent feeders are spared the cost of maintaining the gut in an active state between meals. Energetic models indicate that the benefits of downregulating the gut outweigh the costs of upregulating when feeding occurs only every 5 or more weeks (Secor 2001).

SUMMARY

Amphibians and reptiles exhibit a wide range of feeding structures and modes, reflecting the diversity of habitats they occupy and the wide variety of foods consumed in water or on land.

Aquatic amphibians and reptiles can use inertial suction to draw water and food into the mouth. Some turtles also generate compensatory suction, in which the buccopharyngeal cavity expands to accommodate water that would otherwise be displaced by forward movement of the head and neck.

Larval and paedomorphic adult amphibians generate a unidirectional flow of water during aquatic suction or suspension feeding—in through the mouth and out through the branchial slits. Rapid depression of the buccal floor facilitates prey capture.

Most tadpoles have a modified buccal pumping system that drives water through the branchial baskets, where suspended particles such as algae are trapped by mucus for transport to the gut.

Some tadpoles have mouthparts or ventral skin that is modified to provide high suction in fast-moving waters. Others have a large mouth and sharp mouthparts that facilitate macrophagy, including carnivory.

■ Terrestrial feeding systems may involve cranial kinesis or akinetic skulls, with or without tongue projection. Additional modifications may reflect constraints due to cranial adaptations related to locomotion.

Most caecilians are fossorial and exhibit greatly reduced cranial kinesis. The adductor muscles that normally function in a third-class lever to close the lower jaw are augmented by an enlarged interhyoid muscle, which pulls on the elongated retroarticular process as a first-class lever.

Turtles possess akinetic skulls and have evolved a pulley system—the trochlear process—that allows them to apply high force to the mandibles although the adductor muscle largely occupies the rear of the skull. In pleurodires the pulley is formed by the pterygoid bone of the palate, whereas in cryptodires it is formed by the quadrate and/or prootic bones, in front of the inner ear.

Crocodylians also apply strong force to close the jaw, using enlarged pterygoideus muscles that insert on a flange of the palatine bone.

■ Tongue projection has evolved in many frogs, several clades of salamanders, and the lizard family Chamaeleonidae. Projectile tongues exhibit diverse morphologies but are based on similar principles, including the use of elastic energy storage.

The most extreme tongue-projection systems in salamanders occur in some lungless salamanders, Plethodontidae. In some species the tongue and hyobranchial skeleton are projected out of the mouth by contraction of muscles wrapped around the two epibranchial cartilages. In at least one species the tongue can be projected up to 80% of the salamander's body length and can achieve a velocity of 4.6 m/sec. Frogs exhibit several mechanisms of tongue protrusion or projection, from the slow, highly controlled movement of a muscular hydrostat to the catapulting of the tongue and inertial elongation of its free end.

The most extreme tongue projection, in terms of distance covered relative to body length, occurs in chameleons. Using elastic energy built up by a circular accelerator muscle against the entoglossal process of the hyoid, tongue projection in some species of chameleons can achieve an acceleration of 486 m/sec² and a maximum velocity 5.8 m/sec. The eyes of chameleons are highly modified for independent movement and monocular estimation of distance.

■ Cranial kinesis, movement of bones within the skull, can have important implications for feeding. Kinesis is present in only a few amphibians, but it is widespread among squamates and reaches its highest expression in snakes.

The modified diapsid condition of squamate skulls, with loss of the lower temporal arch, facilitates movement of the quadrate bone, or streptostyly.

Lizards typically possess a mesokinetic articulation between the frontal and parietal bones, as well as a metakinetic articulation between the parietal and supraoccipital bones. With both articulations, the skull is described as amphikinetic.

Snakes lack a bony mandibular symphysis, the firm connection between the two sides of the lower jaw. In alethinophidians this loss allows the mandibles to spread, accommodating relatively large prey. Most scolecophidian snakes have short jaws, few teeth, and a very small gape. They use their highly modified jaws to consume large numbers of eggs and pupae of social insects.

Alethinophidian snakes exhibit several trends in their evolution, including increasingly kinetic jaws, macrostomy (a relatively large mouth), and among colubroids the evolution of venom delivery. A variety of specializations have arisen for dealing with diverse types of prey, including molluscs, armored lizards, and shelled eggs. Most alethinophidian snakes swallow prey whole with alternating movements of the right and left upper and lower jaws.

Complex and specialized venoms appear to have evolved several times within the Toxicofera from a shared genomic endowment of duplicated genes.

Dangerously venomous lizards (to humans) include only the Helodermatidae, but three lineages of snakes have evolved highly effective front-fanged venomdelivery systems.

Venom delivery is fundamentally a strategy for prey capture. Its use in defense is secondary.

There is growing evidence that venom components are adapted to be most effective on specific classes of prey.

Some snakes feed episodically on large prey and exhibit rapid upregulation of their digestive system after consuming a meal.

Go to the **Herpetology** Companion Website at **sites.sinauer.com/herpetology4e** for links to videos and other material related to this chapter.

PART III What Do They Do?

CHAPTER 12 Spatial Ecology

CHAPTER 13 Communication

CHAPTER 14 Mating Systems and Sexual Selection

CHAPTER 15 Diets, Foraging, and Interactions with Parasites and Predators

CHAPTER 16 Populations and Species Assemblages





12 Spatial Ecology

When Alice fell down the rabbit hole in Lewis Carroll's Alice in Wonderland she found herself in an unfamiliar world, shrunk to the size of mice and caterpillars. Flowers and mushrooms became the size of trees, while logs and fallen leaves seemed as large as buildings. This imaginary change in spatial scale, a popular theme in literature and movies from *Gulliver's Travels* to *Honey, I Shrunk the Kids*, is a useful exercise to help understand what it would be like to live as an amphibian or reptile. As we noted in Chapter 1, most of these animals are small—less than 20 g in body mass and being small, they don't move very far.

A red-backed salamander (*Plethodon cinereus*), for example, may spend its entire life in an area smaller than a tabletop in a college biology laboratory (**Figure 12.1**), and even a relatively active lizard or snake may range over an area no larger than a typical classroom or lecture hall. A 45-minute walk is sufficient for a person to cross an average college campus, but even the most mobile amphibians and reptiles may not cover that much ground in weeks, months, or even years. The few species that do cover long distances, such as sea turtles that traverse hundreds of kilometers of ocean, are much larger than most amphibians and reptiles.

This chapter describes patterns of movement by amphibians and reptiles, including the use of limited home ranges for normal daily activities, territoriality, migration, and dispersal. This study of movement patterns and the associated use of habitats by animals comprises the field of **spatial ecology.**

12.1 ■ Ecological Consequences of Movement

Animals move from one place to another for many reasons, but ultimately all movement is related to the acquisition of resources, including food and water, mates, basking or hibernation sites, nesting sites, and shelter—in short, anything required for survival and reproduction. Any movement is likely to entail some costs, including energy expenditure and exposure to unfavorable environmental conditions or predators. Most animals move only when absolutely necessary, but species differ dramatically in how often and how far they move. Patterns of movement affect, and are affected by, almost every other aspect of an animal's biology, including its water and temperature relations, foraging ecology and energetics, mating system, responses to predators, and interactions with other species.

The dynamics of populations are closely tied to patterns of movement. Mortality can be particularly high when individuals move from one habitat to another, as when tiny, newly metamorphosed toads move from ponds to terrestrial habitats or hatchling sea turtles make a mad dash for the ocean. Species that have eliminated this movement phase may have lower juvenile mortality. This in turn can influence the evolution of life-history traits, such as the number and size of eggs that are produced.

Movement patterns affect the dynamics of **metapopulations**, with some habitat patches being populated by individuals that immigrate from other habitat patches, not by recruitment of individuals that were born where they now live (Marsh and Trenham 2001). Movement also affects the genetic structure of populations. Strong **natal philopatry** (the tendency to return to one's birthplace) in juveniles and adults can produce local genetic differentiation (Berven and Grudzien 1990; Smith and Scribner 1990). For example, DNA sequencing studies have shown that many local breeding populations of sea turtles are genetically distinct from one another, even though adult individuals from these populations commonly share the same feeding grounds (Bowen and Karl 1997).

Many species of amphibians and reptiles exhibit significant genetic differentiation among populations if patches of suitable habitat are isolated by landscape features that make movement between patches difficult (Rittenhouse Figure 12.1 Eastern red-backed salamanders (*Plethodon cinereus*) have small home ranges. Many small amphibians live out their lives within a circumscribed home range, such as a single fallen tree on the forest floor. (Photographs: Habitat, © Erin Paul Donovan/Alamy; *P. cinereus*, Harvey Pough.)

and Semlitsch 2006; Wang 2009; Richardson 2012). This is particularly true for species with inherently low dispersal ability, such as small tropical forest-floor frogs (Fouquet et al. 2012) or lizards and snakes that exhibit strong site fidelity (Heath et al. 2012; Lukoschek and Shine 2012) or have highly specialized habitat requirements (Dubey and Shine 2010). Conversely, species with high disper-

sal ability, such as varanid lizards or highly mobile snakes, are less affected by landscape barriers (Smissen et al. 2013) and exhibit considerable gene flow among local populations (Blouin-Demers and Weatherhead 2002).

Patterns of movement in amphibian and reptile populations also have major conservation implications (see Chapter 17). Habitat fragmentation can influence the ability of animals to move through the landscape, thereby affecting survival and reproduction (Janin et al. 2012). Roads, housing developments, agricultural land, forest clear-cuts, and other man-made barriers can limit movement between populations (Todd et al. 2009; Nowakowski et al. 2013), increase mortality among migrating animals (Bouchard et al. 2009; Rittenhouse et al. 2009), decrease genetic diversity within populations (Wahbe et al. 2005; Clark et al. 2010; Holderegger and Di Giulio 2010), and lead to the extinction of small, isolated populations (Driscoll 2004; Becker et al. 2007; Munguia-Vega et al. 2013). Maintaining dispersal corridors of suitable habitat and providing amphibians and reptiles with means of traversing habitat barriers have become major issues in herpetological conservation (Dixo and Metzger 2009; Van Buskirk 2012; Watabe et al. 2012; Krug and Pröhl 2013).

12.2 Methods for Studying Movements

Two essentials for studying the movements of amphibians and reptiles are the ability to identify particular individuals and the ability to relocate them. This means that animals must be marked or equipped with a device to track their movements. The method most commonly used to study movements of small amphibians and reptiles is **mark**-



recapture: researchers mark the animals in some way, release them, then recapture them at a later time and record their recapture positions on a map. Various methods have been used to mark amphibians, including a coded system of toe clips, colored or numbered waistbands and tags, tattooing, heat- or freeze-branding, marking with fluorescent powders, use of subcutaneous passive integrative transponders (PIT tags), recording of natural color patterns, and marking with subcutaneous numbered tags (**Figure 12.2**). Many of these techniques have been used with reptiles as well.



Figure 12.2 Subcutaneous numbered tagging identifies a recaptured individual. The number on this frog's hindlimb can be read through the animal's skin. The tag's legibility is enhanced by viewing it under ultraviolet light. (Photograph by Kristiina Hurme.)

Turtles are usually marked with small notches on the shell or with paint. Snakes are marked by selectively removing scales or by branding, and toe clipping has commonly been used to mark frogs, salamanders, and lizards. Unfortunately, these markings disappear if the clipped toes regenerate, if the skin is shed, or if marks simply wear off. Some, but not all, studies have shown that toe-clipped individuals have lower rates of growth, survival, or reproduction than individuals marked with other methods. Hence, toe clipping has been criticized and defended from both ethical and practical perspectives (May 2004; Funk et al. 2005).

The best method for obtaining detailed information about movements is to equip animals with radio transmitters, each of which broadcasts on a unique frequency. This method allows frequent relocation of animals even in hidden retreats. Radio tracking has been used to study the movements of many kinds of amphibians and reptiles. Originally its use was confined to large crocodylians, turtles, snakes, lizards, and frogs, but miniaturized transmitters are now used with small salamanders and frogs (**Figure 12.3A**) (Madison and Farrand 1998; Connette and Semlitsch 2011; Andreone et al. 2013). Radio tracking usually provides a more complete



Figure 12.3 Radio transmitters allow the movements of amphibians and reptiles to be tracked. (A) A Madagascan rainbow frog (*Scaphiophryne gottliebi*) fitted with a radio transmitter. (B) Satellite transmitters allow researchers to track the long distances travelled by sea turtles such as *Chelonia mydas*. (Photographs: A, Gonçalo M. Rosa; B, Bermuda Turtle Project.)

picture of movement patterns than do mark-recapture studies (Weatherhead and Hoysak 1989).

Sea turtles present a special problem because they move over long distances. Their movements can be studied with satellite-monitored transmitters that relay positional information to investigators on the ground (Figure 12.3B) (Godley et al. 2008). In early studies, sample sizes for satellite tracking studies were small, limited by the cost of the system. Recently, some investigators have deployed transmitters on multiple individuals, thereby providing valuable information on movements of entire populations (Schofield et al. 2013). Another way to study sea turtle movements indirectly is to use genetic sequencing data obtained from individuals at given locations to determine the movements of individuals between nesting beaches and feeding grounds (Dethmers et al. 2010; Naro-Maciel et al. 2012). These data can be combined with data from recaptures of marked individuals and telemetry to produce a complete picture of migration patterns and population structure (Stewart et al. 2013).

12.3 Types of Movement

Terms such as "home range," "migration," and "dispersal" have been used differently for different kinds of animals (Dingle 1996). The term **station-keeping** has been used to describe movements directly related to the acquisition of resources such as food, mates, basking sites, or retreat sites that tend to keep an animal within a home range. Foraging is one type of station-keeping, as is commuting, a pattern of movement back and forth from a fixed location to resource patches. Territorial defense of all or part of the home range also is considered station-keeping.

Movement outside a home range for the purpose of exploring new habitats or resource patches is termed ranging behavior. This type of movement includes not only occasional forays outside an established home range by adults (for example, when males are searching for mates) but also the movements of juveniles from the areas where they were born. The latter have traditionally been termed "dispersal movements" in the herpetological literature. However, the term "dispersal" has been used to describe both the behavior of individual animals and population-level processes. For example, the departure of juvenile anurans from a breeding pond when they move into terrestrial habitats has been called juvenile dispersal, but many of these individuals eventually return to the same pond as adults to breed. Only those that move permanently to new ponds can be considered dispersers in terms of their effect on the genetic structure of populations (Breden 1987). Sometimes animals leave the area where they were born but do not increase their distance from other individuals. Juvenile lizards, for example, are sometimes attracted to areas where other lizards are already living, using their presence as an indicator of habitat quality (Stamps 1994; Vercken et al. 2012). Some lizards move frequently between habitat patches but form aggregations when suitable habitats are in short supply (Nieuwoudt et al. 2003).

The technical term **dispersa***l*, then, is best used for any sort of one-way movement between habitat patches, distinct from **migration**, which usually is considered movement in two directions (although not all migration is bidirectional). In further contrast to dispersal, Dingle (1996) defined migration as a specialized kind of movement that is not directly responsive to resources. Five key features define migration, although they may not be evident in all migrating animals:

- 1. Migration movement is persistent and of greater duration than station-keeping or ranging.
- 2. Migration moves along relatively straight-line paths.
- Migrating animals temporarily suppress responses to resources that normally would terminate movement (e.g., food).
- Migration involves activity patterns related to departure and arrival.
- 5. Energy reserves may specifically support migration.

12.4 ■ Resource Dispersion and the Use of Space

Because all movement is ultimately related to the acquisition of resources, the way in which an animal moves through its habitat is closely related to the spatial and temporal distribution of resources, especially food. We can think of a habitat as comprising a series of resource patches. As an animal moves through the habitat, it passes from one patch to another, making use of resources available in each one.

Resources can be divided into two categories: those that are depleted by the animal and those that are not. Food can be depleted, whereas retreat sites such as burrows, rocks, and fallen logs cannot. Once an animal has used a retreat site and moved on, that resource is available to other individuals, or the same animal may return to the site again and again. In contrast, once an animal has eaten the food in a habitat patch, the patch cannot be used again until the food resource is replenished. The animal must decide whether to remain in a given patch or move to a new patch based on the relative abundance of resources in the available patches, the distance between patches, the risks of moving from one patch to another, and several other factors. Animals that live in restricted home ranges revisit the same patches repeatedly, and the rate at which they do so depends in large part on how rapidly resources in those patches are replenished.

Animals are expected to occupy limited home ranges when resources are so abundant that they are depleted very slowly or when the rate at which resources are renewed is high enough to allow the animal to return to the same patches again and again. For example, nectar-feeding hummingbirds and bumblebees frequently visit the same patches of flowers and even the same individual flowers every day for many days, because the flowers continually produce new nectar.

In contrast, if resources are renewed very slowly after being depleted, then animals will not be able to revisit patches frequently. For example, an animal that feeds on small fruiting bushes can deplete all of the fruit on a given bush in one visit. In that case, the animal must move to another bush to feed, and it may be a year or more before a bush produces fruit again. These types of resources often are patchily distributed in the habitat, and an animal must range over an area large enough to encompass all the patches needed to sustain it year-round. Hence, animals that feed on patchy resources with low renewal rates, such as swarming termites or local concentrations of pelagic marine organisms, tend to have relatively large home ranges. These animals can shift from one activity center to another, or they may even adopt a nomadic lifestyle. In short, the spatial strategies of animals form a continuum from strong site fidelity with very limited movement between resource patches to no site fidelity with extensive movement between patches (Waser and Wiley 1979).

Spatial strategies

Most of the spacing systems and movement patterns described for amphibians and reptiles can be predicted from the abundance, patchiness, and renewal rate of their food resources. Unfortunately, quantitative data on the spatial and temporal distribution of resources used by amphibians and reptiles are scarce, so the examples in **Table 12.1** (which are for reptiles only) are based on a qualitative assessment of resource distribution patterns. The discussion here focuses on reptiles because their spatial strategies have been studied more intensively than those of amphibians.

TURTLES Many freshwater turtles are omnivorous, and their food usually is relatively abundant. The predicted spatial system is one of overlapping home ranges with sharing of clumped resources, such as basking logs. Small turtles that live in highly productive environments, such as bogs, marshes, and shallow ponds, typically have home ranges of less than 2 ha. Examples include the bog turtle (Glyptemys muhlenbergii), spotted turtle (Clemmys guttata), Pacific pond turtle (Emys marmorata), Blanding's turtle (Emydoidea blandingii), and several kinosternid turtles (Schubauer et al. 1990; Rowe and Moll 1991; Carter et al. 1999). Larger turtles, including some predatory species, that live in less productive ponds, lakes, and rivers usually have home ranges exceeding 2 ha and sometimes exceeding 10 ha, as predicted from their larger body size and more patchily distributed resources. Examples include snapping turtles (Chelydra, Macroclemys), map turtles (Graptemys), sliders (Trachemys), red-bellied turtles (Pseudemys) (Schubauer et al. 1990; Pettit et al. 1995), and Australian snake-necked turtles (Chelodina) (Bower et al. 2012).

	Resources				Movement		
Feeding niche	Abundance	Patchiness	Renewal rate	Spacing system ^a	Within patch	Between patches	Examples
Arboreal folivore	High	Low	Moderate	Home range	Low	Low	Green iguana
Marine folivore	High	Low	Moderate	Home range	Low	Low	Galápagos marine iguana, green sea turtle
Herbivore	High	Moderate	Moderate	Home range, temporary aggregations	Low	Moderate	Iguanid lizards, tortoises
Frugivore	High	Moderate	Moderate	Home range, temporary aggregations	Low	Low	Gray's monitor lizard
Terrestrial omnivore	High	Moderate	Moderate	Home range	Low	Moderate	Box and wood turtles, some skinks
Aquatic omnivore (rich habitats)	High	Low	High	Home range	Low	Low	Turtles in bogs and marshes
Aquatic omnivore (poor habitats)	Moderate	Moderate	Moderate	Home range, shifting activity center	Moderate	Variable	Turtles in ponds, lakes, and rivers
Predator of sponges	Variable	Moderate	Low	Shifting activity center	Moderate	High	Hawksbill sea turtle
Predator of jellyfish	Variable	High	Low	Nomadic	Low	High	Leatherback sea turtle
Active predator of vertebrates	Variable	Moderate	Low	Home range, shifting activity center	Moderate	Variable	Many snakes
Ambush predator of vertebrates	Variable	Variable	Low	Shifting activity center, home range	Low	Variable	Viperid snakes
Predator of large vertebrates	Variable	High	Moderate	Home range	Moderate	High	Komodo dragon
Scavenger	Low	High	Low	Shifting activity center, temporary aggregations	Low	High	Komodo dragon
Sit-and-wait insectivore	Moderate	Moderate	High	Home range, territoriality	Moderate	Low	Iguanian lizards
Actively foraging insectivore	Moderate	High	High	Home range	Moderate	High	Non-iguanian insectivorous lizards
Earthworm specialist	Variable	Moderate	High	Home range, shifting activity center	Moderate	Moderate	Worm and garter snakes
Ant and termite specialist	Variable	High	Variable	Shifting activity center	Low	Variable	Horned lizards

TABLE 12.1 Feeding niches, resource distribution, and movement patterns for selected reptiles

^aWhen more than one spacing system is listed, the most common is given first.



Some sea turtles are almost entirely herbivorous. As much as 90% of the diet of a green sea turtle (*Chelonia mydas*) is composed of sea grasses, an abundant and uniformly distributed resource in shallow lagoons. These turtles typically remain in limited home ranges while foraging (Godley et al. 2002). At the opposite end of the spectrum are species that use less abundant, patchily distributed resources with low renewal rates. An extreme example is the leatherback sea turtle (*Dermochelys coriacea*), which feeds mostly on jellyfish and other pelagic invertebrates associated with drift

Figure 12.4 Leatherback sea turtles (*Dermo-chelys coriacea*) move among feeding grounds. (A) Patches of jellyfish can be unpredictable in their spatial distribution, but extremely abundant, as seen in this aggregation. (B) The tracks show the routes of 20 satellite-tagged leatherbacks (A–T) from their release point near Cape Cod, Massachusetts to the point where the last transmission was received (red triangles). (A, photograph by Andrew R. Lewis; B, from Dodge et al. 2014.)

lines and fronts in the ocean. Prey patches are created by winds and currents, so they are not likely to be rapidly renewed once depleted. Some of these prey patches can be enormous, with extremely high densities of prey, allowing a large animal to feed on relatively small prey (Figure 12.4A) (Fossette et al. 2011).

Leatherbacks are nomadic, moving over thousands of kilometers of open ocean in a pattern like that of some whales that feed on similar prey (Hughes et al. 1998; James et al. 2005). Some leatherbacks move across entire ocean basins in a single season, so their movements are even more impressive than those of fish or marine mammals of similar size (Hays and Scott 2013). The turtles do not simply move at random, but consistently travel to areas rich in food (James et al. 2005; Houghton et al. 2006). In the Atlantic, leatherbacks gather in large numbers to feed on jellyfish in the shallow waters off New England and Nova Scotia. The turtles remain in these temperate habitats in the summer and then make long-distance and relatively straight movements into the deeper waters of the Atlantic, through which they travel to wintering grounds in the tropics, where they also breed (Figure 12.4B) (Dodge et al. 2014).

HERBIVOROUS LIZARDS Folivores—animals that feed mostly on leaves—usually have abundant food readily at hand, although the quality of their food may vary seasonally. These ani-

mals are expected to occupy small, stable home ranges and to exhibit relatively little movement. (Home range size must be considered relative to body size, because large species will have larger absolute home range sizes than do small species; see Perry and Garland 2002.) Lizards in this category include the green iguana (*Iguana iguana*) and Galápagos marine iguana (*Amblyrhynchus cristatus*).

Outside the breeding season, green iguanas live in small home ranges, show little aggression toward one another, and spend most of their time resting in one place (Dugan 1982). They make occasional forays out of their normal home ranges to feed on local concentrations of fruit, with many individuals sometimes feeding peacefully in the same tree. Marine iguanas exhibit many behavioral and ecological similarities to green iguanas but feed on algae in the intertidal zone or underwater. They move from terrestrial basking sites to foraging sites and often return repeatedly to the same foraging area. Movements at foraging sites are minimal, and relatively little time is devoted to foraging each day (Wikelski and Trillmich 1994).

Other lizards that are largely or entirely herbivorous include the large ground iguanas of the Caribbean (*Cyclura*) and the Galápagos (*Conolophus*; **Figure 12.5A**), a variety of smaller iguanids such as *Dipsosaurus* and *Sauromalus*, several agamids (*Uromastyx* and *Hydrosaurus*), and at least one skink (*Corucia zebrata*). Terrestrial omnivores include the Australian sleepy lizard (*Tiliqua rugosa*) and the largely frugivorous Gray's monitor lizard, or butaan (*Varanus olivaceous*) of the Philippines. The spatial strategies of these reptiles are similar to those of folivores, with individuals occupying small home ranges, sometimes for many years, exhibiting low rates of movement between food patches, and generally remaining inactive for long periods of time (Satrawaha and Bull 1981; Auffenberg 1982, 1988; Werner 1982; Perry and Garland 2002).

CARNIVOROUS LIZARDS Vertebrate prey animals tend to have a patchy distribution and low to moderate renewal rates. Predators of vertebrates thus are expected to occupy relatively large home ranges (Perry and Garland 2002), or to use a series of shifting activity centers with only weak attachment to a fixed home range. Komodo dragons (*Varanus komodoensis*) are mainly predators and scavengers of vertebrates (**Figure 12.5B**). Individuals vary greatly in size and

(A)



Figure 12.5 Feeding niches affect the range sizes of three lizards. (A) The Galápagos land iguana (*Conolophus subcrista-tus*) is an omnivore that feeds mainly on plants. It moves slowly and has a small home range relative to its body size. (B) The komodo dragons (*Varanus komodoensis*) of Indonesia are carnivores and also scavengers. Here two lizards devour the carcass of a large sea turtle. (C) Gila monsters (*Heloderma suspectum*)

are specialist feeders on nestlings. This radio-tagged lizard was located with its head in a nest of cottontail rabbits (left); pulled from the burrow, the lizard continued to swallow the baby rabbit that was in its mouth (right). Gilas tend to have large home ranges, since nesting sites are easily depleted and may be widely spaced. (Photographs: A, © Carolyn Jenkins/Alamy; B, Achmad Ariefiandy; C, Roger A. Repp.) display a variety of foraging tactics and movement strategies. The largest lizards establish residence in permanent home ranges centered on burrows and basking sites. Radiating out from this core area is a large foraging range (up to 530 ha) that overlaps those of other individuals. The lizards patrol familiar trails and lie in wait for prey along heavily used paths. Carrion is obtained from an even larger area, and lizards often travel 5 km to carcasses, resulting in the formation of temporary aggregations. Smaller Komodo dragons are mostly transient, moving from place to place and feeding opportunistically on a variety of prey (Auffenberg 1981; Ciofi et al. 2007).

Reptile and bird eggs, nestling birds, and baby mammals are particularly patchy types of prey with low renewal rates because they tend to be aggregated at discrete nest sites. Once a nest site is depleted, a predator may have to move some distance to find a new one. Both the Mexican beaded lizard (*Heloderma horridum*) and Gila monster (*H. suspectum*) specialize on this type of diet (**Figure 12.5C**). These lizards have very large home ranges, averaging about 22 ha for *H. horridum* (Beck and Lowe 1991) and up to 66 ha for *H. suspectum* (Beck 1990). Gila monsters and beaded lizards feed on large food packages and remain relatively inactive between meals, moving on less than a third of all days during the activity season. This contrasts with some carnivorous snakes that can move through much of their home range in a single day.

SNAKES All snakes are carnivorous (see Chapter 11). The size of a snake's home range depends on body size and the spatial distribution of its food. Many snakes that actively search for vertebrate prey have relatively large home ranges, including rat snakes (*Elaphe*), racers and coachwhips (*Coluber*, formerly *Masticophis*), and hognose snakes (*Heterodon*) (Weatherhead and Hoysak 1989; Secor 1995; Plummer and

Mills 2000). Some actively foraging snakes, such as water snakes (*Nerodia*) and European grass snakes (*Natrix natrix*), tend to use a limited foraging area for some period of time before shifting to a new area (**Figure 12.6**) (Tiebout and Cary 1987), but they may become more sedentary around rich concentrations of food (Karns et al. 2000).

Slim, elongate snakes, such as mambas (*Dendroaspis*) and racers and coachwhips (*Alsophis, Coluber, Psammophis*, and others), have very large home ranges (see Figure 7.22A). These snakes are visually oriented hunters that travel over much of their home range in a single day (Secor 1995). Viperid snakes prey on small vertebrates, but unlike racers and coachwhips, vipers are predominantly ambush predators that remain immobile for long periods of time while waiting to capture animals that pass by (see Figure 7.22B). Movements within habitat patches are infrequent, and individuals of some species remain in the same place for weeks or months at a time. Most of the movements these snakes make are between habitat patches as they shift from one activity center to another in search of good ambush sites (King and Duvall 1990; Secor 1995).

Snakes that are ambush predators presumably use chemical cues to monitor prey activity and to choose suitable ambush sites. Prairie rattlesnakes (*Crotalus viridis*) in Wyoming stopped searching and remained near stations that were provided with either caged rodent prey or prey odors (Duvall et al. 1990). The costs of movement can be high for snakes, both energetically and because of exposure to predators (Sperry and Weatherhead 2009), so they are expected to minimize costs whenever possible. Particularly rich food supplies can



Figure 12.6 Movements of European grass snakes (Natrix natrix). One radio-tagged male snake (green circles) and one female (red circles) were followed over a 4-month period on a plot in southern Sweden. Blue areas indicate ponds. The size of a circle indicate the number of days the snake stayed in each location. Note the tendency for the snakes to move between several major centers of activity. (After Madsen 1984; photograph by Wolfgang Wüster.)



cause ambush predators to reduce foraging time and amount of movement. In an experimental study, Costa Rican vipers (*Bothrops asper*) were provided with supplemental food. Snakes receiving extra food made less frequent movements, moved shorter distances, and spent less time foraging than did snakes that were not fed (Wasko and Sasa 2012).

Home range size and patterns of movement in snakes are not determined exclusively by foraging strategy, however. Body size, gender, and reproductive state also can affect home range size. In species with mate-searching mating systems (see Chapter 14), males commonly have larger home ranges and make longer movements than do females, especially in the breeding season. These long movements increase the chances of a male encountering a female. Charles Smith and colleagues (2009) used radio tracking to study the movements of copperheads (Agkistrodon contortrix) in Connecticut. During the mating season (June through September), males had larger home ranges and moved more frequently and for longer distances than did females (Figure 12.7). Similar sexual differences in movement or home range size have been reported in cottonmouths (Agkistrodon piscivorus) (Roth 2005) and several species of rattlesnakes (Degregorio et al. 2011; Glaudas and Rodríguez-Robles 2011; Wastell and Mackessy 2011) and in Namagua dwarf adders (Bias schneideri) (Maritz and Alexander 2012), among others.

INSECTIVOROUS REPTILES Most small species of reptiles are insectivorous or specialize on other invertebrate prey such as earthworms. Such resources tend to be more abundant, more evenly distributed, and more rapidly renewed than vertebrate prey. Hence, insectivorous reptiles are expected to occupy relatively small home ranges, a pattern seen in insectivorous lizards and insectivorous and worm-eating snakes (Macartney et al. 1988; Perry and Garland 2002). Insectivorous lizards display a range of foraging modes, from sit-and-wait (ambush) foragers that feed mostly on mobile prey to actively foraging species that feed mostly on cryptic or slow-moving prey (see Chapter 13).

In general, lizards with a sit-and-wait foraging mode tend to have smaller home ranges than do actively foraging lizards of similar size (Verwaijen and Van Damme 2008). Sit-and-wait foragers sometime chase down prey in habitat patches but seldom move between patches, whereas actively foraging lizards move frequently between patches and spend little time in each one (Anderson 1993). The way in which lizards use their home ranges depends on the spatial distribution of prey. For example, the desert grassland whiptail lizard (Aspidoscelis uniparens) feeds mostly on termites that occur in discrete patches within a lizard's home range. Individual lizards have relatively large home ranges but spend most of their time in a core area that is less than 10% of the total home range. Here the lizards dig for termites but seldom return to exactly the same spot once a patch has been depleted (Eifler and Eifler 1998). These lizards belong to a clade of actively foraging species, and they spend much more time moving between patches than digging for prey.

North American horned lizards (Phrynosoma) and Australian thorny devils (Moloch horridus) specialize on ants,

> Figure 12.7 Sexual differences in movements of the copperhead (Agkistrodon contortrix). (A) An adult northern copperhead. (B) Comparison of annual activity ranges for six male (solid lines) and six female (dashed lines) copperheads; each colored polygon outlines the activity range of a single snake. (C) Comparison of monthly total distance moved in the mating season (June-September and nonmating season by males and females (mean ± standard error). Males have larger home ranges than females and travel farther during the mating season. (A, © Design Pics/Alamy; B, C after Smith et al. 2009.)



which also tend to be patchily distributed. These reptiles exhibit elements of both foraging strategies, moving periodically between patches and showing only loose attachment to a home range, but moving very little within patches and sometimes remaining in one area for long periods of time (Munger 1984; Withers and Dickman 1995; Wone and Beauchamp 2003). The similar behaviors and morphology of *Phyrnosoma* and *Moloch* (see Figure 6.2) are an example of convergent evolution.

Home range fidelity and homing

Many amphibians and reptiles exhibit remarkable fidelity to familiar areas, remaining year after year in the same place. Australian sleepy lizards (Tiliqua rugosa) that were radio tracked for up to 5 years seldom shifted to new home ranges (Bull and Freake 1999). European fire salamanders (Salamandra salamandra) were recaptured in the same home ranges for up to 7 years, and European common toads (Bufo bufo) for up to 9 years (Heusser 1968; Joly 1968). Individual gopher frogs (Rana capito) exhibited strong fidelity to burrows under tree stumps, even after traveling more than 3 km to a breeding site (Humphries and Sisson 2012). Even more remarkable are the results of Louise Stickel's (1989) study of home ranges in eastern box turtles (Terrepene carolina) in Maryland (Figure 12.8), which she continued from 1944 through 1981. Most of the turtles that were recaptured over periods of many years (32 years, in one case) showed little or no change in either the location or size of their home ranges.

HOMING BY AMPHIBIANS A high degree of fidelity to home ranges has been demonstrated for many amphibians by experimentally displacing individuals from their home ranges to new habitats. Most species show highly accurate homing to their original home ranges from relatively short distances (adjusted for the body size of the animal), but homing performance often diminishes at long distances. The ability to home after displacement enables animals to return to familiar locations where sources of food, shelter, and other resources are well known. A strong homing tendency in amphibians and reptiles can interfere with conservation efforts that involve translocating animals to new habitats. Translocated individuals often try to return home, causing them to move more than residents, feed less, and face greater exposure to predators and other sources of mortality (Matthews 2003; Germano and Bishop 2009; Roe et al. 2010).

Plethodontid salamanders generally home successfully from distances of up to 30 m but are less successful when displaced longer distances (Wells 2007; Ousterhout and Liebgold 2010). In contrast, the red-bellied newt (*Taricha rivularis*), studied in California by Victor Twitty and his colleagues, exhibits the most impressive homing ability of any amphibian. Twitty displaced hundreds of newts about 2 km upstream or downstream from where they were initially captured. Some individuals remained at the release site the first year, but after 5 years about two-thirds of the newts



Figure 12.8 Eastern box turtles (*Terrepene carolina*) maintain stable home ranges. Louise Stickel's study of eastern box turtles in Maryland over 37 years showed that some individuals maintained the same home range for decades. (Photograph by Kentwood D. Wells.)

had been recaptured, 90% of them in their home stream segments (**Figure 12.9**). In later experiments, newts were displaced over much longer distances to adjacent stream valleys. Many managed to return to their home streams from as far as 8 km, having moved overland across dry wooded ridges (Twitty 1966). This species clearly can return home even when displaced to unfamiliar terrain.

The homing performance of anurans depends in part on how displacements are carried out. Some pond-breeding anurans occupy home ranges around ponds during the breeding season and then return repeatedly to the same terrestrial habitat in the nonbreeding season. When anurans are moved from breeding ponds to land, they usually return quickly from distances of 700 m, and they sometimes show homeward orientation at distances up to several kilometers (Sinsch 1992). Studies of a mixed population of the European waterfrogs Pelophylax lessonae, P. ridibundus, and their hybridogenetic associate P. esculentus (see Section 8.4) revealed a pattern of movement between ponds that corresponded to differences in the ecology of these species. Most adults of all three forms remained in the same pond, but about 12% moved to new ponds. P. ridibundus, which typically inhabits permanent ponds and lakes, was least likely to move, whereas P. lessonae, which inhabits marshy habitats that often contain networks of smaller ponds, was most likely to move (Holenweg Peter 2001). When frogs were displaced from their home ponds, however, there was no effect of genotype on homing performance, although homing decreased with displacement distance (Holenweg Peter et al. 2001). Overall, about 90% of displaced frogs that were recaptured were found at their home ponds, indicating that these frogs exhibit strong breeding site fidelity.



Figure 12.9 Homing by red-bellied newts (*Taricha rivularis***).** This landmark mark–recapture study displaced 564 newts some 2 km downstream from their home stream segment. Although a few individuals remained at the release site, within 5

When males of a terrestrial dendrobatid frog, *Allobates femoralis* (Figure 12.10), were displaced from their territories to other terrestrial sites, 87% returned to their original territories from 200 m away, but only 30% returned from 400 m (Pašukonis et al. 2013). The fact that males of this species defend their home ranges as territories suggests that suitable territories are in short supply, so the frogs would be highly motivated to return home after being displaced.

HOMING BY REPTILES Freshwater and terrestrial turtles vary in their homing performance, from species such as the spotted turtle (*Clemmys guttata*) that do poorly when displaced more than a few hundred meters, to species that can return home from displacements of several kilometers. Aquatic turtles displaced along watercourses tend to home



years almost two-thirds of the displaced newts had returned to their home stream. Bars represent the total number of animals recaptured at each location over the course of the 5-year study. (After Twitty 1966; photograph by Wayne Van Devender.)

from greater distances than do turtles or tortoises displaced over land, perhaps because they often have larger home ranges, or because they can move faster and with less energy expenditure in water. For example, some map turtles (*Graptemys pulchra*) returned home after displacements of up to 24 km along a river, although the total number of individuals returning home was small (Chelazzi 1992). Displacements of several kilometers probably put most turtles outside their usual home ranges.

Gordon Rodda (1985) studied homing by juvenile American alligators (*Alligator mississippiensis*). Individuals displaced from 1 to 10 home range diameters (up to 7 km) either returned home rapidly or showed strong homeward orientation. Subsequent experiments revealed that juvenile alligators maintained a homeward orientation even when displaced much farther (12–34 km), with the accuracy of orientation depending on the method used to displace them. Radio tracking studies of juveniles released up to 16 km from their home ranges also demonstrated an ability to home from unfamiliar areas, although homing performance decreased at distances greater than 5 km.

Caimans (*Caiman crocodilus*) in Suriname usually returned to the precise spots where they were first captured after traveling up to 3 km away (Ouboter and Nanhoe

Figure 12.10 Males of the dendrobatid frog *Allobates* **femoralis are highly territorial.** These South American frogs fight with other males for control of territories and show strong homing tendencies when displaced from their territories. (Photograph by Walter Hödl.)

1988). When individuals of the same species were displaced more than 2 km, more than 80% returned home, with most having traveled over land (Gorzula 1978). The homing of adult saltwater crocodiles (*Crocodylus porosus*) of the Cape York Peninsula in northern Australia was even more impressive, with tagged individuals displaced from their home stream circumnavigating the peninsula to return to their original capture site (**Figure 12.11**) (Read et al. 2007). Individual crocodiles can travel as much as 30 km in a single day, much farther than most reptiles travel in a lifetime.

Relatively little is known about homing by lizards, which is surprising in light of the enormous literature on home ranges and territoriality in these animals. Most studies have focused on North American and European species (Chelazzi 1992). Sceloporus, Uta, and Phrynosoma can home from displacements of less than 300 m from their normal home ranges, but homing from greater distances has not been tested. Most of these studies were done in relatively open desert habitats. The animals were released outside their home ranges, but not necessarily out of view of familiar landscape features.

Some lizards, however, appear to be capable of returning home even when familiar landmarks are not visible. Most adult and juvenile Sceloporus jarrovii returned to their original home ranges when they were displaced up to 200 m in a riparian habitat at the bottom of a canyon (Ellis-Ouinn and Simon 1989). Wall lizards (Podarcis muralis) in Italy were released 50-200 m from their home sites; homing performance decreased with displacement distance (Scali et al. 2013). When male and female Anolis cristatellus were displaced from their home ranges to release sites up to 26 home range diameters (62 m) away, two-thirds of the lizards returned home in 3 days (Jenssen 2002).

Figure 12.11 Homing by saltwater crocodiles (Crocodylus porosus).

(A) An adult saltwater crocodile. (B) Displaced radio-tagged individuals circumnavigated the entire Cape York Peninsula of northern Australia to return to their home stream. (A © GTS Productions/ Shutterstock; B after Read et al. 2007.) Homing performance was unaffected by displacement distance, even though *A. cristatellus* is a highly sedentary species, and individuals were unlikely to be familiar with the more distant areas where they were released.

Limited evidence from homing studies with adult lizards suggests that the strength of attachment to a home range can affect homing performance. For example, homing performance was similar in males and females of *Sceloporus jarrovii* and *Anolis cristatellus*, species in which both sexes are territorial. In contrast, female *Sceloporus orcutti* are not territorial





and exhibited poorer homing performance than did males, which are territorial (Weintraub 1970). Homing performance was relatively poor in Phrynosoma douglassi, a species that exhibits little evidence of territoriality and only weak attachment to a home range. Individuals of Sceloporus graciosus, a territorial species living in the same habitat, exhibited much better homing performance (Guyer 1991). Australian sleepy lizards (Tiliqua rugosa) exhibit strong fidelity to home ranges and a strong tendency to mate with the same individuals year after year. When individuals were displaced during the mating season, males exhibited much stronger homeward orientation than did females and also moved more quickly in a homeward direction. This difference suggests that motivation to return home was stronger in males, perhaps because mating success is related to the males' ability to guard mates in their home ranges (Freake 1998).

Studies of homing by snakes have produced inconsistent results (Gregory et al. 1987; Chelazzi 1992), but this inconsistency may have more to do with the design of the studies than with real interspecific differences in homing ability. Several early studies revealed little evidence of homing behavior. Most of these studies were based on displacements of only a few individuals from summer home ranges to similar habitats. Displaced individuals usually remained near the site where they were released, perhaps because the areas provided sufficient food. Garter snakes (*Thamnophis ordinoides*) that feed mainly on earthworms, a rather uniformly distributed resource, showed little evidence of homeward orientation (Lawson 1994).

In contrast, snakes usually exhibit good homing ability when displaced from communal den sites (Brown and Parker

1976) or from rich food sources such as a fish hatchery or a lakeshore (Lawson 1994). These observations suggest that snakes are motivated to return home when removed from especially valuable resource patches, but they do not necessarily indicate that other species lack homing ability. Studies of yellow-lipped sea kraits (Laticauda colubrina) (Figure 12.12) in Fiji revealed strong homing ability when snakes were displaced from one island to another about 5 km away. The snakes could have been familiar with the entire area, however, because they forage over many kilometers of ocean (Shetty and Shine 2002).

Figure 12.12 Yellow-lipped sea krait (*Laticauda colubrina***).** Snakes displaced between two Fijian islands about 5 km apart readily found their way back to their home island. (Photograph by Xavier Bonnet.)

Finding the way home

When amphibians or reptiles move from shelter sites to peripheral parts of their home range or make occasional excursions outside their home range, they need some mechanism to find their way home to avoid being permanently displaced to unsuitable habitat (Russell et al. 2005). The types of cues that amphibians and reptiles use for local orientation depend on the sensory capabilities of the animals (Chelazzi 1992; Sinsch 1992). Salamanders probably use a combination of visual and chemical cues to identify familiar foraging areas or retreat sites. The European fire salamander (Salamandra salamandra) appears to find its way home after displacement by following a circuitous route connecting landmarks such as rocks and logs rather than by returning along a direct straight-line path (Figure 12.13A). Many amphibians can use less familiar sensory capabilities for orientation, including detection of slope angle, polarized light, celestial cues, and Earth's magnetic field (Sinsch 1992). Red-spotted newts (Notophthalmus viridescens) tend to orient downhill (geotaxis) when placed in unfamiliar surroundings, presumably because moving downhill normally







Figure 12.13 Orienting homing movements using landmarks.

(A) The solid arrow on the left indicates the displacement of an individual European fire salamander (*Salamandra salamandra*) from its home range; the dashed arrrows shows its path when returning home. Shaded areas indicate fallen logs and trees, which the animal uses as landmarks for normal movements within its home range and in returning home after being displaced. (B) Landmark navigation by granite spiny lizards (*Sceloporus orcutti*). Solid arrows show experimental displacements of three individuals; dashed lines show return pathways. Shaded areas indicate rocky outcrops. Most individuals returned home by a circuitous path connecting the outcrops. (A after Plasa 1979, photograph © Arterra Picture Library/Alamy; B after Weintraub 1970, photograph by Troy Hibbitts.)



It is probable that most lizards rely on visual cues for orientation at moderate distances. Chemical cues may be important for identifying retreat sites, burrows, or communal hibernation dens, especially for non-iguanian lizards and for snakes. European vipers (*Vipera aspis*) and granite spiny lizards (*Sceloporus orcutti*) displaced within sight

would lead them to water (Omland 1998). Adult newts collected during spring migrations and placed in an apparatus that allowed the slope angle to be varied exhibited a strong downhill orientation. Red efts, the terrestrial juvenile stage of *N. viridescens*, did not exhibit downhill orientation under the same conditions and showed no tendency to move toward ponds. Several species of newts, including *N. viridescens* and European palmate newts (*Lissotriton helveticus*), have the ability to sense Earth's magnetic field and can use a magnetic map for homeward orientation (Fischer et al. 2001; Diego-Rasilla et al. 2008). of their home areas exhibited better homing performance than did individuals displaced out of sight of home areas. Displaced *S. orcutti* returned home by moving between conspicuous rock outcrops (**Figure 12.13B**). A series of experimental studies with Australian sleepy lizards (*Tiliqua rugosa*) indicated that visual cues probably are important for orientation within a familiar home range, whereas olfactory cues are not essential (Zuri and Bull 2000a,b).

Tortoises may use olfactory cues to orient toward home ranges after displacements of a few hundred meters (Chelazzi and Delfino 1986), and it seems likely that both turtles and crocodylians can use olfactory cues to locate bodies of water at some distance. For several decades, sea turtle biologists have speculated that hatchling turtles might imprint on chemical cues associated with natal beaches and use these cues to identify beaches when they return as adults. Some have even suggested that sea turtles might use chemical cues for long-distance homing. Although the results of some experimental studies are suggestive, they do not definitively support either hypothesis (Lohmann et al. 1997).

12.5 Territoriality

Some amphibians and reptiles aggressively defend all or part of their home ranges as territories. The abundant literature on this subject includes reviews for lizards (Stamps 1977, 1983, 1994) and amphibians (Mathis et al. 1995; Wells 2007). Patterns of home range defense can be predicted from the abundance, patchiness, and renewal rate of resources. Territoriality is part of a spectrum of spacing strategies from exclusive home range defense to complete home range overlap (Waser and Wiley 1979).

Some species exhibit certain elements of territoriality without actually defending an area with aggressive behavior. For example, desert grassland whiptail lizards (Aspidoscelis uniparens) have broadly overlapping home ranges, but there is very little overlap of the core areas where the lizards obtain most of their food. This observation suggests that the lizards exhibit mutual avoidance, even though aggressive interactions among individuals are rare (Eifler and Eifler 1998). A similar pattern is found in Australian sleepy lizards (Tiliqua rugosa); home ranges of males overlap considerably but core areas do not, even though overt aggression is rare (Kerr and Bull 2006). An arboreal Australian snake, Hoplocephalus stephensii, uses tree hollows as retreat sites, and individuals seldom share the same retreat, even though home ranges of individuals overlap (Fitzgerald et al. 2002).

Costs and benefits of territoriality

The principal cost of sharing a home range with other individuals is faster depletion of resources, limiting the ability of a resident to return repeatedly to the same area. Aggressively defending a home range is worthwhile if the increased availability of resources compensates for the costs of defense. Thus, territoriality is favored when resources are moderately abundant, have an even or moderately patchy distribution, and have a high renewal rate. Territoriality is less advantageous when resource abundance is very high or very low, and both patchiness and low resource-renewal rates tend to select against territoriality.

At very high levels of resource abundance, the slight increase in resources available to the defending animal probably will not compensate for the costs of defense. This situation probably accounts for the lack of home range defense by herbivorous and omnivorous reptiles such as iguanas and turtles, even for species that have relatively small home ranges. When resources are concentrated in large patches, such as fallen fruit around a tree, the costs of defense are likely to be too high to make territoriality economically feasible, because so many animals are attracted to the resource patch. Animals in such aggregations are likely to feed peacefully with little interaction, as do some iguanas, or fight-over individual food items, as has been observed for Komodo dragons feeding on carrion (Auffenberg 1981).

When resources are patchily distributed or have low renewal rates, home ranges tend to be large and home range overlap extensive, with little evidence of home range defense. One reason for this pattern is that large home ranges are harder to monitor and defend than small home ranges. Visibility also may be limited in microhabitat patches where food is located (Stamps 1977). Perhaps more important is the fact that a patchy distribution of resources itself favors home range overlap rather than home range defense. This is because the home range must be large enough to meet the needs of the resident throughout the year, but for much of the year only a small portion of the home range is needed to provide resources for one animal. Hence, the cost of sharing the home range is minimal compared with the cost of defending a large area (MacDonald and Carr 1989). Consequently, species that feed on patchily distributed resources, such as small vertebrates or hidden insect prey, usually do not defend home ranges as territories. For example, home range defense is rare among actively foraging lizards and is unknown for snakes, which are derived from actively foraging lizards.

Indeed, home range defense is common in only one group of reptiles, insectivorous lizards that employ a sitand-wait foraging mode. Home range defense is most common in iguanian and gekkotan lizards but also occurs in some lacertids, teiids, scincids, and cordylids, which probably evolved a sit-and-wait foraging mode secondarily from actively foraging ancestors (Stamps 1977; Perry 1999). Cordyliform lizards (Gerrhosauridae and Cordylidae), which are restricted to sub-Saharan Africa, are particularly interesting because gerrhosaurids appear to have retained the ancestral active foraging mode, whereas at least some cordylids have evolved a sit-and-wait mode (Cooper et al. 1997). Some of the most derived species of cordylids exhibit aggressive home range defense and pronounced sexual dimorphism in body size and coloration similar to that of ecologically convergent iguanian lizards (Mouton and van Wyk 1993).

Sex and territoriality

Many lizards exhibit sexual differences in sizes of home ranges and the degree to which they are defended against other individuals. Usually females are not territorial, but instead inhabit overlapping home ranges and show little evidence of aggressive interaction. Males often are territorial and have large home ranges that overlap those of several females. Several lines of evidence suggest that mates rather than food constitute the principal limited resource for territorial males (see Chapter 14). Often the intensity of territory defense increases during the breeding season and wanes once reproductive activities have ceased. Furthermore, experimental studies in which food is added to male territories often fail to induce males to reduce the size of their territories (Stamps 1994).

Females of some lizards do defend exclusive territories, but the size of the defended area actually decreases during the breeding season. In *Urosaurus ornatus*, for example, females become aggressive toward other females in late spring and early summer but restrict their activities to small core areas of their home ranges. This change in use of space may occur because the females focus their activities around suitable nesting sites, or because the energetic burden of carrying a fall clutch of eggs reduces their ability to defend a large home range (Mahrt 1998).

Territorial male lizards vary in the degree to which they defend home ranges as exclusive domains. In addition to having territories that overlap the home ranges of females, many male lizards tolerate subordinate males or juveniles on their territories, even during the breeding season (Stamps 1977). These subordinates probably benefit by gaining access to suitable habitat without moving long distances to find unoccupied sites. They also may be in a position to take over territories if older individuals disappear. Presumably these invaders are tolerated because they cannot compete effectively with resident males for mates, and their impact on food resources in the territory is minimal.

Nevertheless, sexually mature subordinates sometimes attempt to mate with females in the territories of residents when given the opportunity (see Chapter 14). For example, yearling male collared lizards (Crotaphytus collaris) live in the territories of older residents. They exhibit little overt territorial behavior but will try to mate with females when older males are not present. After resident males were experimentally removed, the yearling males rapidly initiated territorial behavior, including patrolling of territory boundaries, displaying, and aggressive interactions with other males (Baird and Timanus 1998). A species of South African armadillo lizard, Cordylus cataphractus, lives in rock crevices. Many adult males have exclusive use of a particular crevice, but other crevices have one or more smaller individuals living in them (Mouton et al. 1999). This unusual grouping behavior probably results from a scarcity of crevices that are suitable as territories.

Site defense

Some amphibians and reptiles do not defend entire home ranges as territories but do defend specific sites within home ranges. Normally the defended sites are resources that are not easily depleted, such as basking perches, burrows, or retreat sites. Site defense is common in some groups of actively foraging lizards that do not defend home ranges (Martins 1994). For example, Australian pygmy blue-tongued skinks (*Tiliqua adelaidensis*) live in spider burrows and mostly feed at the burrow entrance. Burrows are aggressively defended by both males and females, but the skinks showed little aggression when model intruders were placed as little as 10 cm from the burrow entrance (Fenner and Bull 2011).

Site defense also is common among plethodontid salamanders, which sometimes defend retreat sites under rocks or logs (Mathis et al. 1995). These sites provide refuges during dry weather and access to foraging areas nearby. Robert Jaeger and his students have studied the eastern red-backed salamander (*Plethodon cinereus*) for many years. These salamanders prefer large logs, which are relatively scarce. These amphibians advertise ownership of territories with pheromones deposited in fecal pellets, and territories are aggressively defended. The presence of a resident inhibits other salamanders from occupying a site, but if a resident is removed, new individuals rapidly move in.

Some terrestrial salamanders that are ecologically similar to *Plethodon cinereus*, such as *P. vehiculum*, show few signs of territorial behavior, perhaps because they live in wetter habitats where moist retreat sites are not limited. Site defense is less common among frogs than among salaman-



Figure 12.14 Territoriality is not characteristic of snakes. The kukrisnake (*Oligodon formosanus*) is the only snake known to exhibit territorial behavior, and this behavior has only been observed on tiny Orchid Island off the coast of Taiwan; kukrisnakes on Taiwan or the mainland are not territorial. (Photograph by Wen-San Huang.)

ders. Some species of frogs defend rock crevices, burrows, or other retreats in dry weather, and others defend suitable feeding perches. Some terrestrial frogs, such as dendrobatids, defend multipurpose territories that encompass foraging areas, shelter sites, and oviposition sites (Pašukonis et al. 2013). Territoriality among frogs is most often related to defense of resources that are used mainly for reproduction.

Although most snakes are not territorial, there is one exception that can be attributed to an unusual spatial distribution of food. Orchid Island, Taiwan, harbors a dense population of kukrisnakes (Oligodon formosanus; Figure 12.14) and serves as a breeding ground for sea turtles. During the turtle nesting season, the snakes feed heavily on turtle eggs, with several snakes often sharing the same nest. Egg clutches represent a bonanza resource that can sustain snakes for up to 2 months and are relatively easy to defend. Female kukrisnakes, which are larger than males, are relatively tolerant of other females but aggressively repel males from the turtle nests. This behavior provides the females with a sustained source of food until the turtle eggs hatch, even though the resource is sometimes shared with other females. The aggressive defense of turtle nests by female snakes appears to be unique to this population. Kukrisnakes on the main island of Taiwan or in mainland China, where turtle eggs are not available, do not exhibit this type of territorial behavior (Huang et al. 2011).

12.6 Migration

Amphibians and reptiles sometimes leave their normal home ranges to move to different habitats some distance away. Often these migrations are made on an annual basis to and from breeding areas, nesting sites, or hibernation dens, and these are discussed in more detail later in this section. Some migrations, however, are responses to changes in habitat caused by seasonal droughts, floods, or other weather events. For example, some turtles and aquatic snakes move several kilometers from drying ponds to more favorable habitats

Other aquatic reptiles, including crocodiles (Crocodylus johnstoni), caimans (Caiman crocodilus), file snakes (Acrochordus arafurae), and Australian snake-necked turtles (Chelodina longicollis), make regular migrations between seasonally flooded swamps and more permanent bodies of water (Shine and Lambeck 1985; Ouboter and Nanhoe 1988; Graham et al. 1996). Australian water pythons (Liasis fuscus) made regular seasonal migrations in response to habitat shifts by their rodent prey (Madsen and Shine 1996). During the dry season, rats were common in soil crevices in the drying floor of a large floodplain and the snakes moved onto the floodplain to hunt. In the wet season, the area was flooded, forcing the rats out and causing the snakes to follow them to higher ground. Some snakes moved as much as 12 km between wet- and dry-season foraging areas. Some sea turtles in the Atlantic appear to make regular seasonal migrations between feeding grounds as well, moving up to 200 km to warmer waters during the winter (Gitschlag 1996). By contrast, green sea turtles (*Chelonia mydas*) in the Mediterranean move shorter distances into deep water and become inactive in the winter (Godley et al. 2002).

Breeding migrations of amphibians

Synchronized migrations of amphibians to aquatic breeding sites are usually triggered by rainfall, with temperature also being important for temperate-zone species that migrate in early spring. Breeding migrations usually occur at night, but once a migration has started, movement often continues during the day as well. Most amphibians do not move great distances to breeding sites (Wells 2007). The longest movement reported for any amphibian is for a mixed population of European waterfrogs, Pelophylax lessonae and P. esculentus (the latter being a hybridogenetic species derived from hybridization between P. lessonae and P. ridibundus, as described in Section 8.4), breeding in a lake along the border of Hungary and Austria. Some frogs moved as far as 15 km from hibernation sites in peat fens to breeding sites along the lakeshore, but most individuals moved only a few hundred meters (Tunner 1992). Migration distances for other anurans seldom exceed 1,500 m, and most species of salamanders move less than 500 m (Sinsch 1992; Wells 2007).

Amphibians typically exhibit strong fidelity to breeding sites as adults, returning year after year to the same pond or stream segment. A study of newts (*Taricha rivularis*) in California conducted for many years by Victor Twitty and colleagues revealed that individuals continued to return to their home stream segments for up to 11 years after being marked, and they were never recaptured in adjacent streams (Twitty 1966). Thousands of wood frogs (*Rana sylvatica*) were marked in ponds in the mountains of Virginia over a period of 7 years. Adults were always recaptured in their original breeding ponds, even though other suitable breeding ponds were available from 250 to 1,000 m away (Berven and Grudzien 1990).

Some populations of European common toads (Bufo bufo) exhibit such strong site fidelity that individuals continued to migrate to breeding areas several years after the ponds had been drained or turned into parking lots. Nevertheless, researchers in Germany were able to shift the fidelity of toads to a new breeding area by blocking their movements to their original breeding pond and transferring them to a new pond nearby (Schlupp and Podloucky 1994). Anurans that use ephemeral ponds for breeding sometimes change breeding pools. Males in a population of natterjack toads (Bufo calamita) breeding in a network of temporary pools used as many as four different pools in a single breeding season, and some females used sites up to 3 km apart in different years (Sinsch and Seidel 1995). This species favors newly formed ponds and therefore shows a greater tendency to move between ponds than do anurans that use more established ponds.

Breeding migrations of terrestrial reptiles

Most species of reptiles do not exhibit the type of breeding migrations seen in amphibians, but there are a few exceptions. For example, male vipers (*Vipera berus*) in Finland moved rapidly from basking sites to a common mating area several hundred meters away. Female vipers often aggregate at special rookeries to give birth. Tuatara (*Sphenodon punctatus*) in New Zealand often have home ranges separated from suitable nesting sites, and females make relatively short migrations to communal nesting rookeries (Refsnider et al. 2013).

All aquatic reptiles that use terrestrial oviposition sites make regular migrations, as do some terrestrial turtles, lizards, and snakes. Freshwater turtles typically move to nesting sites over distances ranging from about 50 m for small species, such as mud turtles (Kinosternon), to more than 5 km for snapping turtles (Chelydra serpentina) (Gibbons et al. 1990). Females of some species exhibit strong fidelity to general nesting areas and also tend to return to the same aquatic habitat each year after nesting (Micheli-Cambell et al. 2013). Female alligators and caimans sometimes increase the size of their home ranges during the breeding season, but nesting sites are usually located within the home range or only a few hundred meters away. In contrast, Nile crocodiles (Crocodylus niloticus) nesting on islands in Lake Turkana in Africa's Rift Valley often swim considerable distances to nesting beaches (Chelazzi 1992).

Most terrestrial turtles, lizards, and snakes probably do not move long distances to deposit eggs, but find suitable sites within their normal home ranges. A few species of snakes have been reported to make directional movements of up to a few hundred meters from home ranges to specialized oviposition sites, such as manure piles and hollow trees. Female Australian keelbacks (*Tropidonophis mairii*) exhibit strong site fidelity to their own hatching sites, so daughters often nest near their own mothers (Brown and Shine 2007).

Nesting migrations also have been reported for several large iguanid lizards, especially arboreal species or those that live in habitats where nesting sites are scarce. Green iguanas (Iguana iguana) living in the forests of Barro Colorado Island, Panama, nest on a small sandy island just offshore, but most individuals move less than 1 km from their home ranges (Bock et al. 1989). Ground iguanas (Cyclura stejnegert) on Mona Island, Puerto Rico, live in a habitat dominated by limestone, with little soil suitable for nests. Females often migrate up to 6.5 km to nesting areas (Wiewandt 1982). Galápagos land iguanas (Conolophus subcristatus) inhabiting the rocky terrain of Fernandina Island have a similar problem and sometimes move more than 15 km to find nesting sites. Many females climbed to the rim of a 1.400-m volcanic crater and then descended another 900 m to the crater floor to nest. The energetic cost of migration by these lizards equaled nearly half of a female's total reproductive effort. In all of these species, the shortage of nesting sites results in aggressive competition among females and territorial defense of nests (Werner 1983).

Breeding migrations of sea turtles

By far the most spectacular migrations are those of sea turtles, which often travel several thousand kilometers from feeding grounds to nesting beaches (**Figure 12.15**) (Meylan 1982). Early work by Archie Carr, starting in the mid-1950s, demonstrated that sea turtles move over enormous expanses of ocean and yet return with great precision to the same nesting beaches year after year.

Carr's work inspired generations of sea turtle biologists, and the general patterns of migration that he described for turtles in the Caribbean and southern Atlantic have been largely confirmed. One of the most famous sea turtle colo-



Figure 12.15 Olive Ridley sea turtles (*Lepidochelys olivacea*) on a nesting beach in Costa

Rica. Female sea turtles travel thousands of miles from coastal feeding grounds to congregate on such nesting beaches. (Photograph © Ingo Arndt/Minden Pictures/Corbis.)


Figure 12.16 Dispersal of green sea turtles (*Chelonia mydas*) from the nesting ground. Tagged turtles traveled from the nesting beach at Tortuguero, Costa Rica (marked by a star) to widely dispersed feeding grounds. Number of recaptures by country is shown for the period 1955–2003. (After Troëng et al. 2005b.)

nies in the world is the population of green turtles (*Chelonia mydas*) nesting at Tortuguero, Costa Rica, where as many as 50,000 green turtles once were observed coming ashore in a single year. Tens of thousands of turtles have been tagged at this site since the 1950s by Carr and his successors. Large numbers of these turtles gather in feeding grounds off the coast of Nicaragua, but individuals have been recovered on feeding grounds as far away as Panama, Colombia, Venezuela, Brazil, Cuba, and Mexico's Yucatán Peninsula (**Figure 12.16**) (Troëng et al. 2005b). The much smaller numbers of hawksbill sea turtles (*Eretmochelys imbricata*) that nest at Tortuguero also migrate to feeding grounds off Nicara



Another well-studied green turtle colony is on Ascension Island, part of the Mid-Atlantic Ridge more than 2,000 km off the coast of Brazil. Turtles tagged on this island migrate to feeding grounds along the Brazil coast. Here they mix with turtles that nest along the coasts of Suriname and French Guiana. These breeding populations are maintained as genetically distinct because of a strong tendency for females to return to their natal beaches to nest (**Figure 12.17**). Studies using mitochondrial DNA have shown that



Figure 12.17 Genetic distinction in green sea turtles (Chelonia mydas).

Mitochondrial DNA haplotypes were determined for female turtles captured on nesting beaches in Suriname and Ascension Island. These breeding populations use overlapping feeding grounds off the coast of Brazil (green area). The turtles showed no overlap in mitochondrial DNA haplotypes: all of the animals from Suriname had the C haplotype, all but one from Ascension Island had the D haplotype. This distinction in haplotypes indicates a strong tendency for females to return to their natal beaches to breed. (After Bowen and Karl 1997.) the Ascension Island colony probably originated tens of thousands of years ago (Bowen et al. 1989), but how the turtles first happened to locate the tiny island and begin nesting there remains a mystery.

Despite the remote location of Ascension Island, females have no difficulty navigating in a relatively straight line between their nesting beaches and their Brazil feeding grounds. Several individuals monitored by satellite made the trip of more than 2,000 km in less than a month and a half (Luschi et al. 1998). Females that were displaced 60– 450 km in various directions from Ascension Island into the open ocean successfully returned to the island; most of the rest headed for feeding grounds in Brazil (Luschi et al. 2001). Females that were displaced 50 km downwind from the island returned within 4 days, whereas those displaced the same distance upwind required up to 27 days to find their way home. This suggests that wind-borne cues enable the turtles to locate the island after modest displacement (Hays et al. 2003).

Other species of sea turtles also move long distances between feeding and nesting grounds, which usually are located in coastal waters (Meylan 1982; Godley et al. 2007). For example, olive Ridley sea turtles (*Lepidochelys olivacea*) tagged along the coast of Suriname were found as far as 1,900 km away. Loggerhead sea turtles (*Caretta caretta*) tagged in South Africa turned up in the Zanzibar archipelago, nearly 3,000 km away, and one female loggerhead tagged in Queensland, Australia, was recaptured in New Guinea, nearly 1,800 km away. A single individual tracked by satellite for about a year swam a nearly straight course from the coast of Baja California across the Pacific to Japan, a distance of 11,500 km (Nichols et al. 2000).

Leatherback sea turtles (*Dermochelys coriacea*) move over vast areas of ocean and often feed in pelagic habitats, so they are not restricted to feeding in coastal waters. Individuals tagged on nesting beaches in Suriname and French Guiana were recaptured more than 5,000 km away, in locations as disparate as Mexico, Texas, South Carolina, and New Jersey. One individual swam across the Atlantic to the west coast of Africa. Migrating sea turtles can cover these distances surprisingly quickly. Minimum travel speeds based on the time between sightings for several species range from about 20 to 80 km per day. This value agrees well with estimates for satellite-tracked turtles of 1 to 3 km per hour, or about 24 to 72 km per day (Luschi et al. 1996; Nichols et al. 2000).

There are some exceptions to the pattern of long-distance migration by sea turtles (Godley et al. 2007). Turtles in the Mediterranean Sea generally confine their movements to local areas within that body of water. There also is limited evidence that turtles nesting in the Galápagos remain within that archipelago. Some populations of sea turtles that nest along the East Coast of the United States make relatively short-distance movements along the coast but do not move across large expanses of ocean. Flatback turtles (*Natator depressus*) that nest on islands off the coast of Australia also remain in coastal waters. Even in populations in which most turtles migrate to distant feeding grounds, there are some individuals that remain in nearby coastal waters.

Migrations to overwintering sites

Many amphibians and reptiles leave their home ranges in the autumn and move to overwintering sites that provide protection from winter conditions. For example, green frogs (*Rana clamitans*) make regular migrations from ponds where they spend the summer to streams where they spend the winter. The flowing water in these streams seldom freezes completely, and oxygen concentrations in the streams are higher than in frozen ponds (Lamoureux and Madison 1999). Snapping turtles (*Chelydra serpentina*) exhibit a similar preference for flowing water and other areas where oxygen content of the water remains high throughout the winter, and they sometimes move up to 4 km from their normal home ranges to overwintering sites (Brown and Brooks 1994).

For some anurans, migrations to overwintering sites are part of an extended round-trip between breeding ponds and summer home ranges. European common toads (*Bufo bufo*) usually occupy summer home ranges 500–1,500 m away from breeding ponds. Some males begin to move toward breeding ponds in the fall and spend the winter in sites close to the ponds (Sinsch 1988). In the spring these males arrive at the breeding ponds before the first females arrive, thereby giving them an advantage in competition for mates.

Amphibians and reptiles often exhibit strong site fidelity, returning to the same overwintering sites year after year. Manitoba toads (Anaxyrus hemiophrys) were found hibernating in the same prairie mounds for up to 6 years (Kelleher and Tester 1969), and individually marked European fire salamanders (Salamandra salamandra) have turned up at hibernation sites in caves for up to 20 years (Joly 1968). The most dramatic migrations to overwintering sites are those of snakes that use communal hibernation dens. These snakes often make relatively rapid directed movements from foraging areas to hibernation dens and exhibit strong fidelity to specific den sites. Although they do not move together, some rattlesnakes (Crotalus) and garter snakes (Thamnophis) have been observed using similar paths to communal dens. Juveniles generally are unfamiliar with the locations of den sites but probably find them by following the pheromone trails of adults (Ford and Burghardt 1993). Even some sea turtles show strong fidelity to particular overwintering sites, where they dive into deeper water, become inactive, and remain submerged for up to 10 hours at a time (Broderick et al. 2007).

12.7 Dispersal Strategies

Juvenile amphibians and reptiles often leave the areas in which they were born and move into new habitats. Such movements are necessary for many amphibians that lay eggs in water, because aquatic breeding sites do not provide suitable habitats for metamorphosed juveniles or adults. Similarly, aquatic and marine turtle hatchlings emerge from terrestrial nests and move from land to water. In both cases, many of the hatchlings later return to their natal ponds or beaches to breed, and other individuals move to new breeding areas. Only those individuals that move to new breeding areas can be considered permanent dispersers.

For amphibians and reptiles that are terrestrial, movement of juveniles out of natal areas may enable them to find habitat patches that are not already occupied by adults, to avoid cannibalism by adults, or to find suitable mates among unrelated individuals of the opposite sex. Movement of juveniles from natal areas has important consequences for the genetics of populations. Limited movement may lead to inbreeding and reduced genetic variation in the population, whereas permanent movement away from natal areas promotes outbreeding and increases genetic variation in populations.

Dispersal by amphibians

Almost nothing is known about the movements of juveniles of amphibians that breed on land, such as plethodontid salamanders, although there is some evidence that juveniles exhibit very limited dispersal and settle in or near the home ranges of their parents (Ousterhout and Liebgold 2010). There may be sex differences even in short-distance dispersers. In one study of red-backed salamanders (*Plethodon cinereus*) in Virginia, many females moved less than 1 m from the sites where they were first captured as juveniles, and none moved more than 7 m. Males dispersed about twice as far as females (Liebgold et al. 2010). The reason for this difference between the sexes is unknown.

DISPERSAL FROM BREEDING PONDS Many researchers have assumed that aquatic-breeding amphibians tend to return to their natal ponds to breed, but several studies have shown that a small but significant proportion of a population moves to new areas (Smith and Green 2005). Only 18% of more than 5,000 juvenile wood frogs (*Rana sylvatica*) were recaptured as breeding adults in ponds other than their natal ponds (Berven and Grudzien 1990). The dispersal rate of juvenile Fowler's toads (*Anaxyrus fowleri*) was higher (27%), but in that case the breeding ponds were much closer together (Breden 1987).

Some of the most detailed information on juvenile dispersal comes from studies of populations of anurans in an agricultural landscape in Germany, where several ponds were in close proximity to one another (Kneitz 1998). Several thousand juveniles of three species of ranid frogs (*Rana temporaria, R. dalmatina,* and *Pelophylax esculentus*) and one species of toad (*Bufo bufo*) were marked. Between 80% and 98% of the individuals that were recaptured had returned to their natal ponds, and most of the rest were in the next nearest pond. Marked amphibians occasionally have been recaptured 2–5 km from their natal areas, suggesting that long-distance dispersal occurs at frequencies that are too low to be detected in most mark–recapture studies (Wells 2007). DISPERSAL ALONG STREAMS Stream-dwelling amphibians often have different dispersal patterns than pondbreeding species because their movements are limited to the stream channel and its banks. Studies of two species of stream-dwelling plethodontid salamanders in New Hampshire showed that Eurycea bislineata, tended to disperse in a downstream direction, whereas Gyrinophilus porphyriticus usually moved upstream (Lowe 2003). Steep slopes make upstream dispersal more costly for Gyrinophilus, resulting in reduced gene flow between local populations and increased genetic differentiation among populations, even on a microscale (Lowe et al. 2008). In one stream, body condition of Gyrinophilus was greater in downstream areas, but salamanders in better condition were more likely to move upstream, resulting in upstream reaches being populated by migrants from downstream (Lowe et al. 2006). Most individuals in the population did not move very far from their natal areas, but some dispersed up to several hundred meters. These rare long-distance dispersal movements were more likely to occur when average resources were limited and average body condition of salamanders in the population was low. Such long-distance movements allowed individuals to sample a wide range of habitats and settle in better quality habitats (Lowe 2009), thereby increasing their growth rates and survival (Lowe 2010). Presumably the rarity of long-distance dispersal in these salamanders is related to energetic or predation costs that limit dispersal opportunities.

PIONEERING AND INVASIVE SPECIES If all individuals exhibited low dispersal, then populations would never expand their ranges. Some amphibians specialize in invading newly opened habitats. Newly constructed ponds in suitable habitats often are rapidly colonized by a variety of amphibians (Baker and Halliday 1999). Containers of water placed on the floor of tropical forests are soon occupied by frogs such as *Physalaemus pustulosus* and even by the largely aquatic species *Pipa arrabali*. In general, new breeding sites that are close to existing breeding areas are most likely to be colonized (Marsh et al. 1999). The natterjack toad (*Bufo calamita*) of Europe is a pioneering species, with tadpoles that do better in newly formed nutrient-poor ponds than in established ponds with abundant predators and competitors (Banks and Beebee 1987).

The cane toad (*Rhinella marina*; Figure 12.18), a native of Central and South America, was introduced into northern Australia in the 1930s to control sugar cane beetles. This attempt at biological pest control was a failure, but the toads proved to be exceptional dispersers and have become serious invasive pests. Juvenile cane toads tend to show up in new localities before any breeding activity has been observed, suggesting that they are responsible for much of this dispersal (Freeland and Martin 1985). The individuals invading new habitats appear to be in better condition and to grow faster than those lagging behind, perhaps because of decreased competition for food and a lower parasite load at the invasion front (Brown et al. 2013).



Figure 12.18 The cane toad (*Rhinella marina***) is an exceptional disperser.** This native of South and Central America was introduced in Australia in the 1930s as a weapon against sugar cane beetles. Since that time cane toads have successfully invaded a large area of northern Australia, often displacing native species. (Photograph © Amazon-Images/Alamy.)

Dispersing populations of cane toads gradually evolve longer legs relative to their body size, a trait that enhances their ability to move over long distances (Phillips et al. 2006). Other phenotypic changes are appearing in populations at the leading edge of the dispersal. These toads apparently are becoming tolerant of drier and colder conditions than they normally experienced in their native range, allowing them to occupy a larger range in Australia than was originally predicted. The increased tolerance of dry conditions may be due to inherent plasticity in behavioral and physiological traits of cane toads, or to changes in allele frequencies resulting from directional selection on these traits (Urban et al. 2008; McCann et al. 2014).

Dispersal by reptiles

Many lizards and snakes lay eggs within their home ranges. Hatchlings emerge from nests and enter the home range of their mother (Bull and Baghurst 1998) or of a nearby individual. Some hatchlings remain near their natal sites, whereas others move to new areas. Either option entails costs and risks. The costs of dispersal include the energy expended to move and the potential cost of being forced to occupy a habitat of marginal quality because the best sites have already been taken. The biggest risk is probably exposure to predation during the move itself and also later while the juvenile is learning the location of retreat sites in an unfamiliar habitat. The costs of remaining in place include competition for scarce resources, the risk of cannibalism by adults, and ultimately the possibility that mating with close relatives will produce offspring with genetic defects (Auffenberg 1981; Stamps 1994; Castilla and van Damme 1996; Imansvah et al. 2008).

TO MOVE OR NOT TO MOVE? Patterns of movement by juveniles are likely to be affected by a variety of factors, including the rate of adult mortality. If the population of adults turns over rapidly, then habitat may become available relatively quickly, and the best strategy for juveniles may be to remain near where they were born. If adults are long-lived, habitat patches may be occupied for years or even decades, and juveniles may be better off if they disperse, but only if suitable alternative habitat patches are available. As juveniles become sexually mature, reproductive competition may force them to move away from areas occupied by older, more dominant animals.

These generalizations cut across phylogenetic boundaries and can be applied to very diverse kinds of animals. Young sexually mature male Australian freshwater crocodiles (*Crocodylus johnstoni*) disperse much farther from their natal pools than do young females, largely because of aggressive competition from older males (Tucker et al. 1998). Similar male-biased dispersal has been reported in Australian small-eyed snakes (*Rhinoplocephalus nigrescens*), a species in which males compete for females (Keogh et al. 2007). Other snakes also exhibit sex-biased dispersal, although the driving force behind sexual differences in dispersal is not clear (Rivera et al. 2006; Dubey et al. 2008).

In contrast to these species, some reptiles exhibit very limited dispersal. One example is *Anolis apletophallus* (formerly *A. limifrons*) in Panama. This species lives in relatively homogeneous forested habitats and feeds on insects, which are an abundant and rapidly renewing resource. Both adult and juvenile lizards are quite sedentary and occupy small home ranges. Furthermore, once a juvenile establishes a home range, it seldom moves to a new one as an adult. More than two-thirds of individuals captured as both juveniles and adults had juvenile and adult home ranges less than 8 m apart. This species has a high adult mortality rate, with most of the population dying within 1 year, so juveniles do not have to wait long for a home range site to become available (Andrews and Rand 1983).

The behavior of *Anolis apletophallus* contrasts with that of another anole, *A. aeneus*, that was studied by Stamps (1994) in a patchier habitat in Grenada. Hatchlings emerge from eggs laid in woodlands and move to clearings where they establish juvenile territories that they occupy for 2 to 6 months. Once the hatchlings reach a size that allows them to compete for adult territories and avoid being eaten by larger lizards, they return to the woodlands and establish new territories. Thus, the movement of young juvenile *A. aeneus* is not permanent dispersal because the lizards eventually return to their natal habitat, although not necessarily to exactly the same spot.

The effect of population density and a variety of other factors on juvenile dispersal has been studied in some detail for the viviparous European lizard *Zootoca vivipara* (Figure 12.19). This species displays two patterns of postnatal dispersal: juveniles either disperse from the home range of their mother within about 10 days of birth, or they remain



permanently near where they were born. Juveniles from a good-quality habitat with a high density of lizards exhibited greater dispersal tendencies than those from an adjacent poor-quality habitat with a lower population density. This pattern was attributed to a higher level of competition with adults in the good-quality habitat, where adults were expected to live longer, and to a greater competitive ability of individuals moving from high-quality habitats. Competitive ability can be a major determinant of eventual success in settling in a new habitat, because established residents usually have an advantage in competition with immigrants. Individuals that have poor competitive abilities may gain little from attempting to disperse into new habitats, while suffering all of the energetic and predation costs of moving. Dispersal by Z. vivipara appears to be driven mainly by competition for food, with a major source of competition for a juvenile being its own mother (Cote et al. 2007).

The costs and benefits of dispersal for *Zootoca vivipara* are influenced by a complex array of factors operating during gestation and the early life of a juvenile, including the density of competitors, quality of the habitat inhabited by the mother and juvenile, body condition of the mother and juvenile, and degree of relatedness between a juvenile and the adults around it. In general, juveniles are most likely to disperse from dry to moist habitats and from areas with high densities of competitors to areas with fewer competitors, provided that the lizards are in good condition. The initial body condition of juveniles is influenced mainly by the conditions encountered by the mother before or during

Figure 12.19 The viviparous European lizard Zootoca *vivipara.* This species has become a model organism for the study of dispersal strategies. For young lizards, the choice to remain in the natal home range or disperse appears to be driven by the competition for food between juveniles and adults, including their own mothers. (Photograph © Naturepix/Alamy.)

gestation (Massot and Clobert 2000; Massot et al. 2002). Individual juveniles in this species and in other lizards also differ in their inherent tendency to disperse, which in turn is related to phenotypic and personality differences among individuals, such as the tendency to explore their surroundings (Aragon et al. 2006).

Lizards that occupy specialized habitats sometimes have extremely limited dispersal, which can result in the formation of small family groups, or even large aggregations of closely related individuals. This sets the stage for evolution of a greater degree of sociality than is found in most lizards (Doody et al. 2013). Some cordylid lizards in southern Africa, which use either rock crevices or succulent plants as shelters, form aggregations that probably are composed of close kin (Nieuwoudt et al. 2003). The presence of closely related individuals of the desert night lizard (*Xantusia vigilis*) leads to greater philopatry and decreased dispersal by juveniles, which in turn promotes the formation of stable kin groups (Davis 2011; Davis et al. 2011).

The best examples among lizards of limited dispersal leading to social aggregations of related individuals come from studies of Australian skinks in the genus *Egernia* (Chapple 2003). About two-thirds of the *Egernia* species form social aggregations. Populations of *E. stokesii*, for example, live on isolated rock outcrops surrounded by inhospitable habitat that makes long-distance dispersal unlikely. Juveniles and subadults tend to remain in their natal crevices with their parents, and adults apparently remain in the same crevice for life. The animals grow slowly and take several years to become sexually mature. The resulting social system is one of extended families permanently inhabiting particular crevices (Duffield and Bull 2002; Gardner et al. 2007).

Although dispersal between crevices is rare among *Egernia stokesii*, it is not zero. Some individuals become floaters, confined to peripheral areas of the rock outcrop. Some of these floaters eventually join social groups. Limited dispersal opportunities appear to drive this social system, but the lizards may derive positive benefits from aggregation, such as enhanced vigilance and earlier detection of predators by lizards in groups (Lanham and Bull 2004). Three other rock-dwelling species—*Egernia saxitalis, E. cunninghami*, and *E. whitii*—also are found in groups of related individuals. Individuals of *E. saxitalis* and *E. cunninghami* often form nuclear families consisting of a single mated pair and offspring of various ages (**Figure 12.20A**). Yet another species, *E. frerei* lives in burrows rather than rock crevices but also forms aggregations of related individuals (Fuller et

(A)



(B)



al. 2005), as does *E. striolata*, which lives in both rocks and trees (Duckett et al. 2012).

Even more remarkable is the social behavior of another Australian skink belonging to a closely related genus, *Liopholis kintorei* (Figure 12.20B). These lizards live in communal burrows that are constructed and maintained by a group of closely related individuals, with some burrow systems extended for more than 10 meters. These burrow systems are maintained for up to 4 years. Genetic studies have shown that the inhabitants of a burrow system consist of a mated pair and several generations of their offspring. As with the other social skinks, the value of the home burrow as a resource has selected for limited juvenile dispersal, resulting in this unusual social behavior (McAlpin et al. 2011).

DISPERSAL OF HATCHLINGS Some reptiles, such as sea turtles, form nesting aggregations from which large numbers of hatchlings emerge simultaneously. If all of these animals were to remain near the nesting area, competition for limited food resources would be intense. In addition, nesting aggregations tend to attract predators that prey on hatchlings emerging from the nests, so rapid escape to more protected habitats is essential for juvenile survival. Hatchlings often leave the nesting area in groups, a strategy that provides safety in numbers as the animals are attacked by predators. Juveniles sometimes disperse over wide areas,

Figure 12.20 Two social Australian skink species with limited dispersal. (A) A family group of *Egernia cunninghami*, one of several *Egernia* species that have limited dispersal from natal areas, resulting in the formation of family groups that live together in rock crevices. (B) The great desert skink (*Liopholis kintorei*), a member of a closely related genus, also has limited dispersal and lives in social groups, but in this species the group cooperates to build a communal burrow system. (Photographs by Adam Stow.)

where they remain for months or even years, but many eventually return as adults to their natal areas to breed (natal philopatry).

One example of social dispersal is seen in green iguanas (Iguana iguana) emerging from nests on a small island next to Barro Colorado Island in Panama. Hatchlings emerge in groups and wait at nest entrances, observing the behavior of other individuals and scanning for predators before moving across open ground to protective vegetation. They usually move in groups, gathering in patches of reeds before moving across open water to the shore of the main island. Juveniles remain together for several weeks and often follow each other's movements as they gradually spread out in bushes and other vegetation on the island (Burghardt 1977). Juvenile Galápagos marine iguanas (Amblyrhynchus cristatus) also disperse together from nesting areas, with dispersal being synchronized with tidal cycles and exposure of algae used for food (Yacelga et al. 2012). Group dispersal of baby crocodylians from the nest is usually aided by one or both parents. The parents dig the babies out of the nest and transport them to a protected nursery area, where they are guarded and remain relatively social for variable lengths of time (see Chapter 9).

Perhaps the most dramatic example of group dispersal of nestlings is seen in the life cycle of sea turtles (**Figure 12.21**). Baby sea turtles exhibit some social behavior even before emerging from nests, working together to dig their way out of the nest cavity. Once they reach the surface, usually early in the evening, they make a mad dash for the water. Often they are attacked by seabirds and other predators, but moving in large groups provides some protection. Dispersing turtles exhibit frenzied activity, moving as rapidly as possible across the beach and continuing very rapid swimming movements along a direct seaward course once they hit the water. They may maintain this course for many hours or even days (Lohmann et al. 1997).

For decades the whereabouts of these young turtles once they left their natal beaches was a mystery. Archie Carr referred to this period of the life history as "the lost year," although "lost years" is a more accurate description. Juveniles of most sea turtle species spend their early life floating passively in currents near the surface and feeding on pelagic food that accumulates in drift lines (Musick and Limpus 1997). Some nesting beaches may be chosen by females because local currents are favorable for juvenile dis-



persal to open ocean habitats (Shillinger et al. 2012). Once juveniles are in the open ocean, their ultimate distribution depends heavily on ocean currents that transport them to suitable feeding grounds (Blumenthal et al. 2009). A satellite tracking study of newly hatched loggerhead sea turtles (*Caretta caretta*) showed that these young turtles generally avoid predator-rich shallow continental seas and spend most of their time in the open ocean. They remain mostly in surface waters, which are warmer than deeper water, thereby providing a thermal advantage to these growing turtles (Mansfield et al. 2014).

The pelagic phase of the life history lasts for many years in some sea turtle species. The young turtles are carried long distances from their starting points and are distributed by currents over thousands of square kilometers of ocean. Eventually older juveniles of some species settle into a more sedentary, bottom-dwelling lifestyle in shallow-water feeding areas. Turtles sharing a single feeding area typically come from several different breeding colonies (Lahanas et al. 1998; Blumenthal et al. 2009). Only after a very long time (30–50 years for some species) do the adult males and females leave these feeding areas and begin their longdistance migrations to the mating and nesting areas where they were born (Miller 1997; Scott et al. 2012).

The long distances traveled by juvenile sea turtles preclude the use of local cues for orientation, except on the final approach to a nesting beach. Direction finding in sea turtles goes beyond simple compass orientation to true navigation, which requires a turtle to establish both its starting point and its destination. Hatchlings of both loggerheads and leatherback sea turtles (Dermochelys coriacia) are sensitive to Earth's magnetic field. Experiments have shown that young turtles in the open ocean are sensitive to changes in the inclination angle of the magnetic field. This information may be used to approximate the latitude of a turtle's position. When baby loggerheads were exposed to magnetic fields that occurred in different regions of the North Atlantic, they oriented in each field in a direction that would keep them within their normal migration pathway, providing evidence of a true magnetic map sense (Figure 12.22) (Putman et al. 2011).

Sea turtles may also detect local changes in the intensity of the magnetic field. Magnetic sensitivity plus the detection of changes in inclination angle would provide enough information for a magnetic map sense capable of determining both latitude and longitude. Studies of young loggerheads and modeling of leatherback movements indicate that they can make directed course corrections that



The experiment tested the turtles in magnetic fields duplicating locations along their migratory routes. The North Atlantic Gyre (the predominant ocean current) is shown by arrows. In the orientation circles, each dot represents a single hatchling, the arrow in the

center of each circle indicates the mean angle of the group, and the pie-shaped segment shows the 95% confidence intervals of the mean angle. (After Pough et al. 2013.)

increase the chances of arriving at productive feeding areas, possibly using a magnetic compass (Gaspar et al. 2012; Putman et al. 2012). When trained to swim in a particular compass direction toward a light source, they maintain the same compass orientation when tested in the dark. When

the magnetic field is reversed, the turtles reverse their orientation. It seems likely that baby turtles set their initial compass direction as they leave the beach and swim out to sea and then maintain that direction through magnetic orientation as they swim farther offshore.

them back to Florida.

SUMMARY

Patterns of movement affect, and are affected by, almost every other aspect of an animal's biology.

All movement by animals is related to the acquisition of resources. Species differ dramatically in how often and how far they move.

Any movement entails costs, and mortality is often high during movements. Animals thus move only when it is essential. Patterns of movement influence population dynamics and genetic structure. They also have major implications for the conservation of amphibians and reptiles.

Studies of movement patterns require methods for identifying and tracking individual animals. Radio and satellite transmitters provide the most detailed information on movement patterns and have been used on amphibians such as small frogs and reptiles as large as sea turtles and saltwater crocodiles.

Amphibians and reptiles exhibit several kinds of movement, defined by distance moved and permanence of movement from one place to another.

Station-keeping is movement directly related to the acquisition of resources and tends to keep an animal within its home range. Foraging and commuting (moving back and forth between a fixed location and resource patches) are types of station-keeping.

Ranging behavior is movement outside the normal home range in search of new habitats or resources.

Dispersal involves permanent movement from the place of birth to a new habitat patch. Some amphibians and reptiles move as juveniles from their birthplace and remain in new habitat patches for extended periods of time before returning to the natal area to breed as adults, a behavior known as natal philopatry.

Migration involves movement, sometimes on a seasonal basis, between one type of habitat and another, such as movement between a foraging area and a breeding area.

Patterns of movement are related to the spatial and temporal distribution of resources.

Resources that are abundant or are quickly renewed tend to favor small home ranges. Resources that are patchily distributed or have low renewal rates tend to favor large home ranges or even nomadic behavior.

Many freshwater turtles are omnivorous and occupy overlapping home ranges without territorial behavior. Small turtles in highly productive habitats have smaller home ranges than larger turtles in less productive habitats.

Many sea turtles, such as the green sea turtle, are herbivorous and occupy small home ranges in areas with abundant food resources. Leatherback sea turtles, which feed on jellyfish widely distributed in unpredictable patches, are nomadic and roam over entire ocean basins.

Herbivorous lizards usually occupy relatively small, overlapping home ranges, exhibit low rates of movement between food patches, and generally remain inactive for long periods of time.

Gila monsters and Mexican beaded lizards specialize on bird eggs and baby mammals, which have an unpredictable and patchy distribution; these lizards move frequently between food patches but infrequently within patches.

All snakes are carnivorous. Some are active foragers that move frequently within large home ranges. Others are ambush predators that move between food patches but often remain immobile for long periods within patches. Insectivorous reptiles, such as small lizards, feed on evenly distributed resources that tend to be abundant and rapidly renewed; these animals occupy small home ranges.

Amphibians and reptiles that exhibit strong fidelity to a home range often return to the home range after experimental displacement.

Most amphibians can home successfully from relatively short distances, but do poorly when displaced greater distances.

Turtles can return home after displacements of a few hundred meters to several kilometers, depending on the size of their normal home ranges.

Territorial lizards show strong homing performance when displaced moderate distances.

Snakes exhibit variable homing performance, with the most accurate homing occurring when individuals are displaced from valuable resource patches, such as good feeding areas or hibernation dens.

Some crocodylians can successfully home from distances of up to 30 km, which reflects the large areas traversed in their normal activities.

Amphibians and reptiles use a variety of sensory modalities to find their way home, including visual or chemical cues from local landmarks, celestial cues, and a magnetic compass sense. Some long-distance migrants, such as sea turtles, exhibit true navigation using Earth's magnetic field.

Patterns of home range defense can be predicted from the abundance, patchiness, and renewal rate of resources. Territoriality is favored when resources are moderately abundant, have an even or moderately patchy distribution, and have a high renewal rate.

Among reptiles, home range defense is common only in insectivorous lizards.

Both males and females of some lizards are territorial, but in most cases only males defend territories, especially during the breeding season. Individuals that cannot defend their own territories sometimes reside as satellites in the territories of dominant males.

Some lizards defend specific sites within home ranges, such as burrows or rock shelters, but do not defend the entire home range as a territory. Some salamanders exhibit similar site defense.

The only known example of a territorial snake is the kukrisnake from Orchid Island, Taiwan; females feed on a highly concentrated food resource, sea turtle eggs, and exclude males from turtle nests. Some amphibians and reptiles make seasonal migrations from one habitat to another, most commonly from a foraging area to a nesting or breeding habitat.

Amphibians make relatively short-distance migrations of under 1 km from foraging or hibernation habitats to breeding ponds.

Females of some reptiles, such as aquatic turtles that lay eggs in terrestrial habitats, make regular seasonal migrations to suitable nesting habitats.

The most impressive migrations are those of sea turtles, which can involve movements of thousands of kilometers and sometimes traverse entire ocean basins. Sea turtles typically exhibit strong fidelity to the nesting area where they hatched as juveniles.

Because amphibians and reptiles are ectotherms, they often seek out specialized overwintering habitats that protect them from winter cold. Many amphibians and reptiles exhibit strong fidelity to particular overwintering sites. In some cases, such as snakes, individuals migrate to communal hibernation sites. ■ Juvenile amphibians and reptiles often leave the area in which they were born and move into a new habitat where they remain for an extended period of time before eventually returning to their natal areas to breed.

Many amphibians exhibit strong natal philopatry, but some individuals permanently disperse to new breeding habitats. Pioneering species readily disperse to and occupy new habitats, thereby enabling them to expand their ranges.

Lizards and snakes exhibit variable patterns of dispersal, ranging from distances of a few meters from the natal area to several kilometers.

Some lizards that inhabit sites such as rock crevices and burrows exhibit very limited dispersal, which leads to the formation of permanent social groups of closely related individuals.

Sea turtles have prolonged dispersal that can last for years or decades. Juveniles move from nesting beaches to the open ocean, where their movements are largely controlled by currents. Most return to their natal beaches to breed.

Go to the *Herpetology* Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

13 Communication

A nyone who has passed by a swamp or pond on a summer evening is familiar with the sounds produced by frogs and toads. Upon encountering frog choruses in southern Africa, the English explorer and naturalist William Burchell wrote:

No sooner does the delightful element moisten the earth, and replenish the hollows, than every pool becomes a concert-room, in which frogs of all sizes, old and young, seem contending with each other for a musical prize. Some in deep tones perform their croaking bass, while the young ones, or some of a different species, lead in higher notes of a whistling kind. Tenors and trebles, countertenors, sopranos, and altos, may be distinguished in this singular orchestra. The noise produced, particularly in the evenings, is truly astonishing, and nearly stunning. (Burchell 1822, p. 352)

Other people have been less sympathetic. During the 17th century, some members of the French nobility reportedly found their sleep so disturbed by the nighttime calling of frogs that peasants were sent into the swamps to keep the animals quiet.

The sounds produced by frogs and toads are not, of course, designed either to please or to irritate humans but are used by males to communicate with members of their own species. Animals can communicate with other species as well (for example, when a poisonous frog displays aposematic coloration, or a rattlesnake sounds a warning to predators; see Chapter 15). In this chapter we will be concerned only with intraspecific communication. Communication has been defined in different ways by different investigators, but central to any definition is the idea that communication involves interactions between at least two individuals, a signaler and a receiver. In fact, there may be more than one signaler and more than one receiver, and individuals may alternate between roles as signaler and receiver.

13.1 Modes of Communication

Some animal behaviorists define communication in terms of the way in which a signal alters the behavior of another individual. A receiver may respond to a signal by approaching the signaler, retreating from the signaler, attacking, initiating courtship, or in other ways. Other researchers consider communication an exchange of information between two individuals (Bradbury and Vehrencamp 2011). The use that a receiver makes of information conveyed by a signal depends on the context in which the signal is given and the nature of the receiver. Information about the signaler is termed the signal message and is a function of the physical properties of the signal and the way in which it is delivered. A signal may have several different meanings that can be discerned only by studying the reactions of other animals to the signal. For example, the advertisement call of the North American bullfrog (Rana catesbeiana) sends messages about the species identity, sex, spatial location, size, reproductive state, territorial status, and individual identity of the caller (Figure 13.1). The call may have very different meanings to receivers, depending on their sex and reproductive state. To sexually mature males it is a "keep out" signal advertising territory ownership, whereas to gravid females it is an attractive signal indicating the location of a potential mate (Bee and Gerhardt 2001).

Signals often provide a receiver with reliable information about the signaler (e.g., sex or species identity). In some circumstances, however, it may be in the interest of the signaler to provide unreliable information. For example, an individual may produce signals that exaggerate its size or fighting ability and thereby induce potential opponents to withdraw without a fight. In some species, males adopt alternative mating tactics that involve sending visual, chemical, or tactile signals that resemble those produced by females (female mimicry; see Chapter 14). Because the responses of receivers depend on how they perceive the

Figure 13.1 Calling male of the American bullfrog (*Rana catesbeiana***). The calls of this species can convey information about the caller's species identity, sex, spatial location, size, reproductive state, territorial status, and individual identity. (Photograph © Mircea Costina/Alamy.)**

signals of other individuals, animals can be said to use communication signals to manipulate the behavior of receivers. Receivers in turn use signals to assess characteristics of signalers, such as size, fighting ability, or overall quality as mates.

Herpetologists have used many different terms to describe the signals and displays of amphibians and reptiles, but most can be sorted

into a few simple categories, depending on the context in which they are produced. Perhaps the most widespread are **advertisement signals**, usually given by males to advertise ownership of territories or to attract mates. Also common are **courtship signals**, used during close-range sexual interactions between males and females. Most species also have distinctive **aggressive signals** that are used during contests between individuals, and some have **submissive signals** as well. Less common are **contact signals**, used to keep in touch with other individuals in a social group, and **alarm signals**, given when a predator threatens.

Virtually any sensory modality can be used for communication, but the suitability of different modes depends on the sensory capabilities of animals and the characteristics of the environments in which they live. Acoustic, visual, chemical, and tactile signals also differ in the way that they propagate through the environment. Acoustic signals are ideally suited for communication over long distances because sound travels rapidly in air or water. Usually the source of an acoustic signal is relatively easy to locate, and the signals can be perceived at night and when physical barriers separate the signaler and receiver. Messages conveyed in sound can be altered through changes in intensity, frequency (pitch), or timing of various signal components, so animals can use a rich repertoire of acoustic signals to communicate subtle changes in behavior.

Visual signals are effective at short to moderate distances and are easily located, but they also are easily obstructed by physical barriers and are highly dependent on light levels and the wavelengths of light present in the environment. Some amphibians and reptiles, particularly in terrestrial environments, have visual signals in ultraviolet (UV) wavelengths. Some aquatic amphibians also may use UV signals, but only if characteristics of the aquatic environment allow for transmission of UV wavelengths (Secondi et al. 2012). Visual signals can be modified to convey complex messages by combining display elements such as color, movement, and changes in posture. Chemical signals, or **pheromones**, are equally effective at night or during the day, but such signals broadcast into air or water are transmitted very inefficiently unless the medium is moving. Chemical signals often are not very directional, so the source of the signal can be difficult to locate. In contrast to acoustic and visual signals, chemical signals cannot be modified through regular temporal patterning of signal emission, because these patterns tend to be lost as the signal diffuses from its source. Chemical signals convey a variety of messages, including species and sex identity, reproductive condition, and even fighting ability (Mason and Parker 2010; Woodley 2010).

Tactile signals, produced by touching another animal or through surface waves and vibrations, are used mainly for short-range communication but can convey complex messages through changes in the timing or intensity of signal production (Bradbury and Vehrencamp 2011).

13.2 ■ Constraints on Signal Production

The production of communication signals by amphibians and reptiles is subject to many biological and physical constraints. These include body size, energetic and other physiological constraints that affect the cost of signal production, and predation by animals attracted to acoustic, visual, or other signals.

Body size

Many amphibians and reptiles are small, and small size can limit the distance over which an animal can communicate. For example, the distance at which a visual signal can be detected is proportional to the size of the signaler and the amplitude of the display. A small lizard performing a head-bob display will be visible to other animals at shorter distances than a large lizard performing a similar display. Small animals generally produce high-frequency



sounds, and these tend to be more readily absorbed by the ground or vegetation during transmission than lowfrequency sounds (Bradbury and Vehrencamp 2011). Huge mammals such as elephants and whales communicate over tens of kilometers using low-frequency sound, but even the largest reptiles, such as crocodylians, probably do not communicate over more than a few kilometers. The signals of smaller species generally cannot be detected more than a few hundred meters away.

Physiological constraints

Changes in temperature affect most physiological processes of amphibians and reptiles, including the production of communication signals. Temperature usually has a major effect on the rate of signal production, as well as on the temporal features of signals that are determined by active muscle contraction (**Figure 13.2**). Features such as calling rate, call duration, and the number of sound pulses in calls are highly temperature-dependent. These temperaturedependent changes in call structure can have a major effect on the energetic cost of calling, which increases substantially at warmer temperatures. Energetic costs probably represent the most important constraint on the rate at



Figure 13.2 Effect of temperature on pulse rate of the calls of two species of gray treefrogs. At the same temperature, male *Hyla versicolor* and *H. chrysoscelis* show distinct differences in the pulse rate of their calls. This difference in pulse rate presumably enables females of each species to distinguish conspecific from heterospecific males. (After Gerhardt 1978.)

which signals can be produced and the length of time an animal can continue signaling (Wells 2001). Conversion of metabolic energy to sound energy is relatively inefficient (Prestwich 1994), and male frogs that call at very high rates can incur substantial energetic costs.

Predation

Another major cost of signaling is exposure to predation. Communication signals, by their very nature, make animals conspicuous to other individuals. Unfortunately for the signalers, some predators use these signals to home in on prey. For example, a Neotropical bat, Trachops cirrhosus, hunts for frogs by homing in on their calls. The frogs may alter the rate or timing of their calls to reduce the chances of being eaten, even though these changes make it more difficult for females to find the males (Tuttle and Ryan 1981; see Chapter 15). These bats can even home in on the ripples produced in the water by movements of a male frog's vocal sac (Halfwerk et al. 2014). Other vertebrate predators, such as large frogs and opossums, also may use calls to locate frog prey (Ryan et al. 1981; Tuttle et al. 1981). Various species of blood-sucking mosquitoes, midges, and flies also feed on frogs and can be attracted to speakers playing frog vocalizations (Bernal et al. 2006; Grafe et al. 2008). The effect of these insects on the frogs is unknown, although potentially they could weaken frogs by consuming blood or transmitting diseases. Even though female frogs generally do not call, their movements toward calling males can be influenced by the presence of predators. Female Physalaemus pustulosus were less likely to approach calls of males when these calls were associated with the calls of a large predatory frog, Leptodactylus pentadactylus (Bonachea and Rvan 2011).

Predation probably has been an important selective force in the evolution of the display behavior of lizards as well. One study of side-blotched lizards (Uta stansburiana) showed that populations in areas where carnivorous lizards are present tend to move and display less than those in areas where such predators are absent, although actual levels of predation were not measured (Zani et al. 2013). In a northern population of collared lizards (Crotaphytus collaris), males have turquoise body colors and bright yellow heads; in southern populations, they are more cryptic, with duller shades of brown and tan. The difference was attributed to differences in the array of visually hunting predators in the areas inhabited by the two populations, although again, actual rates of predation were not measured (Macedonia et al. 2002). Many lizards have inconspicuous colors that blend in with their surroundings. Some of these lizards have brightly colored display structures that are kept hidden except during courtship or aggressive displays. Neotropical lizards in the genus Anolis usually are brown or green, but they reveal brightly colored throat fans (dewlaps) during sexual or aggressive displays. Chameleons usually are cryptically colored, but they adopt bright coloration when displaying to other individuals (Stuart-Fox and Moussalli 2008).

13.3 Communication and Noise

Once a signal is produced, it must be transmitted to a receiver. The process of transmission is subject to interference by environmental noise, which makes it hard for a receiver to detect or recognize the signal (Vélez et al. 2013). We commonly associate noise with sound, but any communication channel can be affected. For frogs and other animals that use sound to communicate, sources of background noise include wind, rain, waterfalls, and the sounds of other animals. These types of noise often fluctuate in intensity and do not have a predictable temporal pattern. One way to overcome such noise is to produce a signal that contrasts with the unpredictable variations of background noise. The best such signals are stereotyped calls (i.e., calls that exhibit little variation) that are repeated frequently. Most frog calls are stereotyped, and call repetition rates tend to be highest in the noisiest environments, such as large choruses (Schwartz and Bee 2013).

Acoustic noise

A major nonbiotic source of noise for many frogs is sound produced by waterfalls or swiftly moving water. One solution to this problem is to produce calls at frequencies that contrast with those produced by flowing water (Schwartz and Bee 2013). Several stream-breeding frogs in Asia have evolved calls that lie partly or entirely in the ultrasonic range (frequencies above the range of human hearing) and thus contrast with the lower broad-band frequencies of flowing water. The calls of the concave-eared torrent frog (*Odorrana tormota*) contain a mixture of frequencies,



including ultrasonic notes (Feng and Narins 2008; Feng et al. 2009); in *Huia cavitympanum*, the call consists entirely of very high frequency and ultrasonic notes (Arch et al. 2009). Female *Odorrana* produce courtship calls in response to the calls of males, and males respond by giving high-frequency calls in which frequency increases in the noisiest environments (Shen et al. 2008). Yet another strategy for dealing with abiotic environmental noise is to increase the rate or intensity of calling in the presence of wind, flowing water, or other sources of noise (Penna and Zúñiga 2014).

The presence of other frogs calling in the same location, either conspecifics or an assemblage of other species, is a source of environmental noise for many frogs (Schwartz and Bee 2013). If the dominant frequencies of calls of different species overlap, then species with louder, longer, or more continuous calls may mask the signals of species with softer, shorter, or more sporadic calls. One effective way of reducing acoustic interference in large choruses is for males to adjust the timing of their calls, calling during periods when other frogs are quiet. Males of the small Central American treefrog Dendropsophus ebraccatus call in temporary ponds and often are surrounded by dense choruses of a related small frog, D. microcephalus. The latter species calls in distinct bouts, separated by silent periods. D. ebraccatus males insert their calls into silent periods between the calling bouts of D. microcephalus. Experiments in which calls were broadcast to females in an indoor arena showed that males that call during silent periods are more likely to attract mates because females have difficulty hearing calls that overlap with those of the other species (Wells and Schwartz 2007).

Other species of frogs exhibit similar behavior that re-

duces interspecific call interference. Two North American ranids, the bullfrog (*Rana catesbeiana*) and the green frog (*R. clamitans*), share many breeding ponds and call during the same summer months and the same hours of the day. Bullfrogs produce longer and louder calls, often in bouts, thereby monopolizing much of the acoustic space in a pond (Herrick 2013). The calls of the two species overlap in frequency, so each species can hear the calls of the other species. Green frogs avoid calling during bouts of bullfrog calling and insert their calls into the silent periods between bullfrog calls (**Figure 13.3**). Even some noisy insects can interfere with the calls of frogs. The small Neo-

Figure 13.3 Acoustic interactions between American bullfrogs (*Rana catesbeiana*) and green frogs (*R. clamitans*). (A) Oscillograph showing green frog calls (green lines) inserted between bouts of bullfrog calls (black lines). (B) A 30-second sequence of bullfrog and green frog calls, showing the lack of call overlap between the two species. (Courtesy of Susan Herrick.)



Figure 13.4 Airborne and ground-borne signals of *Lepto-dactylus albilabris.* These oscillographs show a single-chirp call recorded with a microphone (airborne signal; top) and a geophone (ground-borne signal; bottom) located 1 m from a calling male. *L. albilabris,* one of the few frog species known to call from underground burrows, is highly sensitive to seismic signals. (After Narins 1990.)

tropical poison frog *Oophaga pumilio* calls during the day on the forest floor. At some times of day, the intense songs of cicadas dominate the acoustic landscape, and the frogs stop calling during bursts of cicada singing (Wong et al. 2009).

Another way to avoid acoustic interference is to use relatively noise-free channels for communication. The Puerto Rican white-lipped frog (Leptodactylus albilabris) calls from burrows. In addition to emitting an airborne acoustic signal, males calling underground produce ground-borne vibrations that can be detected by other frogs (Figure 13.4). Indeed, the organ in the white-lipped frog's ear that is used to detect seismic signals is one of the most sensitive vibration detectors in any vertebrate and is tuned to detect the specific frequencies produced by calling males (Lewis et al. 2001). The advantage of calling in burrows is that very few other animals use the seismic communication channel, and the frog is protected from predators as well. In cases where the male's burrow serves as an oviposition site, acoustic properties of the burrow may affect the structure of the call, thereby advertising burrow quality to females (Cui et al. 2011).

Multimodal signals also can help overcome the effects of environmental noise. In some frogs, the movements of the vocal sac, which may be brightly colored, serve as a visual signal to females or other males. Even if an individual frog's calls cannot be detected in a noisy environment, the movements of his vocal sac provide visual cues to his location (Narins et al. 2005; Richardson et al. 2010; Taylor and Ryan 2013), or the visual signal may enhance the effectiveness of the acoustic signal (Taylor et al. 2011a,b; Preininger et al. 2013).

Visual noise

Animals that use visual signals to communicate often have to make themselves conspicuous against a visually complex background. One way to do this is to move, and most visual displays involve some sort of movement, such as jumping, changes in posture, waving of the legs or tail, movement of the head, or expansion of special display structures such as crests or dewlaps. However, if components of the background environment also are moving, then signalers must contend with the effect of **visual noise**.

A major source of visual noise for animals with visual displays is windblown vegetation (Peters et al. 2008). Experimental work has shown that lizards that depend on visual displays have evolved a variety of strategies for overcoming such noise. Anolis auratus (Figure 13.5) is found in grassy habitats in Panama and must make itself conspicuous against a background of windblown vegetation. This species' visual system is most sensitive to movements that combine high velocity and high acceleration (i.e., fast, jerky movements), features that are characteristic of the lizards' head-bobbing displays but not the movements of windblown vegetation. Furthermore, the displays emphasize movement frequencies to which the visual system is most sensitive, enabling the lizards to detect the displays even under windy conditions. Head movements used in long-distance displays are more pronounced and jerky than those used at close range, suggesting that these elements are used to attract the attention of other individuals (Fleishman 1992).

Comparative studies of *Anolis* display behavior in Puerto Rico and Jamaica have revealed different strategies for coping with visual noise. Jamaican species have short head bobs and rapid dewlap extension, features suited for overcoming



Figure 13.5 A grass anole (Anolis auratus) gives visual displays. Males of this Neotropical species give visual displays against a background of windblown vegetation. The fast, jerky head-bobbing displays of contrast with the visual noise generated by the swaying movement of the grass. (Photograph © luigipinna/Fotolia.)

visual noise in the environment. These species exhibit relatively little plasticity, giving similar displays in noisy and quiet conditions. *Anolis* lizards in Puerto Rico have slower displays, less suited to communication in noise, but are more plastic and increase display rates in noisy conditions (Ord et al. 2007, 2010; Ord 2008). Puerto Rican *Anolis* also reduce the effects of visual noise by displaying during periods when visual noise is reduced, much as some frogs call in the silent periods in the calling of other species (Ord et al. 2011).

The Australian jacky dragon (*Amphibolurus muricatus*) uses a somewhat different strategy to overcome visual noise. Males have a tail-flick display that alerts other lizards to the presence of the displaying male, causing the observing lizard to attend to the main display. In the presence of windblown vegetation, the time required for a lizard to notice the tail flick is increased (Peters 2008). To compensate for this effect, the lizards increase the duration of their tail-flick displays in windy conditions but do not change the rate of the main display (Peters et al. 2007).

13.4 Communication by Salamanders

Chemical, visual, and tactile signals are used in the communication behavior of salamanders, with chemical communication being the predominant mode (Woodley 2010). Salamanders are extremely nearsighted (Roth et al. 1998), and the distance over which they can detect visual signals is limited. Most communication occurs at close range, especially during courtship and aggressive interactions. The communication behavior of most salamander families has not been studied in detail. Ambystomatids have been studied mainly during courtship and mating; some of their behavior will be discussed in Chapter 14 and has been reviewed by Houck and Arnold (2003). The behavior of plethodontids and salamandrids has been studied in most detail, and we will focus our discussion on those families.

Communication by plethodontids

Plethodontid salamanders are active mainly at night, so chemical and tactile signals are the major forms of communication in this family. Nevertheless, even some nocturnal plethodontids make use of simple visual signals.

CHEMICAL COMMUNICATION Most plethodontid communication involves the use of chemical signals. All salamanders have two types of chemical-sensing organs in their noses, the **main olfactory epithelium** and the **vomeronasal organ**, each with neurons projecting to different parts of the brain (Dawley 1998). The main olfactory epithelium is stimulated by small, volatile molecules (airborne odors), whereas the vomeronasal organ is stimulated by larger, nonvolatile molecules. Plethodontids frequently tap their snouts on the substrate. This behavior facilitates uptake of nonvolatile chemicals by the **nasolabial grooves**,



Figure 13.6 Nasal organs of the red-backed salamander (*Plethodon cinereus*). The dashed lines indicate where the skin and skull were removed to reveal the two types of chemical-sensing nasal organs: the vomeronasal organ (contained by the lateral diverticulum) and the main olfactory epithelium. (After Dawley and Bass 1989.)

which run from the upper lip to the corner of the external nares (Figure 13.6). Liquids move through the nasolabial grooves by capillary action and are directed primarily to the vomeronasal organ, not to the main olfactory epithelium. The vomeronasal organ of plethodontids is thickest in the region adjacent to the nasolabial grooves. In eastern redbacked salamanders (*Plethodon cinereus*) and some other species, the organ is much larger in males than in females, presumably because males use chemical cues to locate and identify suitable mates.

Plethodontid salamanders use their chemical senses to detect prey, to identify home sites, and for courtship and other social interactions. Both males and females of some species defend territories around retreat sites and mark their territories with pheromones deposited on fecal pellets by glands in the cloacal region. Not only can P. cinereus distinguish their own territories from those of conspecifics, but they also can distinguish the odors of different conspecifics. Territory owners tend to be more aggressive toward strangers than toward familiar neighbors, presumably because strangers are more likely to try to take over the territory (Jaeger and Peterson 2002). When a male and female share the same territory, they use chemical signals to determine the sex of intruders, and each sex tends to be most aggressive toward members of the same sex (Lang and Jaeger 2000). Females also use chemical cues in fecal pellets of males to assess the quality of food the males are eating. Termites are more profitable prey than ants because they are more digestible, and female salamanders seem to associate more readily with males that have termites in their territories, perhaps because termites provide better resources for the salamanders' young (see Chapter 14).



Chemical signals probably are used by all plethodontids for species and sex recognition during courtship, which begins with a male approaching a female and touching her with his snout. Ellen Dawley (1984) used several species of large Plethodon salamanders to test sex and species recognition using chemical cues. The animals were placed in a glass Y-tube apparatus and given a choice of odors from airstreams emanating from live salamanders of different sexes or species. The experiments showed that the salamanders distinguished the odors of males from those of females. Furthermore, males and females of four species of black and white salamanders once classified as a single species (Plethodon glutinosus, P. aureolus, P. kentucki, and P. teyahalee) all preferred odors of their own species to those of other species living in the same area. The same was true when sympatric populations of P. montanus and P. teyahalee were tested against each other. Genetic studies have Figure 13.7 Tail-straddling courtship walk of *Plethodon shermani*. (A) The female initiates this courtship behavior by straddling the male's tail. (B) After depositing a spermatophore (red arrow), the male shifts his tail from underneath the female and leads her forward, positioning her so that his spermatophore is underneath her clo-aca. (C) With his tail moved to the side, the male extends his hindlegs, pushing the base of his tail into the female's chin. This helps maintain her position over the spermatophore and enables her to pick it up. (After Arnold 1976.)

shown that the interactions between these two species are complex, with some populations exhibiting extensive interspecific hybridization and others appearing to be completely isolated. Behavioral discrimination was strongest in those populations that do not hybridize in the field (Dawley 1987). Similar work by Paul Verrell (1989) showed that two sympatric species of *Desmognathus*, *D. imitator* and *D. ocoee*, also can distinguish conspecifics from heterospecifics by means of chemical cues.

In all plethodontids, a female signals her receptivity by initiating a tail-straddling walk, a behavior unique to this family (Figure 13.7). The female's chin rests on the base of the male's tail. Some male plethodontids have a special gland in the skin at the base of the tail that probably produces a pheromone that is transmitted to the female by way of her nasolabial grooves. The tail-straddling walk also positions the female so a spermatophore deposited by the male can be picked up by her cloaca (Houck and Arnold 2003). Even after she initiates a tail-straddling walk, a female may not be fully responsive and may require additional courtship by the male before picking up a spermatophore.

The principal courtship glands in male plethodontids are located on the chin and are called **mental glands** (Figure 13.8A,B). In species of large *Plethodon* salamanders these glands are large, pad-like structures. The male delivers pheromones from his mental gland during the tail-straddling walk by turning around and slapping his chin on the female's snout (Figure 13.8C). In other



(A)



Figure 13.8 Mental courtship glands of plethodontid salamanders. (A) Mental gland of *Eurycea bislineata*. The dashed line indicates the portion of the gland located below the skin; the small circular area is the exposed secretory portion of the gland. (B) Padlike mental gland of *Bolitoglossa*, with the right image showing a cross section of vertical tubules beneath the pad's surface. (C) A male *Plethodon shermani* slapping his mental gland on the snout of the female during courtship. This behavior is characteristic of plethodontids with the padlike glands shown in (B). (A,B after Houck and Sever 1994; C after Arnold 1976.)

plethodontids, the glands are smaller. Males develop enlarged premaxillary teeth during the breeding season that are either raked across the female's skin or used to puncture the skin when the male presses his chin against the back of the female and then flips his body away from the female ("snapping"). These actions cause glandular secretions to be applied to the wounds, delivering pheromones directly into the female's bloodstream. Two very small species, *Desmognathus wrighti* and *D. aeneus*, carry this process to an extreme. The male actually bites the female, sometimes holding on for several hours to inject pheromones into her bloodstream (Houck and Arnold 2003). Similar behavior occurs in some populations of the larger *D. imitator* (Mead and Verrell 2002).

The pheromones delivered to females by male plethodontids increase female receptivity and enhance a male's chances of mating successfully. The mental glands of *Plethodon shermani* produce a proteinaceous pheromone (Rollman et al. 1999). When applied to the snout of a female, the chemical resulted in greater receptivity of the female to a courting male. Females receiving the pheromone spent less time in the tail-straddling walk before a spermatophore was deposited than did females receiving a saline control treatment. Presumably the advantage to a male in increasing female receptivity is that it reduces courtship time, thereby reducing the chances of interference by another male (see Chapter 14) or the length of time a courting pair is vulnerable to predators.

Subsequent work has shown that the pace of mating is modulated by two pheromones called plethodontid modulating factor (PMF) and plethodontid receptivity factor (PRF) (Woodley 2010). Biochemical analysis of courtship pheromones in species of large *Plethodon* has revealed enormous variation in chemical structure and rapid evolution of pheromones within this genus (reviewed by Woodley 2010), despite the fact that behavioral aspects of courtship are nearly identical among species. These results suggest that sexual selection has favored the evolution of chemical signals unique to each species (Watts et al. 2004). Nevertheless, we lack clear behavioral evidence of sexual selection acting on chemical signals; one experiment showed that even pheromones from a different species served to increase female receptivity (Rollman et al. 2003).

VISUAL COMMUNICATION *Plethodon cinereus* and several other species signal aggression and submission by elevating or flattening the body (**Figure 13.9**) (Mathis et al. 1995; Mathis and Britzke 1999). Territorial individuals are able to discriminate between familiar neighbors and unfamiliar intruders using visual cues, although chemical cues appear to be more reliable (Kohn and Jaeger 2009). There also are both visual and tactile elements in the courtship behavior of *Desmognathus* salamanders and other plethodontids. As they approach females, males of many *Desmognathus* species make complex movements with their forelimbs, including a display called the butterfly in which the male moves



Figure 13.9 Submissive and aggressive postures of *Plethodon cinereus*. The sequence from top to bottom shows increasingly aggressive displays. From the resting posture in which only the head is raised, the animal raises first its trunk and then its tail parallel to but off the ground. In the most aggressive postures (lowest two panels) the back is arched. (After Jaeger and Schwartz 1991.)

his front legs in a circular pattern. The butterfly display is present in the courtship of most species that are closely related to *D. ochrophaeus* but seems to have been secondarily lost in *D. ochrophaeus* itself. The lack of this display element may partially explain the lack of reproductive compatibility between *D. ochrophaeus* and its closest relative, *D. orestes*, although there could be chemical differences in their pheromones as well (Mead and Verrell 2002).

Communication by salamandrids

The courtship behavior of most salamandrids is complex and involves a combination of visual, chemical, and tactile cues. The male and female of some species have considerable physical contact. In the genus *Salamandra*, the male clasps the female from below by looping his front legs over hers. Once the female signals her receptivity, the male deposits a spermatophore and then moves the rear of his body to the side, lowering the female over the spermatophore. Male North American newts (*Notophthalmus* and *Taricha*) clasp the female from above and hold on only during the initial persuasion stages of courtship, releasing the female to deposit a spermatophore. A male *Taricha* courts a female by rubbing his mental gland against the female's snout, whereas a male *Notophalmus* clasps the female around her neck with his hind legs and rubs a gland on the side of his head against her snout (**Figure 13.10**).

Among Old World newts, the male does not clasp the female at all (Halliday 1990; Houck and Arnold 2003). Males do not produce chemical signals to attract females from a distance. Instead, they usually search for females (see Chapter 14) and identify them by chemical cues that provide information about the species identity and sex of potential mates. Once a male and female have come together, a prolonged period of courtship follows during which the male stimulates the female with chemical, visual, and tactile signals.

In Old World newts (*Triturus, Lissotriton, Ichthyosaura, Calotriton, Neuregus,* and *Ommatotriton,* all of which were formerly in the genus *Triturus*), the male positions himself in front of a female and wafts pheromones produced in the cloacal region toward her with fanning movements of his tail. If a female's olfactory bulbs are cut or her nares are blocked, she shows little or no response to male

(A)



courtship (Belvedere et al. 1988). Females of most species of Old World newts signal receptivity after initial courtship by approaching the male. In some species, such as the smooth newt (*Lissotriton vulgaris*), the male responds by retreating from the female while continuing to display and direct pheromones toward her. The retreat display apparently allows the male to assess the female's level of receptivity, as shown by her willingness to follow him. It also may serve as a form of sexual defense (see Chapter 14), because it enables a male to lead a female away from rival males that might interfere with courtship. Males of *L. vulgaris* increase the duration of the retreat display when other males are nearby.

In all species of Old World newts, the male eventually turns around and moves away from the female. If the female follows, the male stops, deposits a spermatophore, and then moves forward just enough to allow the female to move over the spermatophore. The male then stops the female's movement with a braking action of his tail. Both visual and chemical signals probably are important in inducing females to follow males in the spermatophore deposition phase of courtship. Females of some species sniff at the male's cloaca while following. A male may wiggle the tip of his tail, displaying a brightly colored spot (Halliday 1990; Houck and Arnold 2003). In some species, the male's tail tip is elongated into a thin filament that serves to attract the attention of the female, perhaps by mimicking the movements of prey animals such as worms (Cornuau et al. 2012).

The ancestral courtship behavior of Old World newts appears to emphasize transmission of chemical signals through tail fanning. Some form of chemical signaling remains important in all species, especially when they are courting at night (Denoël and Doellen 2010). In some species, chemical signals have been supplemented to various degrees by visual signals, especially lateral display of sexually dimorphic crests and tail fins, which often are marked with bright colors. In some species these color markings include those that reflect UV light, which is not perceived by humans. Experiments with Lissotriton vulgaris showed that when UV light was filtered out, males became less attractive to females. This was not true for the related palmate newt (L. helveticus), however. The latter species often breeds in forest pools in which particulate matter blocks transmission of UV wavelengths, so UV signaling would be of little use to this species, at least in those environments (Secondi et al. 2012).

Figure 13.10 Courtship of the red-spotted newt (*Notophthalmus viridescens*). (A) Unlike the mental glands of plethodontids, the male courtship glands of the salamandrid *N. viridescens* are secretory pits on the side of the head. (B) During amplexus, the male rubs his courtship glands against the snout of the female while grasping her with his hind legs. (After Halliday 1990.)

The most elaborate courtship occurs in some of the largest species of newts, including *Triturus cristatus, T. marmoratus,* and *Ommatotriton vittatus.* These three species have lek mating systems in which many males display in the same area and defend small mating territories (see Chapter 14). These are the most sexually dimorphic newts, with males having greatly enlarged crests and tail fins. Displays that show off these structures to females are found in these species (see Figure 14.12). However, males of these species have lost the ancestral tail-fanning display, suggesting a shift from primarily chemical to primarily visual signaling among lekking species. A phylogenetic study of dorsal crest evolution in the newt clade (Wiens et al. 2011) suggests that large crests evolved once, but were lost repeatedly. Various statistical models used to analyze the data lead to somewhat different conclusions, however, including the possibility of multiple independent origins of crests (**Figure 13.11**).

Why is salamander courtship so elaborate? Complex courtship probably is not needed for species recognition, which is accomplished rapidly by means of chemical cues. On the other hand, extended courtship may be necessary because transferring spermatophores requires close coor-



Figure 13.11 Evolution of dorsal crests in Salamandridae.

A maximum likelihood phylogeny of Old World newts, the only salamandrid clade with dorsal crests. The most parsimonious interpretation of the data is that large dorsal crests evolved once and were repeatedly lost. Some models, however, suggest that the ancestral condition may have been crestless and that there were multiple independent origins of crests. Representative images of crested and crestless individuals are shown. Phylogeny after Wiens et al. 2011. (Photographs: *T. cristatus* © WitR/ Shutterstock; *C. asper* © AGE Fotostock/Alamy; *L. vulgaris* © Dirk Ercken/Shutterstock.) dination between the male and female (Halliday 1990). Male salamanders appear to have a limited supply of spermatophores, so anything a male can do to increase the reliability of spermatophore transfer will be advantageous. The prolonged period of courtship persuasion seen among plethodontids and salamandrids improves the chances of spermatophore transfer by ensuring that the female is ready to receive them (Houck and Arnold 2003). For example, female Lissotriton vulgaris are most likely to pick up a spermatophore if they are courted vigorously by males. Male red-spotted newts (Notophthalmus viridescens) skip the preliminary stages of courtship if females are very receptive, and use more elaborate courtship if they are not (Verrell 1983). Once some form of complex courtship behavior evolved in salamanders, certain features of courtship displays may have been further elaborated through sexual selection. For example, the vigor of a male's display may be a reliable indicator of overall male quality, and females could use such cues in choosing mates (see Chapter 14).

13.5 Communication by Anurans

Vocalizations are by far the most important communication signals for most frogs (see reviews in Gerhardt and Huber 2002; Wells 2007). Anurans are well known for their acoustic signals—indeed, frogs and toads rival birds and insects as the most vocal of all terrestrial animals. The literature on anuran vocal communication is enormous, and until recently researchers largely neglected the role of visual and chemical signals in anuran communication. Recent studies have shown, however, that both these modes of communication are more important for anurans than previously supposed.

Acoustic communication

Frogs have evolved a unique method of sound production, and many frogs have multiple pathways for sound reception. Many species have complex vocal repertoires, with different kinds of calls conveying distinctly different messages.

CALL PRODUCTION Sound production is closely linked to respiration. Frogs force air into their lungs with positive pressure exerted by throat muscles. When muscles in the trunk region are contracted, air is forced out of the lungs and into the buccal (mouth) cavity. In most species, only the male calls, and the trunk muscles of males are much larger than those of females. The muscles are richly supplied with mitochondria, the organelles where aerobic respiration takes place, and with capillaries that supply oxygen to the mitochondria (Wells 2001). These muscles also contain energy stores in the form of lipids and carbohydrate (glycogen), which support the high energetic cost of calling (see Chapter 7). The airstream produced by contraction of the trunk muscles moves through the larynx, causing the vocal

cords and associated cartilages to vibrate at a characteristic frequency. This vibration determines the frequency characteristics (pitch) of the call.

Most frogs have vocal sacs that couple the buccal cavity to the air (Figure 13.12). Frogs with large vocal sacs have much louder calls than frogs that have small vocal sacs or that lack vocal sacs. For example, bufonids in the genus Atelopus have internal vocal sacs but not large external ones; their calls are considerably softer than those of most other frogs and cannot be heard over background noise more than a few meters away (Boistel et al. 2011). Some frogs can transmit calls through alternative pathways, however. Male American bullfrogs (Rana catesbeiana) have much larger tympanic membranes (eardrums) than do females. This difference was long thought to be related to hearing ability, but it now appears that the enlarged tympana of males play a major role in radiating calls to the air (Purgue 1997). This mechanism may be especially advantageous for species that call in water, with much of the vocal sac in contact with water rather than with air.

Pipid frogs, which are strictly aquatic, lack both vocal cords and vocal sacs and have a unique method of producing sound. Species in this family have click-like calls that are produced when the two sides of the larynx, which is modified into a cartilaginous box, are suddenly pulled apart by contractions of laryngeal muscles, much like pulling apart two suction cups (Yager 1992). A surprising recent discovery is that one genus, *Pseudohymenochirus*, seems to have reverted to the ancestral air-driven mode of sound production, even though the structure of the larynx is similar to those of other pipids. The precise mechanism of sound production in this genus is not fully understood (Iri-sarri et al. 2011).

Frog calls come in many different forms: click-like calls with a broad frequency spectrum, tone-like calls with a narrow frequency spectrum, whistles that change in frequency, and a variety of squawks and trills composed of a series of distinct sound pulses (**Figure 13.13**). For frogs other than pipids, the mass of the vocal cords and the size of the buccal cavity determine the dominant frequency of the call (i.e., the frequency with the greatest sound energy). Large frogs usually have low-frequency calls (Gingras et al. 2012).

ADVERTISEMENT CALLS AND CHORUSING BEHAVIOR

Most species of anurans have several distinct types of calls that are used in different behavioral contexts (Gerhardt and Huber 2002; Wells 2007; Toledo et al. 2014). The calls given most frequently by male frogs during the breeding season are usually called advertisement calls because they often serve the dual function of attracting mates and advertising a male's ownership of a territory or calling perch to other males. Males of some species use the intensity of their neighbors' calls to assess the distance between males in a chorus. Other species use differences in the pitch of calls

Figure 13.12 Different kinds of anuran vocal sacs. (A) Median external vocal sac of *Dendropsophus ebraccatus*. (B) The median external vocal sac of *Physalaemus pustulosus* is very large. (C) Internal vocal sac of *Rana clamitans*. (D) Some frogs that call in water have lateral vocal sacs. In the case of *Pelophylax esculentus*, these are paired gular sacs that radiate sound to the air.

(Photographs: A–C by Kentwood D. Wells; D © blickwinkel/Alamy.)





(D)







Figure 13.13 Sonograms and oscillographs of anuran calls. Sonograms are on top in each pair and show frequency (kHz). Oscillographs on the bottom show amplitude (mV). (A) Pulsed advertisement call of *Hyla versicolor*. (B) Two-note advertisement call of *Eleutherodactylus coqui*. (C) Multinote advertisement call of *Dendropsophus microcephalus*, composed of a buzzlike introductory note and eight secondary click notes. (Courtesy of Kentwood D. Wells.) to assess the body sizes of potential competitors, which can affect the outcome of fights. Males of the American bullfrog (*Rana catesbeiana*) and of several other species can even distinguish between the calls of neighboring territorial males and unfamiliar intruders (Bee and Gerhardt 2001; Feng et al. 2009).

The advertisement calls of most frogs and toads consist of a simple whistle, trill, or other type of note repeated many times in succession. However, some frogs have more complex calls that combine several different types of notes. *Dendropsophus ebraccatus* has an advertisement call composed of a buzzlike introductory note followed by one or more secondary click notes. Males calling from relatively isolated positions give mostly single-note calls, but they add secondary notes to calls when calling in dense choruses. Females are more likely to be attracted to complex calls (Wells 1988). The multinote calls of *D. microcephalus* are even more impressive, sometimes containing up to 30 notes (see Figure 13.13C).

Some Old World frogs have even more complex vocal behavior. A treefrog from Madagascar, Boophis madagas-



cariensis, has an extraordinary repertoire of more than two dozen call types, including clicks, buzzes, trills, and tonelike notes (Narins et al. 2000). The stream-breeding frog *Odorrana tormota* in China has perhaps the most unusual vocal behavior of any frog. Males produce an almost infinite variety of complex frequency-modulated calls that are more similar to bird songs than to the calls of other frogs. It even appears that components of some calls are produced by the two sides of the vocal tract independently (Feng et al. 2002).

Chorusing frogs often adjust the timing of their calls to reduce acoustic interference with calls of their near neighbors (Figure 13.14). Male *Dendropsophus microcephalus* further reduce the chances of notes overlapping by increasing the gaps between call notes, responding in only a few thousandths of a second to the notes of another male (Schwartz and Wells 1985). Males of the Puerto Rican coquí (*Eleutherodactylus coqui*) are remarkably precise in their ability to avoid call overlap with neighboring males. They can insert their own calls into silent periods only three-quarters of a second long, even when the occurrence of these periods is completely unpredictable. Males respond only to a few

> close neighbors, with the rest of the chorus simply contributing to the general background noise (Narins 1992). Clearly, a frog chorus is not the disorganized cacophony it appears to be.

> Joshua Schwartz (1987) clarified the adaptive significance of call alternation in experiments with *Hyla versicolor, Dendropsophus microcephalus,* and *Pseudacris crucifer.* He tested three hypotheses: call alternation might (1) make a male's calls easier to locate in a chorus, (2) might allow males to communicate more effectively with other males in the chorus, and

Figure 13.14 Some possible vocal interactions between neighboring conspecific males in a chorus. (A) Calls consist of relatively long notes given at regular intervals, with the calls of frog 2 precisely alternating with those of frog 1. (B) Calls consist of relatively long notes given at regular intervals, with the calls of frog 2 beginning immediately after the end of frog 1's calls. (C) Calls consist of a variable number of closely spaced short notes, with the individual notes of frog 2 alternating with those of frog 1. (D) Calls consist of a variable number of short notes given in rapid succession. The multinote calls of frog 2 immediately follow those of frog 1. (E) Calls consist of trills composed of a rapid series of short pulses. Calls of the two frogs overlap, with no attempt to avoid acoustic interference. (After Wells 2007.)

(3) might reduce interference that can obscure key features of calls used by females in species recognition. Schwartz did not find any evidence to support the first hypothesis. Males of all three species gave more aggressive calls when presented with playbacks of calls that did not overlap their own calls. This observation suggested that males have some difficulty hearing other males when they are calling themselves.

Call notes of *Hyla* and *Dendropsophus* have a pulsed structure, and the distinctive pattern of pulse timing is disrupted if calls are overlapped. When females of these species were presented with a choice of overlapping or nonoverlapping calls from two sets of loudspeakers, they showed a strong preference for nonoverlapped calls. In contrast, female spring peepers (*Pseudacris crucifer*) were equally likely to approach overlapped or nonoverlapped calls. The calls of male *P. crucifer* are simple tones that lack an internal temporal structure, so overlapping of calls does not interfere with call recognition by females. Hence, Schwartz's second hypothesis was supported for all three species, while the third hypothesis was supported for *Hyla* and *Dendropsophus* but not for *Pseudacris*.

SPECIES RECOGNITION Herpetologists have long known that each species of frog has an advertisement call distinct from that of sympatric species. In fact, many new species of frogs have been discovered because they have calls that differ from calls of other species that are very similar in appearance (Gerhardt and Huber 2002; Wells 2007). The relationships of North American leopard frogs in the Rana pipiens complex were not fully understood until differences in their calls were discovered. Other species that look very similar to each other, including the Puerto Rican frogs Eleutherodactylus coqui and E. portoricensis and the North American gray treefrogs Hyla versicolor and H. chrysoscelis, were first recognized as distinct species because of differences in their calls. Other species, such as the Arizona canyon treefrog (Hyla arenicolor), exhibit considerable geographic variation in call structure, and females of some populations prefer calls of their own population to those of geographically distant populations. This variation suggests that more than one species may be present among these populations, or that incipient speciation may be occurring (Klymus et al. 2012; Bryson et al. 2014).

Dozens of experimental studies have demonstrated that female anurans recognize the calls of their own species (Gerhardt and Huber 2002; Wells 2007). In choice tests, females invariably prefer the calls of their own species to the calls of a different species. The calls of two species often differ in several ways, such as dominant frequency, duration, pulse repetition rate, or pulse shape. One cannot assume that all of these differences are important, because some features of calls may be irrelevant to females. Only experiments in which different features of calls are varied independently can show definitively which ones are crucial for species recognition. In general, frogs are most responsive to calls with peak frequencies similar to those of their own species' calls. This is a widespread mechanism that enhances the ability of receivers to detect and recognize conspecific calls in noisy environments (Penna and Meier 2011). This phenomenon was first demonstrated by Robert Capranica (1965), who investigated the acoustic properties of bullfrogs (*Rana catesbeiana*) and identified the components of calls that elicit vocal responses from males. Two frequency peaks are present in bullfrog advertisement calls, at about 200 Hertz (Hz, cycles per second) and 1,400 Hz. Capranica found that calls with both frequency bands present were more effective in eliciting calls from males than were calls from which either the high- or low-frequency peak was absent.

Frogs have two sensory organs in the ear tuned to different frequency ranges. The **amphibian papilla** detects relatively low frequency sounds, whereas the **basilar papilla** is sensitive to higher frequencies. Large frogs such as bullfrogs often have calls that stimulate both sensory organs, which accounts for the greater response elicited by calls that include both high- and low-frequency sounds. Smaller frogs, such as *Pseudacris crucifer*, have higher-pitched calls that stimulate only the basilar papilla. Both organs respond to a broad range of frequencies, but they respond best to sounds in a relatively narrow frequency range that generally corresponds to frequencies of the advertisement call (**Figure 13.15**).

Temporal characteristics of calls often are the basis for species recognition (Vélez et al. 2012). Differences in pulse repetition rate usually are sufficient for females of species with pulsed calls to distinguish calls of their own species from those of other species. Other features of calls—such as dominant frequency, call repetition rate, and loudness—can be varied considerably, and females will still choose calls with the correct pulse rate. However, this does not necessarily mean that females ignore other call features. Calls of Hyla versicolor and H. chrysoscelis differ not only in pulse rate but also in pulse shape, which is a function of the way in which the larynx opens during sound production. Females of H. versicolor show strong preferences for calls with the correct pulse rate, but if pulse rate is held constant, they prefer calls with the pulse shape of their own species to calls with a pulse shape similar to that of H. chrysoscelis (Gerhardt and Huber 2002). Temporal information is processed in parts of the brain where there are neurons programmed to detect certain pulse rates and filter out others. For example, the temporal processing centers in the brains of H. versicolor respond more strongly to pulse repetition rates characteristic of this species' calls than to the much faster pulse rates of H. chrysoscelis calls.

EXTRATYMPANIC SOUND PERCEPTION Most frogs have tympanic membranes that are exposed on the outside of the head. Sound vibrations impinging on the tympanic membrane are transmitted via bones in the middle ear to fluid-



Figure 13.15 Call frequency and tuning of the ear of spring peepers (Pseudacris crucifer). (A) Distribution of dominant frequencies in a sample of calls from a population in Ithaca, New York. The average dominant frequency for the population is 2.9 kHz. (B) Tuning curves of the auditory nerve of a male from the same population. Each point indicates the sound pressure level (SPL) required to elicit a firing response from a nerve fiber. Each curve is for a different nerve fiber. The lowest point on each curve represents the frequency to which that nerve is most sensitive, because the nerve requires the least SPL to fire. The group of nerve fiber curves on the right are those that innervate the basilar papilla, the organ that detects highfrequency sounds. In this individual, the ear is most responsive at about 3.5 kHz, slightly above the average dominant call frequency in the population. Note the uneven scale of the *x* axis. (After Wilczynski et al. 1984.)

filled chambers in the inner ear, where the sound-detecting sense organs are located. In some species there are other pathways for sound transmission as well (Gerhardt and Huber 2002). Anurans have a direct connection from the lungs to the ears via the eustachian tubes, so vibrations of the body wall over the inflated lungs can be transmitted to the ear. Significant sound transmission through the lungs has been reported in *Eleutherodactylus coqui* (Narins et al. 1988) and several other species with tympanic ears. Sound transmission through the lungs is also important in *Bombina orientalis*, a species that lacks a tympanum and a middle-ear cavity, and in other anurans that lack a tympanum, such as toads in the genus *Atelopus* (Hetherington and Lindquist 1999; Boistel et al. 2011).

AGGRESSIVE CALLS AND DEFENSE OF CALLING SITES

Male frogs often defend territories or calling perches against other males, and they have distinct aggressive calls. Some authors subdivide this type of call into more specific categories, depending on the social context in which the calls are given. These include territorial, encounter, fighting, and displacement calls (Toledo et al. 2014).

Aggressive calls usually differ from advertisement calls in temporal features such as duration or pulse repetition rate rather than in frequency, but there is no particular structure common to all aggressive calls (Figure 13.16). The aggressive call of *Pseudacris crucifer* is a long trill that is readily distinguished from the short peep of the advertisement call. Males of *Eleutherodactylus coqui* have aggressive calls composed of an introductory co note and a series of secondary quí notes (co-quí-quí-quí-quí). Aggressive calls of Dendropsophus ebraccatus and D. microcephalus are similar to advertisement calls, but pulse repetition rates of the introductory notes are much faster. The aggressive calls of these two species form a graded signaling system in which males increase the length of the introductory notes of aggressive calls as the distance between opponents decreases (Wells 1988). In P. crucifer, the length of the trill increases as males move closer together (Schwartz 1989).

OTHER TYPES OF CALLS Some frogs give specialized courtship calls in close-range interactions with females (Wells 1988; Toledo et al. 2014). Sometimes these are simply modified versions of the advertisement call. Males of Hyla versicolor give very long calls when females are nearby. Males of Dendropsophus ebraccatus and D. microcephalus give a rapid series of single-note calls. These longer or more repetitious calls make it easier for females to locate a calling male in a noisy chorus. Males of other species give courtship calls that are quite distinct from the advertisement call. Other types of anuran calls include release calls, which are given by males or unreceptive females that are clasped by males, and defensive calls, which are given by frogs confronted by predators. The latter include vocalizations that have been variously called alarm calls, warning calls, and distress calls. They have been documented in many species, although in most cases the intended receiver and the precise function of these calls are poorly understood (Wells 2007; Toledo and Haddad 2009; Toledo et al. 2014).

CALLING BY FEMALE FROGS Female frogs lack vocal sacs, but some females nonetheless produce calls (Emerson and Boyd 1999). Such calls have gone largely unnoticed because females' calls are soft and hard to hear in a noisy chorus.

Figure 13.16 Examples of advertisement and aggressive calls of male

anurans. Sonograms on the top of each panel show frequency (kHz). The oscillographs below the sonograms show amplitude (mV). (A) The advertisement call of Pseudacris crucifer is a frequency-modulated peep (left), whereas the aggressive call is an amplitude-modulated trill (right). (B) Multinote aggressive call of Eleutherodactylus coqui (compare with its advertisement call in Figure 13.13B). (C) The advertisement call of Dendropsophus ebraccatus has a long introductory note and short secondary click notes (left). Its aggressive call (right) has a longer duration than the advertisement call and the introductory note has a higher pulse rate. (Courtesy of Kentwood D. Wells.)

Calling by female frogs occurs in two contexts. In some species, such as Rana virgatipes and several other ranid frogs, females respond to calls of males with calls of their own. This response often induces the male to alter his calls by giving longer calls, or calling at a faster rate, features that probably enhance the ability of a female to locate the male (Given 1993; Roy et al. 1995; Cui et al. 2010). Similar behavior has been described in the aquatic African clawed frog (Xenopus laevis). Male and female X. laevis perform duets that probably facilitate mate location in muddy ponds where visibility is poor (Tobias et al. 1998).

Visual communication

Many frogs use visual signals for communication. This behavior is especially common in frogs that are active during daylight hours, although

visual signaling occurs in nocturnal species as well (Rosenthal et al. 2004; Gomez et al. 2009, 2010; Sztatecsny et al. 2010; Reichert 2012). Commonly used visual signals include display of body coloration, postural changes, elevation or inflation of the body, movements of the throat, waving the front legs, and stretching or waving the hindlimbs. In all cases, the displays make the animal more conspicuous (Hödl and Amézquita 2001; Wells 2007).

VOCAL SACS AND THROATS AS VISUAL SIGNALS Brightly colored or highly reflective vocal sacs or throats, often orange, yellow, or white, are common in male frogs and



probably serve as visual signals (Figure 13.17) (Wells 1978; Schulte-Hostedde and Schank 2009; Biju et al. 2014). In most cases, the behavioral significance of these colors has not been studied. Limited experimental evidence suggests a role for vocal sac coloration in male–male aggressive interactions, mate choice by females (Gomez et al. 2009), or sex recognition by males in species with a scramble-competition mating system (see Chapter 14) (Sztatecsny et al. 2010).

SEXUAL DICHROMATISM Sexually dichromatic breeding coloration is known in several frogs and appears to be phylogenetically widespread, occurring in many unrelat-



Figure 13.17 European common frogs (*Rana temporaria***) in amplexus.** The bright white throats of the males serve as a visual signal that facilitates sex recognition, distinguishing them from the less visible females. (Photograph by Marc Sztatecsny.)

ed clades (Bell and Zamudio 2012). In some cases, sexual dichromatism is transitory; in others, males retain bright coloration for longer periods. One of the best-known examples is the European moor frog (*Rana arvalis*). Males change from brown to bright blue during the mating sea-

son, whereas females remain brown (Figure 13.18). Breeding males also reflect a considerable amount of light in UV wavelengths, whereas females do not (Ries et al. 2008). This species has an explosive, scramble-competition mating system in which female choice appears to play little role in male mating success. Experiments with model frogs painted blue or brown indicated that males avoid clasping blue frogs, thereby avoiding wasting time trying to mate with males (Sztatecsny et al. 2012).

In the Neotropical toad Incilius luetkenii, breeding males adopt a bright lemon yellow color that contrasts with the greenish color of females. This species also has a scramblecompetition mating system. The males' yellow color is lost once mating is over, suggesting a role in sex recognition similar to that in Rana arvalis (Doucet and Mennill 2010). Breeding males of the Australian stony creek frog (Litoria wilcoxii) also turn lemon yellow (Kindermann et al. 2013). Males of Mannophryne trinitatis, a dendrobatid frog from Trinidad, are normally brown but turn black when calling (Figure 13.19), and they jump up and down on prominent display perches to make themselves conspicuous. The change of color takes place in a matter of minutes (Wells 1980). Similar rapid color change by calling males has been observed in another dendrobatid frog from South America, Rheobates palmatus (Lüddecke 1999).

Some males of the North American spadefoot toad *Scaphiopus couchii* are more yellow and more brightly colored than females, although other males resemble females in color. Experiments with clay models indicated a possible preference among females for brighter males (Vásquez and Pfennig 2010). It is possible that bright coloration in males deters other males from attempting to mate with them.

(B)

(A)



Figure 13.18 Color dimorphism in the European moor frog (Rana arvalis). (A) Males of this ranid species temporarily turn from brown to bright blue during the breeding season, thereby facilitating discrimination of females (which remain brown) by males searching for mates. (B) Males usually greatly outnumber females in a chorus. One brown female can be seen in the center of the photograph, clasped by several blue males. (Photographs: A © ImageBroker/Alamy; B by Marc Sztatecsny.)

Figure 13.19 Visual signals in a male *Mannophryne trinitatis.* (A) Males of this dendrobatid species usually have a rather cryptic brown color pattern. (B) A calling male has undergone a rapid color change from the usual brown coloration to black, making him more conspicuous to females. (Photographs by Kentwood D. Wells.)



VISUAL SIGNALS IN POISON FROGS Even when male and female colorations are similar, bright color may function in intraspecific communication. For example, most dendrobatid frogs are brightly colored and this has been shown to be aposematic, warning potential predators that the frogs are protected by distasteful or poisonous skin secretions (see Chapter 15). Normally, the evolution of bright coloration used as an intraspecific communication signal is limited by natural selection if bright colors make the animals more conspicuous to predators. In aposematic species, however, bright colors advertise distastefulness to predators. If brighter coloration is a reliable indicator of toxicity (Maan and Cummings 2012), then natural selection and sexual selection may operate in the same direction, both favoring an increase in brightness (Crothers and Cummings 2013; Cummings and Crothers 2013).

There is increasing evidence that bright colors of dendrobatids are used in mate choice and territorial defense. The best-studied example is Oophaga pumilio, a small Central American dendrobatid that exhibits considerable variation in color pattern, both within and among populations. This is particularly true in the Bocas del Toro region of Panama, where different islands have frogs that differ both in background coloration and in the number and size of dark spots (Figure 13.20). In laboratory experiments where females were allowed to choose between males from their own population and another population, they generally preferred males from their own population, although their choice depended on the degree of color difference. For example, females from an orange population readily discriminated against males from a yellow-green population, but not against males from another orange population. Females of one population in the study also discriminated between males based on spot pattern, although females from the other populations did not (Maan and Cummings 2008).

Studies of mate choice in the field indicated that some color morphs are more discriminating than others in choice of mates. On Bastimentos Island, female *O. pumilio* of the more common red morph are more likely to choose males of their own color than are females of the less common yellow morph (Richards-Zawacki et al. 2012). Bright coloration may also be a signal in territorial encounters between males. In a laboratory experiment, males were more likely to approach other males that were brightly illuminated than those in dimmer light (Crothers et al. 2010). In some *O. pumilio* populations there are subtle differences in male and female coloration, with males being significantly brighter (Maan and Cummings 2009). Sexual dimorphism in color has been reported in other dendrobatids as well (Rojas and Endler 2013).

FOOT-FLAGGING AND OTHER FOOT DISPLAYS Males of several unrelated tropical frogs from Borneo (Staurois, Ranidae), Australia (Litoria, Hylidae; Taudactylus, Myobatrachidae), South America (Hyla parviceps, Hylidae; Hylodes, Hylodidae), and India (Micrixalus, Micrixalidae) have independently evolved foot-flagging displays (Hödl and Amézquita 2001; Preininger et al. 2013; Biju et al. 2014). Some of these frogs have webbing on their hindfeet with a light, highly reflective color that contrasts with the green of the surrounding forest. A displaying male periodically extends one or both of his back legs and spreads the webbing, producing a conspicuous flash of color. Some foot-flagging displays may have evolved from aggressive behavior in which males kick other males with their hindfeet (Biju et al. 2014). Most foot-flagging frogs live along streams with noisy rapids and waterfalls where vocal communication may be difficult, and the visual display probably attracts the attention of females or other males. In some of these species, however, visual signals are accompanied by vocalizations. In some species of Indian dancing frogs (Micrixalus), calling males have conspicuous white vocal sacs that probably complement foot flagging as a visual display (Figure 13.21).

Forelimb movements are used by some frogs to signal aggression. For example, both male and female *Atelopus* frogs in South America threaten other individuals by raising their front feet and waving them in a circle, usually as a prelude to pouncing on an opponent (Crump 1988). When frogs were presented with their own image in a mirror, they responded by increasing their display rate (Lindquist and Hetherington 1998). Somewhat similar limb movements have been reported for brachycephalid toads (Pombal et al. 1994). Male Indian dancing frogs tap their front feet on the calling perch, often just before giving a foot-flagging display (Biju et al. 2014).





Figure 13.20 Color polymorphism among Oophaga pumilio in Bocas del Toro Province, Panama. Each island in this archipelago has a distinct color morph of the dendrobatid frog *O. pumilio*, as do adjacent areas of the mainland; some large islands have more than one morph. Not all color morphs are shown here. Origins of morphs: (A) Aguacate Peninsula. (B) Bastimentos Central. (C) Bastimentos West. (D) Dolphin Bay. (E) Escudo de Veraguas. (F) Mainland. (G) Pastores. (H) Solarte. (Photographs: A–C, F, G by Martine Maan; D, E, H by Laura Crothers.)

Figure 13.21 Foot-flagging display of an Indian dancing frog (*Micrixalus kottigeharensis***).** Like many frogs in families that have foot-flagging displays, this micrixalid frog lives near noisy streams (leading to their alternate common name of torrent frogs), where acoustic communication may be impaired. The brilliant white throat probably serves as yet another visual display. (Photograph by S. D. Biju.)

Chemical communication

Larval anurans have well-developed chemical senses that enable them to detect predators or recognize their close kin, and the ability to detect chemical cues from both conspecifics and predators persists in newly metamorphosed juveniles (Blaustein and Walls 1995). Although relatively little research has been done on chemical communication by adult anurans, there is increasing evidence that chemical signals are more important than previously suspected (Berlanger and Corkum 2009; Woodley 2010).

Anuran skin is richly supplied with various types of glands, some of which are sexually dimorphic, suggesting a role in courtship and mating (Brizzi et al. 2003; Brunetti et al. 2012). Although the functions of most sexually dimorphic anuran glands are unknown, some male frogs have glands in their nuptial pads that secrete chemicals similar in structure to the pheromones of plethodontid salamanders, suggesting possible transmission of male pheromones through the skin of females during amplexus (Willaert et al. 2013).

Male dwarf African clawed frogs (*Hymenochirus*) have special breeding glands that produce a female-attracting pheromone (Pearl et al. 2000), and the skin of males of the



Figure 13.22 Calling male of *Hyperolius concolor.* The yellow padlike structure on the vocal sac (arrow) is a gland that produces a pheromone that may facilitate species recognition by females. (Photograph by Ulmar Grafe.)



Australian treefrog *Litoria splendida* produces a pheromone called splendipherin that is dispersed in water and attracts females (Wabnitz et al. 2000). Females of an Australian myobatrachid frog, *Pseudophryne bibronii*, can use chemical cues to locate males calling in burrows (Byrne and Keogh 2007). Males of another Australian myobatrachid, *Mixophes fasciolatus*, are strongly attracted to airborne odors of other frogs, both of their own species and another species, but the precise message conveyed by the chemical signals is unknown (Hamer et al. 2011).

In mantellid frogs from Madagascar, males have conspicuous femoral glands on the undersides of their back legs. These glands produce volatile chemicals that appear to be species-specific mixtures, suggesting a role as communication signals (Poth et al. 2012). Male hyperoliid frogs have peculiar glandular structures on their vocal sacs (Figure 13.22). These glands secrete species-specific mixtures of volatile chemicals that may aid in species recognition. If so, then the calling display of male hyperoliids would be a trimodal signal, involving acoustic (call), visual (movement of the vocal sac), and chemical communication (Starnberger et al. 2013). The primitive terrestrial New Zealand frog Leiopelma hamiltoni uses chemical cues from fecal pellets to identify other individuals and possibly to mark territories in a manner similar to that used by some plethodontid salamanders (Lee and Waldman 2001).

13.6 Communication by Turtles

Most information about the communication behavior of turtles comes from studies of courtship and, to a lesser extent, aggressive interactions. Most turtles appear to have mate-searching mating systems in which males actively search for females. Courtship by turtles usually is initiated by the male, probably attracted by the movements or odors of a female. Courtship behavior can be simple or complex, with a variety of tactile, visual, and chemical signals. Some turtles vocalize, although the functions of these vocalizations are poorly understood (Liu et al. 2013).

Tactile communication

Courtship in turtles often involves tactile interactions, although it is not always clear if these interactions represent communication signals. Often a male's biggest problem is getting the female to stay still, because it is difficult for a male turtle to mount the shell of a moving female. A common technique for immobilizing a female is to bite at her shell, head, and legs, evidently an ancestral form of courtship behavior that has been observed in many turtle species (Carpenter and Ferguson 1977; Liu et al. 2013). Unreceptive females usually reject courting males simply by swimming away, but females may resort to aggression if males are particularly persistent.

Courtship by some turtles, such as kinosternids, consists of little more than the male chasing and biting the female, but other turtles use more elaborate tactile signals. In general, turtles that swim in the water perform more courtship actions before mounting the female than do turtles that walk on the bottom; the latter often mount the female before performing most courtship actions (Bels and Crama 1994). Bottom-walkers include Blanding's turtle (*Emydoidea blandingii*), which performs several courtship actions while mounted on the female. These include rubbing the chin on the female's snout, swaying the head back and forth over the female's head while mounted on her back, and expelling water from the mouth and nostrils over the snout of the female (Baker and Gillingham 1983). Males and females of some chelid turtles engage in mutual head bobbing and rub



together barbels on their chins (Murphy and Lamoreaux 1978). Other sorts of head rubbing or mutual head bobbing by a male and female have been observed in a variety of other turtle species (**Figure 13.23**). Often it is difficult to determine whether this behavior is tactile, visual, or even chemical communication, or a combination of all three.

Some of the most elaborate tactile courtship behavior by aquatic turtles occurs among emydid turtles in the genera Chrysemys, Trachemys, Pseudemys, and Graptemys. Males swim toward females and face them head-on. Males of most species also have elongated claws on the front feet that they use to stroke or tap the female's head during courtship. This behavior has been termed "titillation," although Liu and colleagues (2013) suggested the neutral term "foreclaw displays," since the function of the displays is not clear. The display may serve to immobilize a female or to increase her receptivity. A male painted turtle (Chrysemys) or slider (Trachemys) approaches a female from the front, extends his front feet, and taps his claws on the sides and top of the female's head for a variable length of time until the female is ready to mate (Jackson and Davis 1972b). Similar behavior has been described for map turtles (Graptemys), but the male of some species in this genus stimulates the female by rubbing or vibrating his head against the side of the female's head. Male cooter and redbellied turtles in the genus Pseudemys approach females from above, extend their front feet over the female's head, and rapidly move their elongated claws on or in front of the female's head (Jackson and Davis 1972a).

Male tortoises, which court females on land, employ a wide variety of signals, with a considerable amount of touching between males and females. Courtship by tortoises is not subtle: a male attempts to immobilize a female by repeatedly biting her on the shell, head, and legs and by ramming her with an enlarged bony process at the front of his plastron (epiplastral ramming). This behavior may go on for hours until the female signals her receptivity by lifting the rear of her shell and exposing her cloaca. A female can reject a male's advances by simply dropping the rear of her shell to the ground. After a variable period of biting and ramming the female, the male will attempt to mount. He may then deliver an additional series of tactile signals in which he repeatedly slams an enlarged area at the rear of his plastron against the female's shell (xiphiplastral ramming) (Auffenberg 1977). Male tortoises often are



Figure 13.23 Three male head movements associated with courtship by sidenecked turtles. In this diagrammatic depiction the female in each pair is more darkly shaded. (A) Head bobbing (vibrating the head vertically). (B) Swaying (vibrating the head and neck horizontally). (C) Swaying the head and neck from one side to the other while mounted on the female's carapace. (After Liu et al. 2013.) very aggressive toward one another, especially when they are competing for females. Aggressive behavior includes epiplastral ramming like that used in courtship, hooking the epiplastral extension under the shell and attempting to overturn an opponent, and biting.

Visual communication

Visual communication among turtles includes the headbobbing displays mentioned previously, which may grade between purely visual and tactile signals. For example, signals used in aggressive encounters between male tortoises include head bobbing, open-mouthed threat displays, and dominance displays in which males elevate their heads as high as possible above the ground (Auffenberg 1977). In aggressive encounters among giant tortoises of the Galápagos Islands, the male that can raise his head to the greatest height usually wins an encounter. Some populations of these tortoises have a saddle-shaped carapace with a notch at the front of the shell that allows the neck to be more fully extended than is the case for tortoises with dome-shaped carapaces (Schafer and Krekorian 1983). The saddle-shaped carapace probably did not evolve to facilitate display, however. These tortoises feed by browsing on tall plants, whereas the ones with dome-shaped carapaces live in a wetter environment and graze on grasses and other low vegetation.

A male tortoise usually responds to the sight of another tortoise by moving his head up and down or side to side. Other males often respond with reciprocal head movements (eventually leading to fighting), whereas females usually do not. These head movements are similar to olfactory movements used by tortoises to sample airborne odors, and these movements may have evolved into communication signals (Auffenberg 1965).

Another form of visual communication that is only beginning to be understood is the display of colors. Turtles have good color vision and often are brightly colored, especially in the breeding season. The most common color displays involve markings on the head, neck, and front legs (**Figure 13.24**). Male freshwater turtles that engage in frontal foreclaw displays during courtship often display these colors to females at the same time. The same is true for head-bobbing displays, which may reveal brightly colored patches on the male's neck (Liu et al. 2013). Young male red-eared sliders (*Trachemys scripta*) have bright coloration on the head, neck, and front legs that gradually darkens with age. Young males tend to court females with foreclaw displays, which reveal these color markings, whereas older, darker males make more use of chasing and biting (Thomas and Montgomery 2002).

The messages conveyed by color markings in turtles are not entirely clear, and no studies have altered colors to determine their functions (Liu et al. 2013). However, several studies have suggested that coloration is an honest signal of a turtle's state of health. Both male and female red-eared sliders have red patches behind the eyes as well as yellow stripes on the chin. Turtles were presented with an immune challenge to determine the strength of the immune response. Those with higher immune responses had brighter coloration in both regions (Polo-Cavia et al. 2013). Female Spanish terrapins (*Mauremys leprosa*) have brighter and more orange leg stripes than do males, and females with stronger immune responses had brighter coloration (Ibáñez et al. 2013).

Chemical communication

Many features of courtship behavior in turtles suggest that chemical cues are important in species and sex recognition and in stimulating the female during courtship. Male tortoises generally investigate any tortoise-shaped object by sniffing. Most tortoises apparently use chemical cues to determine the species, sex, and reproductive condition of other individuals (Auffenberg 1977; Ruby and Niblick 1994; Galeotti et al. 2007).

Males and females of the North American genus *Gopherus* have **subdentary glands** on their chins. Males have larger glands than females, and dominant males have larger glands than subordinates. The glands become enlarged during the breeding season, especially in males, and secre-



Figure 13.24 Male wood turtle (*Glyptemys insculpta*) showing bright breeding coloration. Turtles have good color vision and may use this in visual displays. The yellow-orange coloration of wood turtles varies, with the males often becoming vibrantly colored during the breeding season. (Photograph by Tobias Landberg.)

tory activity increases. Tortoises sometimes rub glandular secretions onto enlarged scales on the front feet and extend the feet to allow the courting partner to sniff them. They also appear to broadcast chemical signals by elevating the chin and moving the head up and down. Gland secretions contain more than a dozen protein compounds of different molecular weights, as well as several kinds of lipids and volatile free fatty acids. Individual variation in composition of these secretions may allow individual recognition, which in turn would facilitate the establishment of a stable dominance hierarchy in a local population (Alberts et al. 1994).

Among aquatic turtles, the male often pursues the female and sniffs her cloacal region, presumably using chemical cues to identify the species and sex of prospective mates. Male green sea turtles (Chelonia mydas) respond differently to breeding and nonbreeding females, suggesting the presence of some chemical indicator of reproductive condition (Crowell Comuzzie and Owens 1990). Freshwater turtles have a variety of specialized glands, but in most cases their function is poorly understood. However, experimental studies have shown that males of several species can discriminate between chemical cues from males and females, or from their own species and another species. These experiments involve giving males a choice of aquaria with water conditioned by a male, female, or no turtle. In European pond turtles (Emys orbicularis), Spanish terrapins (Mauremys leprosa), and North American musk turtles (Sternotherus odoratus), males tested during the breeding season consistently preferred odors of females to odors of other males or of control water, although the preference often disappeared in the nonbreeding season (Muñoz 2004; Poschadel et al. 2006; Lewis et al. 2007). In Spanish terrapins, both males and females also could distinguish between chemical cues from large or small individuals of the opposite sex, although it is not clear whether this was simply a function of odor concentration (Ibáñez et al. 2012).

Acoustic communication

Acoustic communication is the least-studied mode of turtle communication. Tortoises are the most vocal turtles. Males produce a variety of sounds, including repetitive moans or groans during courtship and mating (Auffenberg 1977). The function of these vocalizations is poorly understood, as is the mechanism by which they are produced. Tortoises lack true vocal cords, but the larynx does have elastic bands that may vibrate to produce sounds (Sacchi et al. 2004). A phylogenetic analysis suggested that sounds produced during courtship and mating are an ancestral trait in cryptodires, but acoustic signals are now found mostly in terrestrial or semiterrestrial species (Galeotti et al. 2005). In the marginated tortoise (Testudo marginata), courtship intensity (measured by number of bites and rams delivered by the male) and rate of vocalization both were positively correlated with a male's success in mounting a female (Sacchi et al. 2003). Female Hermann's tortoises (T. hermanni) exhibited a preference for playbacks of male calls at high rates; calling rate may be a reliable indicator of male health or quality (Galeotti et al. 2004).

The first report of underwater vocalization by an aquatic turtle was in the Australian snake-necked turtle (*Chelodina oblonga*). This species has a surprisingly large repertoire of calls, with up to 17 different categories recorded. During the breeding season, males produce a repetitive pulsed call that can be sustained for nearly 10 min at a time. This call appears to be an advertisement call to attract females in an environment in which vision is restricted by poor light or turbidity in the water (Giles et al. 2009); if so, this would be the only known example of male turtles advertising themselves to attract mates.

Another little-explored context for vocal signaling in turtles is communication between mothers and their young. Turtles generally are thought to lack parental care, but female and young Amazon River turtles (*Podocnemis expansa*) produce a variety of calls and communicate with each other, both at the nest and in the water. One possible function of such communication is to coordinate mass migrations from the river to flooded forest in the wet season (Ferrara et al. 2013, 2014a). Vocalization by hatchling-green sea turtles (*Chelonia mydas*) may coordinate emergence from the nest (Ferrara et al. 2014b).

13.7 Communication by Crocodylians

Two features of crocodylian communication set these animals apart from other reptiles. Crocodylians are the most vocal of reptiles, employing a wide variety of vocalizations for both long- and close-range communication. They also are unusual in the extent to which they combine acoustic, visual, and tactile signals into complex displays. Crocodylian communication signals can be divided into four general categories, based on the context in which the signals are given: advertisement displays, given by males or females, that announce ownership of a territory or attract mates; aggressive displays, usually given during encounters between males; courtship displays, given during interactions between males and females; and signals exchanged between parents and their offspring (Senter 2008).

Communication by alligators

The American alligator (*Alligator mississippiensis*), an inhabitant of swamps, marshes, lakes, and ponds in the southeastern United States, is the best-studied crocodylian (Vliet 1989). Its most conspicuous display is a loud, repetitive roar called bellowing (**Figure 13.25A**). This display attracted the attention of early explorers in the Southeast, among them William Bartram (1791), who said that the roaring of alligators caused the air and water to shake and the earth to tremble. Perhaps he exaggerated, but the bellowing display does include both airborne sound and waterborne vibrations. It is produced by the contraction of trunk muscles (A)





that force air through the glottis, producing a low-frequency sound (Vergne et al. 2009). When males give this display, the audible bellow is followed by subaudible vibrations (i.e., vibrations of a frequency too low to be heard by humans) that cause water droplets to dance above the alligator's back while propagating underwater waves for some distance (**Figure 13.25B**). Females also bellow, but they do not produce subaudible vibrations (Senter 2008).

Bellowing both advertises an animal's ownership of a territory and attracts potential mates. It is hard to estimate the distance over which the bellows can be heard by conspecifics; it depends on the call's frequency structure and intensity as well as the level of environmental background noise. Estimates for airborne transmission in a fairly noisy captive situation yielded transmission distances of about 170 m, whereas lower frequencies that propagate through water could be heard up to 1.5 km away (Todd 2007).

On mornings during the breeding season, American alligators often engage in a bellowing chorus that can last an hour or more. Similar choruses have been reported in Chinese alligators (*Alligator sinensis*) (Wang et al. 2009a). *A. sinensis* is relatively solitary and territorial outside the breeding season, but during the mating season both males and females aggregate in ponds and lakes, and individu-

Figure 13.25 Bellowing display of a male American alligator (Alligator mississipiensis).

(A) During the vocal component of the display, a male raises his body high in the water and emits a bellow—sound waves that travel through the air. (B) Following the bellow, the male sinks into the water. Once most of his back is submerged, he produces subsonic vibrations that propel water droplets as much as 60 cm into the air and produce pressure waves that travel through the water. (Photographs: A, © Kenny Williams/Alamy; B, courtesy of Vladimir Dinets.)

als of both sexes participate in chorusing. The precise function of chorusing by Chinese alligators is unknown, but both males and females respond equally strongly to playbacks of either male or female calls, suggesting that the calls facilitate aggregation at mating sites. Chinese alligators live in areas with no other animals that produce similar sounds, and both males and females respond to a wide range of acoustic stimuli that resemble natural bellows. The absence of competing sounds presumably results in relaxed selection for precise sound recognition (Wang et al. 2009b).

A less frequent advertisement display by the American alligator is head slapping, which is performed mostly by males. The physics of underwater sound transmission make head slaps the easiest sounds for other alligators to

locate, whereas subaudible pressure waves are the hardest. Vladimir Dinets (2011, 2013a) has suggested that head slaps identify the position of a displaying male, while subaudible vibrations indicate the size of the male.

Male alligators often respond aggressively to bellowing or head slapping by other males. Aggressive behavior includes chasing, lunging, and biting the opponent, as well as a variety of visual displays. A male signals aggression by lifting his head out of the water with his tail arched above the water surface. Submission is signaled by lifting the snout out of the water at an oblique angle or by simply submerging and swimming away. Victorious males sometimes assume an inflated posture with the body high in the water (Vliet 1989; Senter 2008).

A female alligator attracted by these displays initiates courtship by placing her snout on the male's head or snout. A period of mutual head and snout rubbing follows, during which both sexes emit a series of distinctive coughlike vocalizations. Males sometimes also produce subaudible vibrations during courtship. If the female is receptive, the male and female proceed by circling one another in the water, rubbing their heads together, moving over the back of the partner, blowing bubbles through the mouth, and blowing a stream of water into the air from the nostrils. It a female is not receptive, she responds to the male with a series of bellow-growl vocalizations and then submerges or swims away from him (Vliet 1989).

Communication by crocodiles

Many of the displays described for American alligators have been observed in other crocodylians, but the structure, timing, and sequence of display components vary among species (Dinets 2013b). Crocodiles tend to be less vocal than alligators. This is probably because crocodiles often live along open riverbanks or lakeshores, where close-range visual displays are more useful than acoustic displays (Garrick and Lang 1977; Wang et al. 2009a). Nile crocodiles (Crocodylus niloticus) can occur at very high densities and constantly encounter other individuals. This situation requires frequent use of submissive displays, such as snout lifting by males approached by a larger individual or by females during the initial stages of courtship. Male crocodiles perform snout lifting also during courtship, but it has never been seen in this context among alligators (Senter 2008). In general, crocodiles tend to have more sex-specific displays (e.g., females apparently do not bellow or head slap), whereas in alligators the two sexes perform many of the same displays. This difference may be related to the pronounced territorial behavior of female alligators.

Communication by juvenile crocodylians

Crocodylians are unusual among living reptiles in the degree to which communication signals are used in interactions between juveniles and between juveniles and adults. Baby crocodylians begin exchanging vocal signals while still inside the egg, responding to the calls of siblings in the nest. This communication may help coordinate synchronous hatching within a brood (Vergne and Mathevon 2008). The calls attract the attention of the female, who usually remains near the nest and guards it during incubation. The female digs the hatchlings out of the nest and often transports them to a nursery pool. The young then remain with the mother for an extended period—several weeks in the case of crocodiles and up to 2 years in the American alligator (see Chapter 9).

The juveniles often live together in a relatively cohesive group, responding to each other's movements with grunting vocalizations that may serve as contact calls. Juvenile crocodylians also produce distress calls with a structure that grades into that of the contact grunts. Experimental studies with several species have shown that distress calls elicit protective responses from parents (Britton 2000). The structure of these calls varies among species, among populations of the same species, and among individuals in the same population, but this variation seems not to affect the behavior of the animals. Adults are not very discriminating in their responses, but respond to a wide range of signals that resemble juvenile distress calls, and juveniles respond to contact calls of their own or other species (Vergne et al. 2007, 2011, 2012; Sicuro et al. 2013).

Do crocodylians use chemical signals?

A poorly understood aspect of crocodylian communication is the extent to which they make use of chemical signals (Mason 1992). All crocodylians have glands under the chin that produce a musky odor, and there are scent glands in the cloacal region as well. Musky odors have been detected during bellowing and head-slapping displays of alligators, and an oily substance has been observed in the water during head-slapping displays. In addition, the mutual chin and head rubbing during courtship of many species may be related in part to delivery of chemical signals. The chemical constituents of crocodylian glandular secretions have been extensively characterized (Weldon and Wheeler 2000), but their precise function as communication signals remains largely unknown. Crocodylians lack a vomeronasal organ, which other reptiles use to detect pheromones (Senter 2002), and behavioral evidence for pheromonal communication is lacking.

13.8 Communication by Squamates

Most squamates have well-developed visual systems with color vision. They also have three distinct chemosensory systems: the olfactory system, taste buds (lost in some lineages), and the vomeronasal system (Schwenk 1995). The last opens directly into the oral cavity and receives chemical stimuli by way of the tongue (see Figure 15.11). The tongue picks up chemicals by licking the substrate or by flicking rapidly in the air. Squamates generally use both visual and chemical signals for communication (geckos also use acoustic signals), but the relative importance of each mode of communication varies in different lineages and is correlated with with feeding behavior.

Iguanians use the tongue to capture prey and transport it into the mouth, which is the ancestral condition for all lepidosaurs (see Chapter 11). Use of the tongue in feeding constrains its evolution as a specialized chemosensory organ. Members of other squamate clades generally capture prey with their jaws. This evolutionary innovation freed the tongue from its ancestral role in feeding and set the stage for the evolution of enhanced chemosensory functions (Schwenk 1993). The specialization of the tongue as a chemosensory organ reaches its peak in the varanid lizards and snakes, both of which have deeply forked tongues that are used exclusively for chemoreception.

Visual communication

Visual communication is the best-studied mode of communication in iguanian lizards. Iguanians produce complex visual signals that involve combinations of color and movement that make the animal more conspicuous to conspecific males or females. Until recently, the role of visual communication in non-iguanian lizards had been neglected, but recent research has shown that visual signals are important for some non-iguanian lizards and often complement chemical signals.

IGUANIAN LIZARDS Males of many species of iguanian lizards are territorial, at least during the breeding season. A territorial lizard typically spends much of its time surveying its territory from a conspicuous perch or patrolling the territory by moving from perch to perch. Periodically, the lizard performs a series of displays that vary from simple vertical movements of the head with the rest of the body stationary to elaborate two- or four-legged push-ups. The displays often are performed spontaneously rather than being directed at a particular receiver (Martins 1993). These have been called assertion displays or broadcast displays in the lizard behavior literature, but they serve the same function as advertisement displays in other animals-to advertise ownership of a territory and to attract females (Baird 2013). The displays usually include a stereotyped component known as the signature display or signature bob, which encodes the species identity of the performer in the temporal pattern of the display. Species living in the same region have distinct head-bobbing displays, and there is little doubt that these displays are important in maintaining reproductive isolation among sympatric species. Other components of the display may exhibit individual or gender differences.

The advertisement displays of *Anolis* lizards and their close relatives have been studied in more detail than those of most other lizards (Jenssen 1977; Losos 2009). These

largely arboreal lizards are common throughout the Neotropics. They are generally cryptically colored, but they have dewlaps that can be extended to reveal bright patches of color ranging from purple and blue to red, orange, yellow, or white. Some species have elaborately colored dewlaps with spots of one color superimposed on a background of another color (**Figure 13.26**). Often these display structures have colors that contrast with the prevailing background to make them especially visible to receivers. *Anolis* lizards that live in forests dominated by low-light conditions often have dewlaps that emphasize highly reflective colors such as white, yellow, or pink, whereas those living in more open, higher-light environments have red, blue, or purple dewlaps.

Studies of neural responses of *Anolis* lizards, along with behavioral experiments, have shown that dewlaps with the greatest brightness contrast with the natural background environment are those that are most likely to be detected by lizards. The actual color of the dewlap in a particular species probably results from a complex set of selective pressures, including the amount of shade in the habitat, predominant wavelengths of light in the environment, the background (vegetation or open sky) against which a displaying lizard typically is viewed by conspecifics, and the possibility of detection by predators (Fleischman 2000). Even within a single species, dewlap color may differ among populations, and these differences are correlated with the light environment. In Puerto Rico, male *Anolis cristatellus* from high-light environments have darker, less reflective dewlaps that do

(A)



(B)



(C)





Figure 13.26 Visual dewlap displays of Anolis lizards.

The dewlaps of male *Anolis* have species-specific characteristics. Examples of variation in size and shape are seen in (A) Orton's anole (*A. ortonii*) and (B) the many-scaled anole (*A. polylepis*). Examples of variation in color and pattern include (C) the lyre anole (*A. lyra*) and (D) the yellowtongued forest anole (*A. chrysolepis*). (Photographs: A, D, © Morley Read/Alamy; B, © Hugh Lansdown/Shutterstock; C, © Morley Read/Shutterstock.)
those from low-light environments (Leal and Fleishman 2004). Surprisingly, variation in dewlap colors for *A. distichus* on Hispaniola shows the opposite pattern—brighter dewlaps in drier, more open habitats (Ng et al. 2012).

Species living in the same geographic region usually have different colors on their dewlaps, except in cases where two species are very different in size, shape, or body color. It has long been assumed that these color differences are important for species recognition, and this hypothesis has been supported experimentally for a pair of sympatric species in the Dominican Republic, Anolis marcanoi and A. cybotes. Males of these species look very similar, but A. marcanoi has a red dewlap, whereas that of A. cybotes is vellow or white. When Jonathan Losos (1985) painted the dewlaps of each species to resemble those of the other species, the altered males were readily attacked by heterospecific males, indicating that color is important for species recognition. In subsequent experiments, projected video recordings of displays of both species elicited displays from A. marcanoi males, but they synchronized their display behavior more closely with stimuli from their own species (Macedonia et al. 1994).

Even stronger evidence of species recognition was obtained in similar experiments with the Jamaican species *Anolis grahami*. Males of this species gave more displays to video playbacks of displays of their own species than to displays by other species (Macedonia and Stamps 1994). Additional experiments using robotic lizards enabled investigators to vary both dewlap color and head-bob display pattern simultaneously. Test males gave more dewlap displays to robot presentations that resembled conspecifics in both color and display pattern than they did to those in which either color or display pattern was altered (Macedonia et al. 2013).

While the advertisement or assertion displays of territorial male lizards elicit aggressive responses from other males or cause them to retreat, these same displays are attractive to females. Caged *Anolis nebulosus* females presented with films of displaying males projected onto tiny screens at the ends of cages, showed a strong tendency to move toward the screen showing the display (Jenssen 1970).

Once a female lizard approaches a displaying male, he usually responds with a series of courtship displays. Courtship displays of some lizards are very similar to those used in territorial advertisement, but the courtship display of many species has a distinctly different tempo of head bobbing and dewlap extension. For example, male lizards in several families approach females while giving a rapid series of shallow head bobs (a display variously described as jiggling, shudder-bobbing, or courtship nodding) that appears to convey a nonaggressive message to females (Carpenter and Ferguson 1977; Kelso and Verrell 2002).

The most elaborate displays performed by male iguanian lizards are those used in aggressive interactions with other males. These displays typically involve a basic headbob or push-up display like those used for territory advertisement, but these elements may be modified by additional behaviors such as dewlap extensions, erection of crests, movements of the tail and limbs, body compression or inflation, inflation of the head and throat or engorgement of these regions with blood, and changes in color. There is considerable similarity in basic display structure among iguanian lizards, suggesting that evolution of aggressive displays has been relatively conservative (Carpenter and Ferguson 1977; Carpenter 1978). Nevertheless, overall display complexity, determined by the number of modifying elements added to the basic push-up or head-bob display, varies widely among species.

In contrast to advertisement displays, which sometimes are given spontaneously even in the absence of nearby conspecifics, aggressive displays are dynamic and change in response to the behavior of competing males. Studies using video playbacks of aggressive displays to males of the Australian jacky dragon (Amphibolurus muricatus), a territorial lizard, have shown that males adjust their own display rates to that of the video playback and give more submissive displays to recorded males displaying at high rates (Ord et al. 2002). This response suggests that males use display rates of competing males to assess their fighting ability. Further evidence of such assessment comes from video playbacks of displays in which the concentration of displays in time was varied; displays given in clusters were most likely to suppress aggressive displays by the test male (Van Dyk et al. 2007). In some species, particular aspects of a display may be reliable indicators of fighting ability. In North American collared lizards (Crotaphytus collaris), males display to other males with an open mouth, which reveals the size of the jaw-closing muscles. White patches at the corners of the mouth, which also reflect UV wavelengths, make these muscles more conspicuous (Figure 13.27A). The breadth of the muscles is correlated with bite force, independent of body or head size, and is probably a good indicator of fighting ability (Lappin et al. 2006).

The use of color in territorial advertisement and aggressive interactions is widespread among iguanian lizards (Cooper and Greenberg 1992). Males often develop bright colors during the breeding season. For example, males of *Urosaurus, Uta, Uma,* and *Sceloporus* often have colorful patches on the sides of the belly and on the throat. These markings are used to advertise ownership of territories and are shown off during push-up displays (**Figure 13.27B**). There has been repeated loss of sexually dimorphic belly patches in different clades within the genus *Sceloporus,* which is correlated with a shift from using arboreal or rock-dwelling habitats to using terrestrial habitats. It may be that the costs of having bright coloration (perhaps increased exposure to predators) has favored loss of this sexually selected trait in certain habitats (Wiens 1999).

Males of species that have lost the blue coloration, such as Sceloporus virgatus, rely more on chemical signals and have reduced the frequency of visual displays (Ossip-Klein et al. 2013). Conversely, males of species with blue coloration, such Figure 13.27 Territorial and threat displays of male lizards. (A) Openmouth threat display of a male collared lizard (Crotaphytus collaris). The white patches in the corner of the mouth, which also reflect UV wavelengths visible to the lizards, focus the viewer's attention on the size of the jaw-closing muscles, an indicator of fighting ability. (The bright orange objects on the lizard's shoulder are mites; see Figure 15.20.) (B) Push-up display of a male granite spiny lizard (Sceloporus orcutti). The bright blue breeding coloration also advertises territory ownership. (Photographs: A by A. Kristopher Lappin; B by Mark Chappell.)

(A)



(B)



as *S. undulatus*, are less responsive to chemical signals of other males than are species lacking blue coloration (Hews et al. 2011). Despite the evolutionary loss of blue coloration in *S. virgatus*, males retain the behavioral response to such colors; when males were painted with blue color on their abdomens, their displays elicited more submissive responses from other males than did the displays of unpainted males (Quinn and Hews 2000). This observation suggests that natural selection, probably mediated by predation pressure, has acted on signalers but not on receivers, which suffer no cost in retaining the response to blue color displays.

There are other costs to maintaining bright breeding coloration. Brightly colored males are more likely to be attacked by other males because they are perceived as reproductive competitors. In many species, small males delay development of breeding coloration, probably because they cannot compete with large males and therefore avoid costly interactions with larger individuals (Martín and Forsman 1999). The elevated testosterone levels that produce bright coloration in males also increase physiological costs through increased aggressiveness (Marler et al. 1995) and greater susceptibility to parasite infection (Salvador et al. 1996).

One of the most spectacular color displays of any lizard is that of the Australian frillneck lizard (*Chlamydosaurus kingii*). Males have an enormous frill around the head, marked with bright reddish orange coloration in some populations. Males erect the frill during contests with other males, displaying the bright coloration, while also giving an open-mouth threat (**Figure 13.28**). Males are highly territorial in the breeding season, defending conspicuous perches on tree trunks against other males. Many disputes

Figure 13.28 Threat display of the Australian frillneck lizard (*Chlamydosaurus kingii*). Male-male competition in this highly territorial species involves the erection of the large, brightly colored neck frill combined with an open-mouth threat display. (Photograph courtesy of Sarah Pryke.) are settled without actual fighting, and both body size and the color of the frill are good predictors of contest outcome. The bright orange color on the frill is derived from carotenoid pigments, which are acquired in the diet and may be an honest indicator of male quality (Hamilton et al. 2013).

Males of some iguanian species exhibit polymorphic differences in color pattern that are related to differences



in dominance status. Male tree lizards (Urosaurus omatus) from the southwestern United States have color patterns that vary both within and among populations. In most populations, males have an orange or yellow area on the throat with a central green or blue spot that varies in size. Throat color is determined by levels of testosterone and prolactin early in the development of the male (Moore et al. 1998). Experimental manipulation of throat color demonstrated that males with more blue on their throats dominate those with less blue (Thompson and Moore 1991). Throat color is not, however, the only determinant of the outcome of fights. Larger males consistently dominate smaller individuals, even when throat color is not as blue, and males that have been dominant in previous fights are more likely to win contests (Carpenter 1995). In another study, blue-throated males performed more push-up displays than other males, and large males displayed more than small males. However, display behavior was not clearly correlated with various measures of body condition or quality that might indicate fighting ability (McElroy et al. 2007). Interpreting these results is complicated, because differences in throat color and dominance status are related to differences in the tactics used by males to acquire mates (see Chapter 14).

Males in some populations of *Urosaurus ornatus* turn very dark or even black during the breeding season. Darkening



can occur in a matter of minutes and is used by territorial males to advertise their dominance status. In a comparative study of two populations in New Mexico, males in a high-density population were found to be more aggressive and exhibited a greater degree of dorsal darkening than did males in a lower-density population (Carpenter 1995). The males from the high-density population also had less polymorphic throat coloration, because most males had blue throats. When throat color was similar, darker males won contests with lighter males. The degree of dorsal darkening is not fixed in these populations. When males from the low-density population were placed in enclosures at high density, they gradually assumed a darker dorsal coloration (Zucker 1994a). The dark dorsal coloration is a more effective long-distance territorial signal than is blue throat coloration because it provides more contrast with the background colors in the environment. Presumably the dark color also makes males more conspicuous to predators. Dominant territorial males darken only when females are available, perhaps because the potential increase in mating success outweighs the risks (Zucker 1994b).

Chameleons are well known for their ability to change color rapidly. Rapid color change as a visual display makes the display easily detectable by rival males or by females but reduces exposure to predation by limiting color displays to specific social situations (Stuart-Fox and Moussalli 2008). Male chameleons often change from a cryptic color pattern to much brighter colors when courting females, and they have other distinctive color patterns that are used during aggressive interactions with other males. Male Cape dwarf chameleons from South Africa (*Bradypodion pumilum*) have a pink or orange patch on the side of the body outlined with dark blue markings that also reflect UV wavelengths (**Figure 13.29A**). In staged contests between males, the size of the color patch was a good predictor of fighting ability (Stuart-Fox et al. 2006).

Male veiled chameleons (*Chamaeleo calyptratus*) signal aggression with colorful vertical stripes on the sides of the body, as well as markings on the head (**Figure 13.29B**). The brightness of the lateral stripes was a good indicator of a male's motivation to fight, whereas both the brightness and rate of change in head color predicted a male's chances of winning a fight (Ligon and McGraw 2013). Males that lost fights became rapidly darker in color until they were

Figure 13.29 Color signaling in male chameoleons.

Members of the Chamaeleonidae are well known for their remarkable and rapid changes in coloration. (A) During the breeding season, male Cape dwarf chameleons (*Bradypodion pumilum*) display pink or orange lateral streak outlined with dark blue markings that reflect UV wavelengths. (On this individual, the pink streak extends from the face to the hind leg.) (B) The bright vertical stripes on a male veiled chameleon (*Chamaeleo calyptratus*) signal aggression. (Photographs: A by Devi Stuart-Fox and A. Moussalli; B by Russell Ligon.)



Figure 13.30 Sexual dimorphism in the Mexican collared lizard (Crotaphytus dickersonae). Gravid females develop bright orange markings, whereas males are a brilliant blue color. (Photograph by A. Kristopher Lappin.) almost black, providing an unmistakable signal of submission (Ligon 2014). Furthermore, the amount of darkening was affected by the level of aggression experienced by the losing male.

Some female iguanian lizards develop bright coloration during the breeding season (Cooper and Greenberg 1992). Gravid females of the Mexican collared lizard (*Crotaphytus dickersonae*) develop bright orange spots, a strikingly different color pattern from the bright blue coloration of the male (**Figure 13.30**). Nonreceptive females of *Holbrookia propinqua* develop orange markings on the belly and sides of the body. Brightening of female coloration typically is accompanied by increasing aggressiveness toward males, but color displays alone may be sufficient to deter a male from trying to court a nonreceptive female.

Male *Sceloporus virgatus* have reduced color patches compared with other males in the genus, but female *S. virgatus* develop bright orange marks on their throats in the breeding season, although the brightness varies among individuals (**Figure 13.31**). Brightness of coloration peaks during the female's receptive period and gradually fades as she becomes nonreceptive. Males were more likely to court females with large, bright color patches (Weiss 2002). These color patches also may indicate female quality, because the size of the orange patches was a good indicator of female body condition, while the saturation of the color was positively cor-

(A)



(B)





Figure 13.31 Color signaling by female Sceloporus virgatus. Although the use of color has been reduced in males of this species, females develop bright orange throat

patches during the breeding season. Breeding coloration of three females, showing individual variation in the intensity of color signals. (Photographs by Stacey Weiss.)

related with body size and negatively correlated with mite infestation (Weiss 2006).

Female chameleons are cryptically colored outside the breeding season. During the breeding season, some species develop one set of colors that indicates receptivity to courting males and another set that indicates nonreceptivity after mating. Male veiled chameleons adjust their courtship behavior in response to the receptivity of females, directing the most vigorous displays toward receptive females (Kelso and Verrell 2002). Experiments with the common chameleon (Chamaeleo chamaeleon) showed that males direct most of their courtship toward models painted with the colors of receptive females and toward live females with coloration altered to resemble that of receptive females (Cuadrado 2000). Presumably it is advantageous to females to signal nonreceptivity because they avoid the costs of being harassed by males that are searching for mates. It is advantageous to males to respond to such signals because they avoid wasting time and energy courting females that are unlikely to mate with them (Olsson and Madsen 1998). Female Cape dwarf chameleons (Bradypodion pumilum) do not signal receptivity with color change. Instead, nonreceptive females are very aggressive toward males, and because females are larger than males, they pose a significant threat of injury. Males adjust their intensity of courtship by assessing a female's size and aggressiveness (Stuart-Fox and Whiting 2005).

A neglected area of research in lizard communication is the use of markings that reflect UV wavelengths. Many birds have UV markings that are known to be important in both interactions among males and mate choice by females. Many lizards have the sensory capacity to see in the ultraviolet, and some species have UV-reflecting markings. In the Australian agamid lizard *Ctenophorus ornatus*, females have UV-reflecting throat and chest patches that are not obvious in the visible spectrum. These markings are more conspicuous in the UV than are those of males, and males prefer to associate with females with the most conspicuous UV markings. These markings do not appear to convey information about variation in female quality, but may reflect differences in receptivity (LeBas and Marshall 2000).

NON-IGUANIAN LIZARDS Males of some non-iguanian lizards, including scincids, cordylids, and lacertids, develop bright colors during the breeding season (Cooper and Greenberg 1992), and all of these lizards use some visual displays in aggressive and courtship interactions, although chemical signals predominate in many species. Breeding coloration of males and females often differs, and may provide cues for sex recognition by males searching for mates. Males of an Australian skink, Eulamprus heatwolei, appeared to use visual cues to locate females, but used chemical cues to assess the females' receptivity (Head et al. 2005). Experiments with the lacertid lizard Podarcis hispanica in which both color and odor cues were manipulated indicated that chemical cues take precedence over visual cues in sex recognition (López and Martín 2001). In P. bocagei, the normally brown females develop a green coloration similar to that of males after mating. Green females were less likely to be courted by males, were never seen copulating, and were the only females seen to reject male courtship advances (Galán 2000). These observations suggest that, as in many iguanian lizards, female non-iguanian lizards use color to signal their lack of receptivity to males. Subordinate male South African flat lizards, Platysaurus broadleyi, sometimes adopt the color pattern of females, perhaps enabling them to sneak into the territories of dominant males. However, this tactic is effective only at long distance, because these so-called she-males are unable to mimic the chemical signatures of females (Whiting et al. 2009).

Until recently, there was little evidence that male coloration is important in female choice of mates in lizards (Olsson and Madsen 1998), but recent research has shown that coloration can convey important information about male quality. Male European green lizards (*Lacerta viridis*) defend territories during the breeding season. They develop blue coloration on the head and throat, which also reflects strongly in UV wavelengths (**Figure 13.32**). UV reflectance



Figure 13.32 The breeding coloration of male Lacerta viridis reflects ultraviolet light.

Although the males of most non-iguanian lizards search for females to mate with and compete directly with other males, *L. viridis* males are territorial during the breeding season, using color on the head and throat to advertise their quality to females. The male's bright blue head and neck reflect UV wavelengths, which are perceived by other lizards, including mate-choosing females. (Photograph by Wayne Van Devender.) can be experimentally blocked by applying UV-blocking chemicals to the throat patch. In a laboratory experiment, females presented with a choice of males with normal and reduced UV reflectance preferred to associate with normal males. Actual mating was not observed, but the results suggest a role for UV coloration in female mate choice (Bajer et al. 2010). In a field study, male green lizards with brighter throats were larger and had larger heads, both of which are traits correlated with fighting success. Throat brightness was negatively correlated with ectoparasite load (mites), suggesting that color, and particularly UV reflectance, provides accurate information about male health (Molnár et al. 2012). When UV reflectance of males was experimentally blocked, the duller males were more likely to lose contests with other males than were brighter males (Bajer et al. 2011).

Color markings, including UV-reflecting patches, appear to signal male quality in other non-iguanian lizards and sometimes predict fighting success. Males and females of the European ocellated lizard (Lacerta lepida) have UVreflecting eyespots on the sides of the body and UV-reflecting marks on the sides of the belly. These markings are larger in males, and eyespot size is correlated with male size, but not with female size. In addition, the color markings of males have greater UV reflectance than those of females (Font et al. 2009). Other lacertid lizards that exhibit difference in UV-reflecting signals in males and females include various species of wall lizards (Gallotia, Podarcis), although in most cases the functional significance of these signals is poorly understood (Huyghe et al. 2005; Pérez i de Lanuza et al. 2014). Male South African flat lizards (Platysaurus) have UV-reflecting color patches on the throat, which appear to signal fighting ability in these territorial lizards (Stapley and Whiting 2006; Whiting et al. 2006).

Chemical communication

Chemical communication is much more difficult to study than visual communication. Humans are not very chemically oriented, and our ability to detect chemical signals is far inferior to that of lizards and snakes. Special equipment and expertise in organic chemistry are required to identify and characterize the chemical signals of other animals.

IGUANIAN LIZARDS The chemical signals of iguanian lizards have received much less attention than their visual signals. Many species have femoral glands located on the undersides of their back legs. These glands generally are better developed in males than in females and become active during the breeding season, secreting a nonvolatile combination of lipids and proteins. The lizards smear these secretions on rocks and other substrates in their territories, where they are actively investigated by other lizards with tongue flicking or licking (Mason and Parker 2010). The femoral gland secretions of at least one species, *Dipsosaurus dorsalis*, absorb UV radiation, making the secretions visible to the lizards, which can see UV wavelengths (Alberts 1989).

These scent marks almost certainly serve as territorial markers analogous to those of many mammals. The secretions themselves may provide considerable information about the territory owner. In green iguanas (*Iguana iguana*) there appears to be sufficient variation in the protein composition of femoral gland secretions from different individuals to provide information about sex, individual identity, and kinship relationships, assuming that the lizards can detect these differences. These chemical signals may play a role in the establishment of dominance relationships among males during the breeding season, when they defend small mating territories in close proximity to one another (Alberts 1993).

NON-IGUANIAN LIZARDS Chemical communication seems to predominate in most non-iguanian families. These lizards have well-developed olfactory systems, but most chemical signals are detected by the vomeronasal system. Chemical stimuli are sampled by touching the substrate or other lizards with the tongue. Sampling airborne or substrate chemicals by tongue flicking is common among teiids, lacertids, helodermatids, varanids, and snakes (Mason 1992). Male skinks can follow chemical trails of females produced by a specialized cloacal gland (the urodeal gland) that enlarges during the breeding season. Rates of tongue flicking or tongue touching are frequently used as indices of the ability of lizards and snakes to make chemical discriminations. It is assumed that squamates convey nonvolatile chemicals to the vomeronasal organs when they lick a substrate or touch it with their tongue.

The use of chemical signals by skinks has been studied in some detail (Cooper and Vitt 1986). Male North American skinks of the genus Plestiodon (formerly Eumeces) are aggressive toward other males of their species during the mating season, but they do not defend territories. Males determine the sex and species of other lizards by touching them with their tongues, and males of other species generally are ignored. When male P. fasciatus were smeared with cloacal material from male P. inexpectatus, they were attacked by P. inexpectatus males. Despite the similar appearance of some sympatric skinks, males seldom try to court females of the wrong species but will do so if the females are smeared with cloacal material from the male's own species. Chemical information can sometimes override other types of signals. For example, the heads of some Plestiodon males turn bright orange during the mating season, and this color is an aggressive advertisement to other males. Females with heads painted orange were initially attacked by males but were courted once the males had touched them with their tongues.

Several species of large skinks in the genus *Egernia* in Australia use piles of feces to mark areas near basking sites. Experimental tests with one scat-piling species, *E. striolata*, demonstrated that these lizards could distinguish their own scat piles from those of unfamiliar conspecifics. This result suggests that scent marking provides information about the individual identity of resident lizards that probably enhances their ability to defend preferred basking sites (Bull et al. 1999). Several other members of the genus *Egernia* are unusual among lizards in that they live in stable social groups in rock crevices (see Chapter 12). These skinks can discriminate between members of their own group and those of other groups using either body odors or scats (Bull et al. 2000).

Male gekkonids, lacertids, teiids, helodermatids, and varanids lick or touch females with their tongues during courtship. Male varanids direct their attention mostly to the sides of the head, the region where the back legs join the body, and sometimes the female's back. Male geckos also lick a female's skin, and experimental studies of leopard geckos (Eublepharis macularius) have shown that males use skin pheromones to distinguish males from females (Mason 1992). Komodo dragons (Varanus komodoensis) deposit feces in conspicuous places along regularly used trails and especially at basking sites, where they are investigated intensively by conspecifics. Although this species does not defend its home range as an exclusive territory, these chemical markers may enable individuals to avoid areas currently being used by other lizards (Auffenberg 1981). In lacertid lizards of the genus Acanthodactylus, chemical signals also elicit both avoidance by males and aggressive behavior, whereas females exhibit little response to male secretions (Khannoon et al. 2011).

Chemical communication has been studied extensively in several European lacertid lizards. Individuals of *Iberolacerta cyreni* can discriminate familiar from unfamiliar individuals using chemical cues from both fecal pellets and femoral gland secretions (Aragón et al. 2001). Signals deposited from femoral gland secretions are made up of a combination of steroids, such as cholesterol, and other chemicals. Males of this species apparently can use these signals to assess the fighting ability of rivals, with the concentration of cholesterol being the most important component of the signal (Martín and López 2007).

Females also use femoral gland secretions to assess various aspects of male quality, including size, age, reproductive status, and health. Secretions with high concentrations of dehydrocholesterol and ergosterol are produced by larger, older males and those with strong immune responses, an indicator of overall health (López et al. 2006). In experiments in which females could choose substrates marked by different males, they preferred chemical signals of larger, older males and those in good health (Martín and López 2006). When substrates were experimentally manipulated to increase the proportion of ergosterol, females preferred the enhanced substrates to controls. Females also preferred substrates marked with secretions from large, old territorial males to those from smaller, younger satellite males (Martín and López 2013).

European wall lizards of the genus *Podarcis* (Figure 13.33) also have been investigated for chemical communication (reviewed by Font et al. 2012). Mate recognition appears to be mainly a male behavior—males discriminate between conspecific and heterospecific chemical cues, whereas females do not. Males also use chemical cues of other males to assess individual identity, size, age, and fighting ability (Carazo et al. 2007, 2008), whereas females do not appear to choose mates based on male chemical cues (Carazo et al. 2011).

SNAKES Snakes, which are derived from a non-iguanian clade of lizards, rely heavily on chemosensory information to locate prey and to communicate with members of their own species. Their highly forked tongues function exclusively as chemosensory organs, capable of fine-scale detection of chemical trails produced by conspecifics or prey (Schwenk 1994). Odor particles are transferred by the tongue to the vomeronasal organ, which in turn conveys information about the chemicals to the snake's brain (Filoramo and Schwenk 2009). If the tongue is removed or the functioning of the vomeronasal organs is experimentally impaired, male snakes do not trail or court receptive females (Halpern 1992). Most snakes have a mating system that involves males searching for females (see Chapter 14), and the tongue is sexually dimorphic in some species, being longer and more deeply forked in males than in females



Figure 13.33 European wall lizard (*Podarcis muralis*). Members of the genus *Podarcis* have been widely used in studies of chemical communication. (Photograph by Kentwood D. Wells.)

(Smith et al. 2008). Snakes also tongue flick in air to detect volatile chemical cues. The tongue-flicking behavior creates vortices of moving air that allow a snake to sample airborne chemicals and convey them to the vomeronasal system (Ryerson 2014). Hence, the common assumption that airborne pheromones can be detected only through the main olfactory system (see Shine and Mason 2012) is probably incorrect.

Male snakes do not produce signals to attract mates. Some species, such as the red-sided garter snake (*Tham-nophis sirtalis parietalis*), form large mating aggregations as they emerge from communal hibernation dens, but males of most species search for widely dispersed females. It has been known for decades that male snakes follow chemical trails produced by pheromones in the skin of females. Skin pheromones produced by females appear to be sufficiently long-lived to allow males to follow pheromone trails for some distance (Wilmes et al. 2012).

Pheromones of female snakes are derived from skin lipids that probably evolved originally to retard cutaneous water loss and secondarily acquired a communication function (Mason and Parker 2010). Pheromones produced by female red-sided garter snakes are composed of nonvolatile chemicals called methyl ketones. The basic structure of these compounds is similar among closely related species of snakes, but pheromones exhibit sufficient quantitative variation in the proportion of different methyl ketones to enable males to identify females of their own species by chemical cues alone (Uhrig et al. 2014). Hence, reproductive isolation in snakes probably is mediated mainly by chemical cues (Shine et al. 2002; Gabirot et al. 2012).

Once a male snake has located a female, a period of courtship follows (**Figure 13.34**). As with trailing of females, intensive courtship in males is influenced by chemical signals produced by the female, which in turn are mediated by female reproductive hormones, especially estradiol (Parker and Mason 2012; Uhrig et al. 2012). Courtship usually begins with the male exploring the female's body with tongue flicks, particularly on the dorsal surface. The male then engages in a period of tactile stimula-

Figure 13.34 Courtship by redsided garter snakes (*Thamnophis sirtalis parietalis*). (A) Multiple males court a larger female (center). (B) Male tongue-flicking a female to detect her skin pheromones. (Photographs by Christopher Friesen.)

tion, the details of which vary among families. The male of most species moves forward along the back of the female, rubbing his chin against her body and sometimes making a series of jerking movements with his head. In some colubrid snakes, the male also lies on top of the female and sends waves of muscle contractions forward or backward along his body. Other types of body movements, sometimes described as twitching or spasmodic contractions, have been observed for colubrids, elapids, and viperids. Some male colubrids also bite the female gently, usually when the female is coiled up and not in the proper position to be courted by the male. Male boids have hard spurs, remnants of the hindlimbs, that are used to stroke the female during courtship. The final stage of courtship begins with the male using his tail to search for the female's cloacal opening before inserting one of his hemipenes for copulation (Gillingham 1987).

Pheromones of female red-sided garter snakes lack squalene, which is present in the skin pheromones produced by males. Some males lack squalene when they first emerge from the den, and the pheromones of these males mimic the pheromones of females. These "she-males" are often courted by other males in mating aggregations. Originally this chemical mimicry was thought to enable males to avoid being pushed aside by other males and increase their



(B)

chances of mating with a female, but subsequent studies have failed to reveal a clear mating advantage for she-males (Shine et al. 1999). However, it may be that female mimicry confuses other courting males, thereby increasing the chances that unmated females will be available once a male is ready to begin courtship (see Chapter 14 for additional discussion of the mating system of the red-sided garter snake). Another hypothesis is that males newly emerged from hibernation sites are cold, and inducing other, warmer males to court them allows them to warm up more quickly, thereby enhancing their own ability to court females (Shine et al. 2012).

Chemical communication does not end once copulation has been completed. Males of some snakes produce a hard copulatory plug composed of proteinaceous and lipid compounds that is inserted into the female's cloaca after she is inseminated. These plugs reduce the potential for sperm competition, especially in species in which multiple males are in close proximity to females. Copulatory plugs have been studied mainly with red-sided garter snakes. The plug may remain in the female's cloaca for up to 4 days and inhibits mating by other males, which can distinguish between chemical trails of mated and unmated females (O'Donnell et al. 2004). Initially it was thought that the plug simply served as a mechanical block that prevented other males from copulating with a recently mated female, but Patrick Ross and David Crews (1977) argued that the copulatory plugs of Thamnophis radix contain a pheromone that inhibits courtship by males. More recent work with T. sirtalis parietalis supported the original interpretation of plugs as mechanical block to mating and revealed that fluids transferred during copulation, and not the plug itself, were responsible for the decreased attractiveness of mated females (Shine et al. 2000). Another hypothesis for the function of mating plugs is to prevent sperm from leaking out of the female's cloaca, thereby increasing a male's chances of fertilizing her eggs (Friesen et al. 2013).

Acoustic communication

Most lizards can detect airborne sounds, but only the nocturnal geckos regularly use acoustic signals for communication. Geckos are unique among lepidosaurs in having vocal cords and therefore are the only lepidosaurs that can produce sounds more complex than simple hisses and gasps (Marcellini 1977; Rittenhouse et al. 1998). Lizards in some other families, such as skinks, sometimes produce defensive vocalizations when handled, but only geckos are known to have complex vocal repertoires used in a variety of social interactions. Males of many gecko species are territorial and vocalize to advertise territory ownership and to attract females. These vocalizations have been termed multichirp calls in the gecko behavior literature and are functionally equivalent to the advertisement calls of frogs. They generally consist of a repeated series of short notes with a relatively broad frequency spectrum.

Although call structure is similar in many geckos, calls of sympatric species appear to be sufficiently different to be species-specific mate recognition signals. Most reports indicate that these calls are directed toward particular males or females, but in some cases they are given spontaneously as well. Gecko vocalizations generally are poorly studied, and it is not clear that all vocalizing geckos use their vocalizations as intraspecific communication signals. Pygopodids—elongated, legless lizards that do not resemble other geckos—produce sounds when handled by human observers, and their ears are capable of hearing these sounds, but the behavioral function of the sounds is unknown (Manley and Kraus 2010).

Male barking geckos (Ptenopus) in southern Africa emerge from burrows in the desert at dawn and dusk and call in choruses reminiscent of frog choruses (Haacke 1969). These geckos have the most complex sound-producing organs described in lizards, with vocal cords and a larynx somewhat like a frog's in structure (Rittenhouse et al. 1998). The calls of Ptenopus are unusually loud for the size of the animal, perhaps being amplified by expansion of the trachea and throat during vocalization. Calling at the entrance of a burrow may amplify the sound as well. Like many frogs, male barking geckos have bright vellow color on their throats, which is absent in females and probably serves as a visual territorial signal. Males defend the areas around their burrows as territories, with large males being more successful than small males in winning fights and acquiring mates. The role of female choice in determining male mating success in barking geckos is unknown, although females have been observed approaching calling males from a considerable distance (Hibbitts et al. 2007).

Some geckos give distinct *churr* calls during aggressive interaction between males. These often consist of a series of notes that are longer than those of the multichirp calls, with the calls being broken into a series of pulses. *Churr* calls are used both in intraspecific aggressive encounters and to threaten humans or other predators. Both males and females of some species also produce single-chirp calls that resemble individual notes of the advertisement call; the function of these calls is unclear, but they appear to be used in a defensive or aggressive context (Marcellini 1977).

An especially complex vocal repertoire is found in the large Asian tokay gecko (*Gekko gecko*). This species is unusual in having a multipart advertisement call that begins with a rattling sound that is followed by a series of two-syllable chirps, the *to-kay* sound that gives the lizard its common name (Tang et al. 2001). Little is known about the functional significance of these call components, but it is possible that this species resembles some frogs in using different parts of the advertisement call to convey aggressive messages to males and attractive messages to females. Geographic variation in tokay gecko calls corresponds to color and genetic differences, suggesting that more than one species is present in Asia (Yu et al. 2011).

SUMMARY

Amphibians and reptiles use a wide array of communication signals that convey information to conspecifics about species identity, sex, size, age, territory ownership, sexual receptivity, and even individual identity.

Many sensory modes are used for communication, with the most common being visual, chemical, acoustic, and tactile signals.

Visual and acoustic signals can be used at close range or from a distance; chemical and tactile signals usually function at close range.

Communication by amphibians and reptiles is subject to many physical and biological constraints.

Body size constrains signal production; small animals communicate over shorter distances than large animals.

Physiological constraints include temperature, which affects all aspects of the biology of ectotherms, and the energetic costs of signal production.

An ecological constraint on signaling is the risk of predation; predators may home in on the signals produced by amphibians and reptiles. Acoustically signaling animals such as frogs may alter their calls to reduce the chances of predation.

Predation also shapes the evolution of visual signals in animals such as lizards, which may have less conspicuous signals in areas with many predators than in those with few predators.

Once a signal is produced, it is subject to interference by noise before it reaches the receiver. Noise can affect any signal modality, but acoustic and visual noise are the best studied.

A major source of acoustic noise for frogs is waterfalls or swiftly flowing water, which can mask frog calls. Frogs have evolved a variety of strategies for dealing with acoustic noise, including altering the frequency of their calls and using visual signals in noisy environments.

The calls of other frogs in the same environment are a biological source of acoustic noise. Many frogs adjust the timing of their calls to avoid acoustic interference from other species.

Another strategy to reduce acoustic interference is to use vibrational communication, which provides a largely noise-free communication channel. Some frogs are highly sensitive to vibratory signals.

Anolis lizards often display in visually noisy environments created by windblown vegetation; their signals have evolved movement patterns that contrast with the background visual noise.

Some lizards alter the temporal pattern of their visual signals in response to changes in visual noise.

Salamanders communicate with chemical, tactile, and visual signals, but not with acoustic signals.

Plethodontid salamanders use mostly chemical and tactile signals in courtship, although some species have simple visual signals as well.

- Chemical signals in plethodontids are detected by the vomeronasal organ; chemicals are transported by capillary action from a substrate to the vomeronasal organ through the nasolabial grooves.
- Plethodontids can detect both substrate- and airborne chemicals. These signals convey information about species identity, sex, reproductive status, territory ownership, and sometimes individual identity.
- In all plethodontids, courtship involves the female following the male in a tail-straddling walk. Many male plethodontids have mental glands on the chin, which they use to deliver pheromones to the female, either by slapping the gland on the female's snout or by biting the female and injecting the pheromone into her bloodstream.
- Some plethodontids use changes in posture to signal aggression.

Courtship in salamandrids involves a combination of visual, chemical, and tactile signals. In Old World newts, small species rely mostly on chemical signals, whereas large species often have complex visual displays and have evolved large crests on the body and tail and often are brightly colored.

Frogs and toads are well known for their vocalizations.

The calls of most frogs are produced by air being pushed out of the lungs through the larynx, which causes the vocal cords and associated cartilages to vibrate.

Most male frogs have vocal sacs that amplify their calls. Some female frogs call, but they lack vocal sacs.

Frog calls have a variety of forms—whistles, clicks, trills, and croaks. Many frog repertoires are complex, consisting of several distinct types of calls.

Advertisement calls are the most common vocalizations given by frogs; they are directed at both male and female receivers.

Frogs often call in choruses of many individuals, which can result in considerable acoustic interference. Males often adjust the timing of their calls to avoid such interference.

Advertisement calls are species-specific, with both frequency and temporal information being important in species recognition.

The auditory nerves and brains of frogs are tuned to the specific frequencies of their calls, thereby enhancing

call recognition. Temporal patterns of conspecific calls are decoded in the central nervous system.

Many male frogs have distinct aggressive calls, which they emit when competing for territories or for females; some aggressive calls are graded, with changes in call structure reflecting changes in aggressiveness.

Frogs have a variety of other call types, including courtship calls that males give in close interactions with females.

Some female frogs also call, often in response to the calls of males. Because females lack vocal sacs, their calls are very soft.

Recent research has shown that both visual and chemical signals are more important for anurans than was previously thought.

The many frog species employ a variety of visual signals, including brightly colored vocal sacs or throats, foot-waving displays, postural changes, and movements of the front feet.

Some frogs are sexually dichromatic, usually with males being much brighter than females. In some species, such as the European moor frog, bright coloration enables males to distinguish females from males and thereby avoid trying to mate with other males.

The visual signals of poison frogs in the family Dendrobatidae are unusual in that bright colors not only advertise the frogs' distastefulness or toxicity to predators, but also may be used in mate choice and territorial defense.

Chemical communication has been the least studied type of communication in frogs. Many male frogs develop special glands in the breeding season that probably produce pheromones attractive to females, but the function of most such glands is poorly understood.

Turtles use mostly tactile, chemical, and visual signals, but a few species produce vocal signals. Research on communication among turtles has been limited mostly to courtship behavior and occasional aggressive interactions.

Tactile communication involves males biting females during courtship, rubbing their heads against the female's head, or touching the female's head with elongated front claws.

Visual communication involves head-bobbing displays and displays of bright colors on the head, neck, and front limbs of the male.

Some male turtles develop specialized glands during the breeding season that probably produce pheromones that are attractive to females, but the functions of these chemical signals have not been well studied.

Only tortoises and a few species of aquatic turtles produce acoustic signals. These signals are often used in aggressive interactions among males, and in some cases as communication signals between females and their young.

Crocodylians are unusual in the extent to which they combine various modes of communication tactile, visual, and acoustic—into complex displays.

Alligators are particularly vocal, giving a wide range of vocal signals, some of which carry over long distances.

Crocodiles tend to be less vocal than alligators, and rely more on visual and tactile interactions in courtship and aggressive interactions.

Female crocodylians communicate with their offspring, and the offspring communicate with one another, through acoustic signals.

The evolution of communication signals in lepidosaurs is influenced by their sensory systems.

Many lizards are among the most colorful of reptiles and rely heavily on visual signals for communication.

Iguanian lizards use the tongue for transport of prey into the mouth, so the use of the tongue as a chemosensory organ is constrained. Non-iguanian lizards and snakes generally capture prey with their jaws, so in these species the tongue is free to evolve as a specialized chemosensory organ, especially in snakes.

Many male iguanians are territorial during the breeding season and often use visual signals to advertise their territories and attract mates. Signals include headbobbing displays, displays of colorful structures such as dewlaps, and displays of bright body coloration.

Aggressive displays of iguanian lizards often involve displays of color on the body, as well as open-mouth threat displays that may provide information on a male's fighting ability.

Many female iguanians develop color signals during the breeding season, often to signal their lack of receptivity toward courting males.

Male *Anolis* have colorful dewlaps that are extended in courtship and aggressive displays. Colors have evolved to contrast with the background colors in the environment. Dewlap colors are species-specific and play a major role in species recognition.

Chameleons are famous for their ability to rapidly change color, especially during aggressive interactions, when changes in aggressiveness may be signaled by spectacular changes in body and head colors.

Non-iguanian lizards were previously thought to rely mostly on chemical signals, but recent research has shown that non-iguanian lizards also make extensive use of visual signals, including displays of head and body coloration and even markings that reflect UV wavelengths.

Both iguanian and non-iguanian lizards use chemical signals. Many male lizards have femoral pores on their

hind legs that deposit waxy secretions on rocks or other substrates that advertise ownership of territories.

Femoral gland secretions contain steroids such as cholesterol, and each species typically has a unique chemical profile. In some cases, individual lizards have unique chemical profiles that allow for individual recognition.

Snakes rely heavily on chemical signals, and their tongues function solely as chemosensory organs. Males

use their tongues to track other individuals, especially females during the breeding season.

Receptive female snakes produce pheromones in their skin that attract males and enable males to track their movements.

Acoustic communication in squamates is limited to nocturnal geckos, which often have complex repertoires of vocalizations resembling those produced by frogs.

Go to the *Herpetology* Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

14 Mating Systems and Sexual Selection

n 1871 Charles Darwin published *The Descent of Man, and Selection in Relation to Sex.* The book set off a storm of controversy because of its discussion of human evolution, but more than half the book was devoted to the study of animal behavior and, in particular, Darwin's theory of **sexual selection**. Although this part of the book was much less controversial at the time, it has proved to be one of Darwin's most enduring contributions to biology. Indeed, the continuing influence of his theory of sexual selection presented in his more famous book, *On the Origin of Species*, published in 1859.

Darwin formulated his theory of sexual selection to explain the evolution of certain traits in animals that could not be explained by the action of natural selection. Naturalists had long recognized that males and females of many animals do not look exactly alike. Often males are larger, more brightly colored, or equipped with special weapons such as horns and antlers. Darwin's book provided a survey of sexual dimorphism and secondary sex characters of all sorts of animals. Although he focused heavily on birds and mammals, he included some herpetological examples (Figure 14.1). Darwin attributed the elaborate horns of male chameleons, the colorful tail fins of male newts, and even the voices of male frogs to the action of sexual selection. Darwin argued that such traits could not have evolved through the action of natural selection, which generally would favor traits that increase the survivorship of individuals. Indeed, many of these traits might actually decrease individual survivorshipfor example, brightly colored males might be more vulnerable to predators, or males might injure or kill one another with their dangerous weapons. He concluded that such traits, which he called secondary sex characters, had evolved because they increase a male's chances of mating with females, thereby increasing the male's reproductive success even at the possible cost of his own reduced survivorship.

Darwin recognized two components of sexual selection that could lead to the evolution of secondary sex characters and other sexually dimorphic traits, such as differences in body size. The first was competition among males for access to females. This idea was relatively noncontroversial, because 19th-century naturalists were well aware that males of many animals fight vigorously during the breeding season for control of females. Such fighting clearly could lead to selection for effective weapons. However, Darwin suggested that more subtle forms of competition were important as well, such as displays directed at other males. The second component of sexual selection was female choice. Darwin argued that females of many animal species compare the displays or other traits of males and choose to mate with those they judge to be the most attractive or strongest individuals. This idea was more controversial at the time, in part because Darwin attributed to animals a sense of beauty equivalent to that of humans. Even some of Darwin's strongest supporters parted company with him on this issue, and the study of female choice languished for nearly a century before eventually becoming a major focus of modern studies of sexual selection.

During this time the study of sexual selection was not a major focus of herpetological research, but one of the few early herpetologists who did understand its importance was G. Kingsley Noble, who devoted an entire chapter of his book *The Biology of the Amphibia* (1931) to secondary sex characters. Noble also conducted the first detailed experimental study of the functions of sexually dimorphic colors of lizards (Noble and Bradley 1933). The modern era of herpetological research on mating systems and sexual selection began in the late 1970s with the appearance of several major papers on the social behavior of salamanders (Arnold 1976; Halliday 1977), frogs (Wells 1977a,b, 1978; Howard 1978a), and lizards (Stamps 1977). These have been followed by reviews dealing with mating systems and sexual selection in both amphibians



Figure 14.1 Examples of sexually dimorphic structures of amphibians and reptiles. These illustrations are from Charles Darwin's *The Descent of Man, and Selection in Relation*

to Sex (1871). Males are shown at the top of each pair. (A) Great crested newt (*Triturus cristatus*). (B) Owen's chameleon (*Trioceros owenii*, formerly *Chamaeleo oweni*).

(Verrell 1989; Halliday and Tejedo 1995; Sullivan et al. 1995; Wells 2007) and reptiles (Olsson and Madsen 1998).

This chapter focuses on the mating systems of amphibians and reptiles and the relationship of these mating systems to the process of sexual selection. Rather than discussing each group separately, the chapter is organized around several major conceptual themes. The first section reviews modern thinking about sexual selection in the context of mating system organization. This is followed by a review of the major types of mating systems found in amphibians and reptiles. The third section discusses the major determinants of variation in male mating success in different types of mating systems, including the importance of female choice. The final section deals with the evolution of sexual dimorphism and the influence of sexual selection on particular morphological, physiological, and behavioral traits.

14.1 ■ The Relationship of Mating Systems to Sexual Selection

Sexual selection is a form of directional selection that acts on genetically variable phenotypic traits that affect the reproductive success of individuals of one sex. In other words, if increased fighting ability, brighter coloration, or louder calls tend to increase a male's chances of acquiring a mate and contributing offspring to the next generation, then these traits can be considered sexually selected traits (Andersson 1994). Sexual selection, therefore, is like natural selection in being an evolutionary process that results in changes in gene frequencies within populations. However, different components of selection often work in opposite directions because of the costs imposed on an animal by sexually selected traits. For example, the production of loud calls by male frogs may be favored by sexual selection if this enhances a male's attractiveness to females. Such calls can be costly, however, because they can attract predators or deplete a male's energy reserves, thereby reducing his chances of survival. Indeed, most sexually selected traits tend to be costly, and some traits may be fully expressed only in males that are in good physical condition.

Males usually are subject to more intense sexual selection than females because individual variation in mating success is greater for males than for females. This difference derives in part from differences in the amount of energy that males and females invest in the production of gametes (sperm and eggs). Females typically produce eggs that are provisioned with yolk reserves to support growth and development, and energy investment may be even greater if embryos are retained in the female's body and provided with nutrition, or if the female engages in extensive parental care after eggs are laid. Consequently, the reproductive success of females is limited mainly by energy intake, and it may take some time for a female to produce a new clutch of eggs once she has laid her first clutch. If one male can fertilize all of her eggs, then a female's reproductive success is not likely to be strongly affected by the number of times she mates. Hence, selection for acquisition of multiple mates will be relatively weak in females.

Males, on the other hand, produce sperm that have only enough energy reserves to make their way to an egg to be fertilized. Hence, the cost of sperm production generally is lower than the cost of egg production, even though males produce millions of sperm. Males usually have enough sperm to fertilize the eggs of many females, and a male's reproductive success is largely dependent on the number of mates he acquires. Consequently, traits that enhance a male's ability to acquire many mates are likely to be strongly affected by sexual selection (Andersson 1994; Arnold and Duvall 1994). This is particularly true when the male



contributes little or nothing to parental care, which is the case for most amphibians and reptiles. Under such circumstances, males tend to be **polygynous**—that is, they attempt to acquire several mates in each breeding season, although usually only a small proportion of the males in a population succeeds in doing so. Monogamy, a mating system in which a single male and female remain paired together, is rare among amphibians and reptiles but does occur among some dendrobatid frogs and some lizards.

One way to quantify the relative intensity of sexual selection acting on males and females is to use a Bateman Figure 14.2 Sexual selection in the rough-skinned newt (Taricha granulosa). (A) An adult rough-skinned newt. (B) Distribution of genetically documented mating events for male and female newts. Many males failed to mate at all, whereas all females mated at least once. (C) Plot of reproductive success versus mating success (Bateman gradient). The steeper slope for males indicates that sexual selection is stronger in males than in females. (After Jones et al. 2002b; photograph by Todd Pierson.)

gradient, a method first applied to fruit flies by Angus J. Bateman (1948). Bateman graphed the relationship between the number of mates obtained by males and females and the number of offspring produced. If sexual selection acts primarily on males, the slope of the Bateman gradient is expected to be greater for males. In other words, the number of mates should have a stronger influence on male reproductive success than on female reproductive success. A study that used genetic techniques to determine the paternity of larvae of the rough-skinned newt (Taricha granulosa; Figure 14.2A) found that both males and females frequently acquired more than one mate, although multiple mating was more common among females (Figure 14.2B). As predicted by sexual selection theory, the number of mates had a much stronger effect on the reproductive success of males than of females (Figure 14.2C) (Jones et al. 2002b). Similar results were obtained in a study of marbled salamanders (Ambystoma opacum) (Crowshaw 2010), whereas in studies of tiger salamanders (A. tigrinum) and small-mouthed salamanders (A. texanum), Bateman gradients were similar for males and females (Gopurenko et al. 2007; Williams and DeWoody 2009).

14.2 Mating Systems of Amphibians and Reptiles

The behavioral tactics used by males to acquire mates depend on the temporal and spatial distribution of females (Wells 1977a, 2007; Duvall et al. 1993; Mathis et al. 1995; Sullivan et al. 1995). Females can be aggregated or dispersed in space, and they may be available to males for a long time or only very briefly. When the breeding period is short and large numbers of females are found together in one place, the usual mating system is an **explosive mating aggregation** characterized by scramble competition among males for the gathered females (see the next section).

At the opposite extreme, females may be widely dispersed but available over a longer breeding season. In such cases males have few options other than searching for receptive females over large areas. When females are moderately aggregated in space and available over a relatively long period, a variety of mating systems are possible. One option is for a male to search for an individual female, follow her, and actively guard her from other males until the female is ready to mate. If females live in relatively small, stable home ranges that are spatially aggregated, males may encompass the home ranges of several females within a defended territory, effectively resulting in multiple mate guarding. In some groups, males use acoustic or visual signals to attract mates. Sometimes signaling males are widely dispersed, but many species aggregate into choruses or gather at traditional display areas, called leks, to attract females. Finally, if males can monopolize resources needed by females for successful reproduction, such as good egg-laying sites, then males will defend territories containing those resources.

The use of DNA fingerprinting and other molecular techniques to determine the paternity of offspring has revolutionized the study of mating systems in all vertebrates. Genetic studies of many bird species, for example, have shown that seemingly monogamous species often engage in extra-pair mating, and multiple paternity of egg clutches is common. Consequently, it is important to differentiate between a species' behavioral mating system and its genetic mating system. Behavioral monogamy is rare in amphibians and reptiles, and even the most consistently monogamous lizard-the Australian sleepy lizard (Tiliqua rugosa)—exhibits some extra-pair mating (Bull 2000). On the other hand, another Australian skink, Egernia stokesii, lives in stable social groups of up to 17 individuals, yet exhibits a surprisingly high level of genetic monogamy within a breeding season (Gardner et al. 2002).

Many species of crocodylians, turtles, lizards, and snakes exhibit both multiple mating and multiple paternity of offspring (Davis et al. 2001; Olsson and Madsen 2001; Pearse and Avise 2001; Refsnider 2009), as do salamanders (Croshaw 2010). In cases where multiple paternity occurs, sperm of different males can be evenly mixed, with each male having an equal probability of fathering offspring. It also is possible for the sperm of either the first male (Jones et al. 2002a) or the last male (Pearse and Avise 2001) to fertilize a disproportionate number of a female's eggs. The variability of genetic mating systems and the frequency of multiple paternity of egg clutches has important implications for the evolution of sperm competition, as we will discuss later in this chapter.

Scramble competition mating systems

When receptive females are available to males for relatively short periods of time and are spatially aggregated, often the most efficient way for males to obtain mates is some form of scramble competition in which males compete to locate females as quickly as possible, invest relatively little time in mating with each female, and attempt to mate with as many females as possible. In some cases there may be limited guarding of individual females and struggles among males for access to mates, but violent aggression tends to be rare. Males often outnumber females, sometimes by as much as 10 to 1. There are several possible reasons for these highly skewed sex ratios, including greater annual mortality of females, delayed sexual maturity in females, and a tendency for males to breed every year, whereas females sometimes do not. In addition, individual females often are receptive for relatively short periods or may leave the breeding area after mating. Because many females are mating simultaneously, opportunities for multiple mating by males often are limited, and many males do not mate at all. This type of mating system also provides few opportunities for females to choose among the available males, and male-male



(B)



Figure 14.3 Mating behavior of the American toad (Anaxyrus americanus). (A) Pairs of males and females in amplexus are aggregated around the oviposition site, while unmated males attempt to displace mated males from their females. (B) Two males compete for the opportunity to fertilize the eggs of a single female. (Photographs by Kentwood D. Wells.)

competition tends to be the most important determinant of variation in male mating success.

SCRAMBLE COMPETITION AMONG ANURANS Scramble competition occurs in many species of anurans that form explosive mating aggregations in early spring, such as North American wood frogs (Rana sylvatica), European common frogs (R. temporaria), American toads (Anaxyrus americanus), and European common toads (Bufo bufo) (Davies and Halliday 1979; Howard 1980, 1988; Ryser 1989; Sztatecsny et al. 2006). This type of mating system also is found among desert-dwelling anurans that use temporary rain pools for breeding, such as spadefoot toads (Spea, Scaphiopus) (Sullivan 1989), and tropical species that breed only after heavy rains, such as the Neotropical treefrog Agalychnis saltator (Roberts 1994). The selective pressure favoring a very short breeding period often is the short life of the breeding pond, but other factors, such as the danger of cannibalism by larger conspecifics or predation by other species, can select for synchronous breeding as well (Petranka and Thomas 1995).

Sometimes hundreds of individuals arrive at a pond on a single night. Breeding periods range from 1 night in some species to nearly 2 weeks in others. Males generally arrive slightly earlier than females and usually greatly outnumber them. Often there is a mad scramble among males searching for females (Figure 14.3A). Males move around the pond while calling, grabbing any other individuals they encounter, sometimes even grabbing individuals of the wrong species (Marco and Lizana 2002). Males are quickly released, but females are tightly clasped and defended against other males attempting to displace the clasping male. Several males sometimes struggle for control of a single female (Figure 14.3B). Because of the skewed sex ratios in these aggregations, most males fail to mate in any given season, and the short breeding period results in relatively few males obtaining more than one mate (Figure 14.4).

SCRAMBLE COMPETITION AMONG SALAMANDERS Some ambystomatid salamanders that breed in winter or early spring also form explosive mating aggregations (Verrell 1989; Sullivan et al. 1995). In contrast to anurans, these salamanders have internal fertilization, and mating may

be separated from egg laying by several days. Often hundreds of salamanders move into a breeding pond on a single night. As in explosive-breeding frogs, males usually outnumber females.

The behavior of the spotted salamander (Ambystoma maculatum) is typical of explosive-breeding salamanders. Males mill about on the bottom of the pond searching for females. When a female is encountered, a male deposits several mushroom-shaped spermatophores around the female. Fertilization occurs when the female picks up the cap of the spermatophore, which contains the sperm mass, with the lips of her cloaca. Sometimes several males court a female simultaneously, resulting in a large number of spermatophores being clustered in a small area (Figure 14.5) (Arnold 1976), and a female may pick up spermatophores from more than one male (Myers and Zamudio 2004). Pushing and shoving among males competing for females are common as well. This form of scramble competition occurs in other ambystomatids with short breeding seasons, such as A. macrodactylum and A. talpoideum (Verrell and Krenz 1998).

Some hynobiid salamanders form explosive mating aggregations, but these have external fertilization, so rather than scrambling to court females, groups of males gather around egg sacs immediately after they are deposited by a female and compete to release sperm onto the eggs (Hasumi 1994). Usually the first male to encounter an egg sac tries to prevent other males from depositing sperm (monopolist tactic), whereas later arriving males attempt to forcibly fertilize eggs (scrambler tactic). When the sex ratio in a breeding group is heavily skewed toward males, the result is the formation of mating balls in which multiple males clasp the same egg sac (Hasumi 2001).

SCRAMBLE COMPETITION AMONG REPTILES In contrast with amphibians, most reptiles do not have short breeding seasons or form dense aggregations that are likely to result in scramble competition for mates, but there are exceptions. The best example of explosive mating aggregations comes from studies of red-sided garter snakes (*Thamnophis sirtalis parietalis*) in Manitoba. This species has been used as a model system to investigate the behavior and endocrinol-



Figure 14.4 Mating success of male

anurans. Bars show the distribution of the number of mates per male in pondbreeding anurans with explosive breeding periods (*Bufo bufo* and *Rana sylvatica*) and prolonged breeding periods (*R. clamitans* and *R. catesbeiana*). (After Wells 1977b; Howard 1978a; Davies and Halliday 1979; Howard 1980.)



Figure 14.5 Patterns of spermatophore deposition by the spotted salamander (*Ambystoma maculatum***).** Males scatter large numbers of spermatophores around a female on the bottom of a pond. Blue circles indicate single spermatophores. Red circles indicate spermatophores deposited on top of other spermatophores, a form of sexual interference. Males are oriented randomly with respect to the female during spermatophore deposition, as indicated by the short lines on the circles. (After Arnold 1976.)

ogy of reproduction by snakes (Mason and Parker 2010). These snakes gather by the thousands in communal hibernation dens during the winter. When spring arrives, males emerge before females and wait around the entrances of the dens to intercept females (**Figure 14.6**). Females produce a pheromone in the skin that is attractive to males. Large



Figure 14.6 An explosive mating aggregation of red-sided garter snakes (*Thamnophis sirtalis parietalis*). In Manitoba, Canada, thousands of these snakes overwinter in communal hibernation dens. In the spring, males (which emerge before females) gather at the den entrance, where they intercept and mate with the females. (Photograph by Christoper Friesen.)

females are more attractive than smaller ones, a result of higher concentrations of a key chemical component of the mate-attracting pheromone (LeMaster and Mason 2002). Large males tend to focus their attention on the largest females, whereas smaller males are relegated to courting small females, leading to size-assortative mating in the population (Shine et al. 2001b). When females are courted near the hibernation den, the result can be a writhing ball of snakes, with many males jostling one another but with little overt aggression. Females resist this constant harassment by males and quickly move away from the den, where they are courted by smaller groups of males. Much of the actual mating appears to take place in these smaller groups away from the den site (Shine et al. 2001a).

Female receptivity is relatively brief, in part because females resist further mating attempts once they have mated

(Mendonça and Crews 2001). Males transfer a pheromone during mating that renders females unattractive to other males, and males block the cloaca of the female with a gelatinous plug that further reduces the chance that she will immediately mate with another male (Shine et al. 2000b). The main advantage of a mating plug is that it frees the male from having to guard his mate from other males and allows him to seek additional matings. An unusual feature of this mating system is that males often are seen courting other males. This odd behavior results from production of a female-like pheromone by males just after they emerge from hibernation. This pheromone may confuse other males, reducing their mating success and increasing the number of receptive females that are available when the newly emerged males are ready to initiate courtship (Shine et al. 2000a).

The mating systems of most turtles are poorly known, but some aquatic species in which males appear to search over large areas for mates display a form of scramble competition. When males come upon females that are spatially concentrated, as in a small pond, the mating system is best described as scramble competition. Promiscuous mating is common and often results in multiple paternity of egg clutches (Pearse and Avise 2001). Similar competition occurs in sea turtles in which males and females aggregate offshore from nesting beaches (Jessop et al. 1999). Often several males attempt to court the same female and interfere with the mating attempts of competing males (**Figure**



Figure 14.7 Scramble competition by green sea turtles (*Chelonia mydas*). Males and females aggregate near nesting beaches, where males compete to mate with females before the individuals disperse widely across the ocean. Here a mating (center) and secondary (top) male compete for the female on the bottom. (Photograph © Gary Bell/Corbis.) **14.7**); multiple paternity of egg clutches is common (Lee and Hays 2004). The mating system of some dense populations of tortoises also appears to be scramble competition, with males chasing numerous males and females until they locate a receptive mate (Johnson et al. 2009).

Mate searching

When animals are widely dispersed in their habitats, males and females may have difficulty finding one another. If males do not produce long-distance signals to attract females, they find mates by searching for them. Extended mate searching grades into scramble competition, depending on the degree of spatial clumping of females.

MATE SEARCHING BY AMPHIBIANS Male red-spotted newts (*Notophthalmus viridescens*) move about on the bottom of a pond, approaching any newt moving nearby (Massey 1988). Usually males seize females and hold them in amplexus (see Figure 13.10B). This posture allows the male to stimulate the female with courtship glands on the side of his head, which he rubs against the female's snout. Amplexus also is a form of mate-guarding behavior, because clasping the female makes interference by other males difficult. One field study showed that males with wide tail fins were most successful in acquiring mates, perhaps because the tail fin facilitates swimming during mate searching. Other newts, such as the smooth newt (*Lissotriton vulgaris*), also engage in mate searching but do not clasp females (Verrell 1989).

MATE SEARCHING BY REPTILES Mate searching appears to be the predominant mating system of snakes, most of which are solitary (Gregory et al. 1987). Prairie rattlesnakes (Crotalus viridis viridis) in Wyoming emerge from hibernation dens in the spring and immediately begin moving over relatively long distances in search of rodents, their principal prey. Males and females are widely dispersed over the available habitat by the time the mating season begins in midsummer. For a period of 6 to 8 weeks, males move around more than do females, searching for mates. Data from individuals equipped with radio transmitters showed that most males did not succeed in finding even a single female, whereas most females did mate and presumably produced young. Because the location of females is unpredictable, models of searching behavior suggest that the best strategy for males would be to move in a relatively straight line until a female is encountered, and this appears to be what prairie rattlesnakes do (Duvall et al. 1992). The likelihood of male rattlesnakes finding females once they are nearby is enhanced by the ability of males to follow chemical trails produced by pheromones in the female's skin (Mason 1992). Mate searching by snakes often results in males having much larger home ranges and moving longer distances than females (see Chapter 12).

Male lizards that forage over wide areas for food, such as teiids, lacertids, varanids, and scincids, usually search for females over relatively large areas. Both males and females of the Australian water skink (*Eulamprus heatwolei*) are relatively sedentary and occupy overlapping home ranges. Home ranges of males generally are larger than those of females; on average, the home ranges of males overlap those of 2–3 females. Some males are territorial, whereas others adopt a floater tactic and search for females. Mating with multiple partners is common, and most egg clutches are fathered by more than one male (Morrison et al. 2002). Males that exhibited high levels of activity and movement were the most successful in acquiring mates, probably because they encountered the most females (Keogh et al. 2012). When males were given the opportunity to compete with one another for access to females, large males fathered more offspring than did small males (Keogh et al. 2013).

In contrast to these relatively sedentary skinks, monitor lizards tend to be highly mobile. Male white-throated monitors (*Varanus albigularis*) in the Namib Desert sometimes move more than 6 km in a single day while looking for females, and their home ranges may cover as much as 18 km². Receptive females are reported to make themselves conspicuous by climbing into trees, where they release an airborne pheromone that attracts males (Phillips 1995; Phillips and Millar 1998).

Mate guarding

When searching for mates is costly, a male may enhance his reproductive success by investing time in guarding individual females and preventing other males from mating with them. The amount of time and energy invested in mate guarding depends not only on the density of male competitors, but also on the availability of additional females as potential mates. When male competitors are abundant and females are relatively scarce, selection tends to favor prolonged mate guarding. When male competitors are scarce but females are relatively abundant, males may guard individual females only briefly and invest more time in searching for mates.

MATE GUARDING BY AMPHIBIANS The amplexus behavior of red-spotted newts, which enhances the ability of a male to monopolize a female, is one form of mate guarding. Several other types of mate-guarding behavior have been reported for salamanders (Verrell 1989; Halliday and Tejedo 1995; Houck and Arnold 2003). Male tiger salamanders (Ambystoma tigrinum) court females individually and, if approached by other males, sometimes physically push a female away from competitors. Males of other ambystomatids and some salamandrids (Pleurodeles, Taricha) clasp females during early stages of courtship and sometimes carry the female away from competing males. Wrestling bouts between intruding and clasping males also have been observed (Houck and Arnold 2003). Males of many species of plethodontid salamanders are very aggressive toward other males, chasing and biting any individuals that intrude on their courtship attempts. Males of some of these species



Figure 14.8 Male and female *Atelopus varius* in amplexus. Males often become emaciated after long periods of amplexus. (Photograph by Martha L. Crump.)

have enlarged teeth and jaw muscles that are used in aggressive encounters between males and during courtship of females (Deitloff et al. 2014).

Most anurans have some sort of amplexus in which the male clasps the female to fertilize her eggs (see Chapter 8). Not only does this behavior help position the male to release sperm directly over the eggs being released by the female, it also prevents other males from acquiring that female as a mate. This type of mate guarding is taken to unusual extremes in the Neotropical bufonid genus Atelopus (Figure 14.8). These toads are terrestrial for most of the year but move briefly to streams to breed during the wet season. Males defend territories against other males throughout the year but allow females into their territories. When a male encounters a female, he usually tries to clasp her in amplexus, even weeks or months before the breeding season. Females resist these attempts, but sometimes males succeed in clasping females and remain in amplexus for several weeks, and even for several months in some species (Crump 1988). Clearly this is disadvantageous for the females, because they must carry the males around on their backs for prolonged periods of time. There may be costs to the males as well, such as reduced opportunities to feed. Presumably Atelopus males have adopted this tactic because females are encountered infrequently.

MATE GUARDING BY REPTILES Mate guarding by turtles usually takes the form of aggressive contests for possession of females. For example, aggressive encounters between male wood turtles (*Glyptemys insculpta*) generally result in larger individuals winning fights (Kaufmann 1992). Most of the fights occurred when an intruder challenged a male attempting to court a female. Male tortoises usually inhabit overlapping home ranges, and aggressive contests between males take place almost exclusively during the breeding season in the presence of receptive females (Auffenberg

1977; Ruby and Niblick 1994). Male desert tortoises (*Gopherus agassizii*) move around more than females during the breeding season, and a male often visits several different females. Males sometimes remain for several days in the same burrow with a female. Such cohabitation is rare outside the breeding season and suggests that males are actively guarding females from other males while engaging in periodic courtship behavior to bring them into sexual receptivity (Niblick et al. 1994).

Mate guarding is common among nonterritorial lizards that search for mates in large home ranges. The amount of time that a male remains with an individual female varies considerably. Time spent guarding one female decreases the amount of time a male can search for additional mates. In situations where females are relatively abundant, males would be expected to invest relatively little time in guarding each female. A male *Lacerta schreiberi*, for example, typically remains with a female for only a few hours and aggressively fends off mating attempts by other males (Marco and Perez-Mellado 1999). Some males mate with as many as four different females.

Males of the European sand lizard (*L. agilis*) not only guard females before mating, but also for up to 3 days after mating. The payoff for such prolonged guarding can be large, because mating by a second male anytime within 24 hours of a first mating results in multiple paternity of egg clutches. Females are promiscuous and will mate with any males that court them. Large males acquire more mates and guard females longer than do small males. DNA fingerprinting studies have shown that long periods of mate guarding increase the chances that the guarding male will be the principal father of a female's offspring (Olsson and Madsen 2001).

Mate guarding by males clearly enhances reproductive success, but it also can be energetically costly. Male whiptail lizards (*Aspidoscelis costata*) closely guard receptive females, and guarding males are much more likely to mate than are nonguarding males (Zaldívar-Rae and Drummond 2007). However, males that are guarding females reduce their food intake while increasing rates of aggressive behavior directed toward other males. This suggests that males suffer a double energy cost of lower food intake and higher energy expenditure on fighting (Ancona et al. 2010).

Mate guarding by some skinks is a prolonged affair, and in extreme cases can effectively lead to a monogamous mating system. For example, males of the North American broad-headed skink (*Plestiodon laticeps*) sometimes stay with the same female for more than half of the 2-week mating season (Cooper and Vitt 1997). Males of *Niveoscincus microlepidotus*, a small viviparous skink from Tasmania, guard individual females for up to a month during the breeding season—a strategy that probably prevents them from mating with many different females (Olsson and Shine 1998).

Pair bonds in another skink, the Australian sleepy lizard (Tiliqua rugosa), last even longer. This is a large and relatively sluggish lizard, with a lifespan exceeding 12 years. Both males and females are nonterritorial, living in home ranges that overlap with those of other individuals. During the mating season, males seek out females and remain with them for long periods of time, following them while they search for food and occupying the same retreat sites (Figure 14.9). An unusual feature of this system is that male-female pairs often stay together long after the mating season is over, suggesting that there is some advantage to pairing beyond simple mate guarding (Leu et al. 2010). Although males are occasionally seen fighting with one another, aggressive defense of mates is rare, and even when males leave their mates for some period of time, other males show little interest in them (Murray and Bull 2004). In fact, males that are most persistent in accompanying females are less aggressive than those that do not stay with females (Godfrey et al. 2012).

Another unusual feature of this system is that sleepy lizards repeatedly pair with the same mate in successive years, even though their home ranges overlap those of other potential mates. When mates separate temporarily, they appear to find each other by following chemical trails on the ground, as well as airborne odors. They also search in known locations where their mates are likely to be found. About 80% of all males were consistently monogamous,

> but a few individuals mated with more than one female in a given breeding season (Bull 2000). When pairs were experimentally separated, males were more likely than females to return to their partners (How and Bull 2002).



Figure 14.9 Male Australian sleepy lizard (*Tiliqua rugosa*) following a

female. Males and females of this species often form long-term pair bonds that can last for several years. (Photograph by Dale Burzacott.)

Mate guarding is less conspicuous among snakes than lizards, but occurs in some species (Shine 2003). The prolonged copulation of some snakes (which can last for hours or even days) can be considered a form of mate guarding because it prevents mating by other males (Olsson and Madsen 1998). In some species, mate guarding takes a more aggressive form, including violent fighting for possession of individual females. Male European adders (Vipera berus) often accompany females for several days until they are ready to mate, and also guard them after mating. Males respond very aggressively toward other males and may engage in prolonged wrestling bouts in which the males coil around one another, each attempting to force his opponent to the ground (Figure 14.10). They never bite one another, however. On rare occasions three or even four males may fight one another simultaneously, but most fights involve only two males (Madsen et al. 1993). Fights between males that differ considerably in body size generally are short, with the larger male always winning. Fights between more evenly matched opponents are much longer, sometimes lasting for hours, but again, the larger male almost always wins. Similar fighting among males for possession of females has been reported for many other species of snakes, including boids, colubrids, elapids, and viperids (Schuett et al. 2001).

Multiple mate-guarding strategies

When females are aggregated, males may be able to guard more than one female. Males of most small, insectivorous lizards with a sit-and-wait foraging mode are territorial during the breeding season (see Chapter 12). Males typically spend a lot of time and energy displaying to other males, chasing intruders, and courting females. Food, basking



Figure 14.10 Wrestling contest between two male European adders (Vipera berus). The fight is a test of strength, with each male trying to press his opponent to the ground. (Photograph © Nature Picture Library/Alamy.)

sites, display perches, and retreat sites all are encompassed within their territories. Usually the territories of males are larger than the home ranges of females (Stamps 1977, 1983). There are many examples of male lizards guarding relatively sedentary aggregations of females occupying small home ranges, although it is not always clear whether males are defending groups of females or the resources that attract females (Cuadrado 2001; Kwiatkowski and Sullivan 2002).

The ability of a male to monopolize females, and hence his tendency to mate polygynously, depends in part on the size of home ranges occupied by females. When females have small home ranges, perhaps because food is very abundant, males can monopolize several females while defending a relatively small territory (**Figure 14.11A**). As female home-range size increases, males would have to defend larger and larger areas to encompass several female home ranges. Presumably the costs of territory defense increase with increasing territory size. At some point, defending a territory containing multiple females would require too much energy, or the territory would become so large that a male could not effectively monitor the movements



Figure 14.11 Home-range sizes of lizards. (A) Relationship between home-range size of females and density of females for a variety of lizard species. (B) Relationship between home-range size of females and the ratio of male to female home-range size in a variety of territorial and non-territorial lizard species. As the home-range size of female lizards increases, the ratio of male to female home-range sizes becomes closer to 1:1, as predicted. (After Stamps 1983.)

of intruders. At this point males should concentrate their efforts on defending fewer females more effectively. Hence, the size of male and female home ranges should become more similar as female home-range size increases (**Figure 14.11B**), and males should be less polygynous. At very large female home-range sizes, guarding of individual females becomes a more viable mating strategy than guarding multiple females in a defended territory. In general, actively foraging lizards, such as teiids and lacertids, have larger home ranges than do sit-and-wait foragers (see Chapter 12). These species usually are nonterritorial, with similar homerange sizes in males and females, and males usually guard individual females.

Leks and choruses

Males of some species of amphibians and reptiles with prolonged breeding seasons form aggregations at traditional mating areas and defend small territories where they advertise themselves to prospective mates. In many cases these small territories do not contain resources that are attractive to females, nor are they large enough to encompass the home ranges of several females. Males display to attract mates, and females may base their choice of mates on characteristics of the males themselves, such as their size, color, or vigor of their displays. This type of mating system resembles the leks of some birds and mammals.

The term *lek* is a Scandinavian word used to describe a gathering of males on a traditional display ground to attract females. Females generally are free to move about the lek and choose their mates, although males often try to keep females from leaving their territories (Höglund and Alatalo 1995). Leks of reptiles such as the green iguana (*Iguana iguana*) and the Galápagos marine iguana (*Amblyrhynchus cristatus*) are not necessarily located near areas where females nest or give birth. Male amphibians, on the other hand, often aggregate at ponds, marshes, or streams because females must lay eggs at those sites. Hence, despite their similarity, the leks of reptiles and choruses of frogs may have quite different evolutionary origins.

AMPHIBIAN LEKS AND CHORUSES Several species of Old World newts have lek mating systems. Males gather in limited parts of ponds and defend small territories against other males. Females passing through the area are greeted with elaborate visual displays, including handstands that accentuate the broad tail fins and colorful markings of the males (Figure 14.12). Because these display structures and colors are important for both male–male competition and attracting females, newts with lek mating systems, including *Triturus cristatus, T. marmoratus,* and *Ommatotriton vittatus,* are the most sexually dimorphic newts and, indeed, are among the most colorful of all salamanders (Hedlund and Robertson 1989; Wiens et al. 2011).

The predominant mating system among frogs and toads involves choruses of males that attract females to aquatic breeding sites (Gerhardt and Huber 2002; Wells 2007). Usu-



Figure 14.12 Courtship display of the great crested newt (*Triturus cristatus*). The display emphasizes the size of the male's body, tail, and crest, all of which are important cues for females choosing mates. (After Halliday 1977.)

ally males space themselves throughout the available habitat and defend their calling sites with aggressive calls and physical attacks on intruders. Depending on the species, males call from the water or from elevated perches such as rocks or tree branches. In most species, these calling sites are not immediately adjacent to suitable oviposition sites, so females approach calling males, enter into amplexus, and then carry the males on their backs to egg-laying sites. Once a male has mated with one female, he usually returns to the chorus and advertises for additional mates.

Competition among males in such choruses often takes the form of vocal interactions, with individuals attempting to out-signal their neighbors by increasing the rate, intensity, or complexity of their calls. Direct aggressive competition among males for possession of females is rare, and females have an opportunity to move through the chorus and compare males before selecting a mate. Anuran choruses share many of the attributes of bird leks, although the displays of frogs are primarily acoustic rather than visual.

REPTILE LEKS Some crocodylians form lek-like aggregations along riverbanks and lakeshores during the breeding season, but the mating systems of these animals have not been studied in detail. Males in some populations defend suitable basking sites as territories all year, but males in other populations are territorial only during the breeding season. Females tend to aggregate on the territories of the largest males (Lang 1989). Other crocodylians have mating systems that are closer to resource defense. For example, male American alligators (*Alligator mississippiensis*) defend territories dispersed in marshy habitats and often are out of sight of other males. They rely on long-distance acoustic signals (bellowing) to advertise their territories and attract females.

(A)



(C)



Male green iguanas (*Iguana iguana*) sometimes establish breeding territories in dead trees, which provide conspicuous display sites but no food (Rodda 1992). Males spend most of their time giving head-bob and dewlap displays, defending the boundaries of their territories against other males, and courting females. They can become quite emaciated by the end of the breeding season. Females aggregate in the territories of the largest males, where they eventually mate. Smaller males cannot defend territories but remain at the periphery of territories defended by larger males and attempt to copulate with females as they pass by.

The Galápagos marine iguana (*Amblyrhynchus cristatus*) also has a lek mating system (**Figure 14.13**). Male territories are clustered even when population densities are relatively low, and the location of territories is not related to physical characteristics of the habitat (Wikelski et al. 1996). Males

(B)



Figure 14.13 Lekking behavior of the Galápagos marine iguana (Amblyrhynchus cristatus). (A) A male (right) on his lek breeding territory shows the red breeding coloration characteristic of some populations of this lizard. (B) Two males fighting for possession of a territory. (C) Density of iguanas during the breeding season. Darker gray shading indicates high-density areas where many females congregate; lighter shading represents low-density areas with few females. Territorial males cluster and aggressively defend territories only in the high-density areas. (D) Number of copulations per male per female as a function of the number of males on a lek. Males on large leks acquired more mates. (After Wikelski et al. 1996; photographs by Martin Wikelski.)

are attracted to sites where other males have established territories, presumably because these sites provide access to females that collect near the most attractive males (Partecke et al. 2002). Males on clustered lek territories obtain more mates than do peripheral males that defend individual territories (see Figure 14.13C and D). Females prefer to mate with the largest territorial males, but smaller, nonterritorial males attempt to sneak copulations when territorial males are absent. Most aggressive behavior is directed toward the largest males on centrally located territories. Attacking males seldom displace territorial residents, but aggression may disrupt the courtship and mating of dominant males. Females typically visit a limited number of males on the lek, probably because they are constantly harassed by territorial males. Mate choice by females incurs significant energy costs for males, presumably because females tend to mate with males that display at high rates (Wikelski et al. 2001; Vitousek et al. 2007).

Resource defense

If males can monopolize resources that are attractive to females, often the most efficient mating system is defense of those resources as exclusive territories. This strategy appears to be uncommon in amphibians and reptiles, probably because the low energy requirements of these animals make territorial defense of food resources inefficient, but it may occur in some species that feed on spatially aggregated prey. Defense of other kinds or resources, such as egg-deposition sites, is more common.

RESOURCE DEFENSE BY SALAMANDERS Resource defense is most common in amphibians with external fertilization, because males must be present when eggs are laid and therefore are able to defend oviposition sites against other males (Verrell 1989; Sullivan et al. 1995; Wells 2007). Male hellbenders (*Cryptobranchus alleganiensis*) establish territories under rocks on the bottom of streams and rivers, whereas male giant salamanders (*Andrias*) use tunnels in riverbanks as nests. Other males are attacked, but females are allowed to enter the territory and are courted by the male. Females lay eggs in the male's territory and then leave, while the male remains with the eggs and guards them. Additional females may subsequently enter the nest site and lay their eggs, and these females sometimes cannibalize eggs already in the nest.

Extensive studies of the eastern red-backed salamander (*Plethodon cinereus*) have shown that both males and females defend territories centered on cover objects such as rotting logs that also provide rich food supplies of termites, ants, and other invertebrates. Home ranges of the females sometimes overlap the territories of several males (Jaeger and Forester 1993; Mathis et al. 1995). The precise nature of the mating system of this species is not yet clear and may vary among individuals in the same population. The spatial overlap of home ranges of males and females suggests that this species has a resource-defense mating system. Females probably compare several males or their territories before choosing a mate. Both large males and males with large territories seem to be preferred. In addition, males that have fed on termites appear to be more attractive to females than those that have fed on ants, presumably because termites are a better-quality, more digestible food. Females use the fecal pellets of males to determine the type of food found in their territories. The quality of a male's food also affects the composition of secretions produced by courtship glands those with high-quality diets have more protein in their glandular secretions, possibly providing an indirect measure of territory quality (Chouinard 2012).

RESOURCE DEFENSE BY ANURANS Although the predominant mating system of anurans with a prolonged breeding season is the formation of lek-like choruses, some species have resource-defense mating systems. Two wellstudied examples are the North American green frog (Rana *clamitans*) and the American bullfrog (*R. catesbeiana*) (Wells 1977b, 1978; Howard 1978a). Both of these species have breeding seasons lasting 2 to 3 months during the summer. Males set up territories early in the breeding season and defend them with aggressive calls and wrestling with other males (Figure 14.14A). Some individuals maintain their territories for almost 2 months. Territories are situated around suitable oviposition sites, where eggs are laid in surface films (Figure 14.14B). Females sometimes visit the territories of several males before choosing a mate. The quality of the oviposition site defended by a male appears to be more important in mate choice than the size of the male or his behavior, although the largest males typically control the best territories. Among American bullfrogs, water temperature was an important component of territory quality (Howard 1978b). Eggs laid in cool water took

(A)



Figure 14.14 Reproductive behavior of the green frog (*Rana clamitans*). (A) Two male green frogs wrestle for control of a territory. (The red patch on the male on the left is an identifying tag.) (B) Male and female green frogs in the male's



territory. The female's body is hidden under the male; her legs are visible through the egg mass she is laying. Floating vegetation holds the eggs at the water's surface. (Photographs by Kentwood D. Wells.)

longer to develop and were subject to intense predation by leeches, whereas eggs laid in water that was too warm developed abnormally. The largest males controlled territories in which eggs developed at the fastest rates and suffered the least predation (**Figure 14.15**). Territorial males shifted their activities to different parts of the pond as temperatures changed throughout the season.

RESOURCE DEFENSE BY LIZARDS Many male lizards are territorial during the breeding season, but it is often difficult to determine whether males are defending resources that are attractive to females, or groups of females already settled in the habitat. One species that appears to attract females to high-quality territories is the side-blotched lizard (*Uta stansburiana*). Certain males, especially those with blue throats (see Figure 14.23), defend piles of rocks in open areas as territories. The best-quality territories are those that offer a range of temperatures that facilitate behavioral thermoregulation, as well as crevices that serve as retreat sites. When territory quality was manipulated by removing rocks from some males/ territories and adding them to the territories of other males, males with diminished territory





quality remained in place but increased their territory size to encompass more rocks. Those males in improved territories reduced their territory size, thereby saving on defense costs (Calsbeek and Sinervo 2002a).

In a similar study, females moved from lower- to higherquality territories, which increased the reproductive success of males on high-quality territories (Calsbeek and Sinervo 2002b). Female reproductive success also increased on high-quality territories, because females in those territories produced larger eggs than did those on poor-quality sites. The manipulations resulted in some small males having higher-quality territories than did some large males. Although females showed a strong preference for high-quality territories, genetic studies showed that they also preferred large males as fathers for their offspring. Multiple paternity is common in this species, and eggs fertilized by large males were more likely to produce sons, whereas those fertilized by small males were more likely to produce daughters. Offspring of large males also were larger and in better condition at hatching than were offspring of small males.

14.3 ■ Variables Affecting Male Reproductive Success

Most studies of sexual selection and mating systems of amphibians and reptiles have focused on determinants of male mating success, because this is what affects the intensity of sexual selection. When males have many opportunities to mate in a single season, some males are likely to mate many times, but many others will not mate at all. This means that the variance in male mating success will be relatively large, and consequently sexual selection on male traits that affect mating success will be strong. On the other hand, if most males can obtain only one mate in a season, variation in male mating success will be smaller, and sexual selection on male traits will be weaker. This situation can be complicated, however, by differences in sex ratios in populations. Even when males have few opportunities to obtain more than one mate, as is often the case in explosive-breeding aggregations, competition among males will be intense if there is an excess of males in the breeding population. In that case, strong sexual selection on male traits is expected.

The mating systems described in the first part of this chapter provide the framework for the operation of sexual selection on male traits because they determine the types of traits that are likely to be important for male mating success. Exactly which male traits are affected by sexual selection depends on the nature of the mating system and which stage of the mating process has the greatest impact on male mating success. For example, in a species such as the prairie rattlesnake (*Crotalus viridis*), male mating success probably is limited by the time required to find each mate. Consequently, any traits that can reduce search time will tend to increase male mating success. A capacity to follow chemical trails produced by females might be one such trait that would be strongly favored by sexual selection, because a male that can follow scent trails is more likely to find a mate than a male that cannot follow these trails. Finding females is relatively easy for red-sided garter snakes (*Thamnophis sirtalis*) because female snakes aggregate at hibernation dens, and male mating success is more likely to be limited by mate handling time. Within 12 hours of mating, *T. sirtalis* males are ready to mate again; this is about half the time required by *T. radix*, a species with a much longer breeding season (Whittier et al. 1985).

Sexual selection on male traits also is affected by direct competition among males for access to females and the behavior that results from that competition. For example, male prairie rattlesnakes search for females but seldom fight with other males, so they essentially engage in scramble competition to find mates; thus traits that enhance their ability to find mates may be favored over those that enhance fighting ability. In contrast, European adders (Vipera berus) not only search for females but fight to keep other males away from their mates. Thus, traits that enhance fighting ability would be favored by sexual selection. The same would be true for male toads that form explosive mating aggregations-they not only scramble to find mates, they also fight over females. Males of territorial species engage in contests for possession of territories, so traits that improve

male fighting ability would be favored by sexual selection. However, if females also choose mates from among the established territorial males, then traits that increase a male's attractiveness to females or his ability to acquire resources needed by females could be important as well.

Male persistence and allocation of resources

One factor that often affects male mating success is the ability of a male to continue breeding activities for a long period of time. For example, the amount of time a male frog spends in a chorus often is a major determinant of mating success (Halliday and Tejedo 1995; Wells 2007). Yet a common pattern is for most males to be active on only a few nights, perhaps because the energy costs of calling limit male breeding activity (see Chapter 7). Males often depend on stored energy reserves to make it through the breeding season, and they must reduce their activity as reserves are depleted. Although they sometimes replenish energy reserves by feeding, male amphibians and reptiles often reduce feeding during the breeding season because time spent searching for prey conflicts with time needed for territory defense, courtship, and mating. For example, male Galápagos marine iguanas often do not feed while present



Figure 14.16 Energy cost of breeding for male Galápagos marine iguanas (Amblyrhynchus cristatus). (A) Percentage of males not feeding on a given day. The mating period is in early January. (B) Amount of time males were away from their territories on foraging trips. (After Trillmich 1983.)

on a lek, and those that do feed make only short forays away from their territories (Figure 14.16). Lekking males can lose up to 26% of their body mass in a month (Trillmich 1983).

Studies of the lek-breeding Italian treefrog (*Hyla intermedia*) have shown that both the length of time a male spends in a chorus and his calling effort are correlated with mating success (Castellano et al. 2009), with chorus attendance being the most important determinant of mating success (**Figure 14.17**). As in many other studies (e.g., Jaquiéry et al. 2010), most males in the population were in the chorus for only a few nights, but a small number of individuals were present for as much as 2 weeks. The latter group acquired as many as 5 mates in a season, whereas more than 70% of the males in the study failed to mate at all.

Both chorus attendance and calling effort were limited by body condition. Within a single night of calling, some features of calls changed over time. For example, calling rate and pulse rate within calls decreased as the number of hours of calling increased, although this relationship was not consistent for all males. This change in calls suggests that fatigue caused some males to alter some properties of their calls to conserve energy, while still maintaining a relatively stable level of calling activity (Castellano and Gamba 2011).



Figure 14.17 Chorus attendance and mating success for males of the lek-breeding Italian treefrog (*Hyla interme-dia*). The graph shows the relationship between the number of nights of calling and the number of mates males obtained per season. (After Castellano et al. 2009.)

Male competitive ability

Competitive ability is most frequently measured as body size, because large males almost always win more fights than small males (Wells 1978; Bowcock et al. 2013). Large body size has been shown to enhance the mating success of many amphibians and reptiles (**Table 14.1**). In explosivebreeding anurans, where struggles among males for possession of females are common, large males are more likely than small males to mate (**Figure 14.18**). The same is true for territorial species such as green frogs (*Rana clamitans*) and American bullfrogs. In contrast, male body size often is not very important for frogs that form choruses or leks because they only occasionally fight among themselves (Halliday and Tejedo 1995; Wells 2007).

Large body size increases male mating success for many species of reptiles, especially those that compete directly

TABLE 14.1 Examples of amphibians and reptiles in which large body size increases male mating success				
Species	Mating system	Mechanism of sexual selection		
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Anurans		and a second state of the second s
Anaxyrus americanus	Explosive aggregation	Male competition
Bufo bufo	Explosive aggregation	Male competition
Physalaemus pustulosus	Chorus (lek)	Female choice
Rana catesbeiana	Resource defense	Male competition and female choice
Rana clamitans	Resource defense	Male competition and female choice
Rana sylvatica	Explosive aggregation	Male competition
Salamanders		
Desmognathus ochrophaeus	Mate guarding	Male competition
Triturus cristatus	Lek	Female choice
Lizards		
Amblyrhynchus cristatus	Lek	Female choice
Anolis garmani	Resource defense	Male competition and female choice
Plestiodon laticeps	Mate guarding	Male competition and female choice
Iguana iguana	Lek	Male competition and female choice
Lacerta agilis	Mate guarding	Male competition
Uta palmeri	Resource defense	Male competition and female choice
Snakes		
Natrix natrix	Mate searching	Male competition
Nerodia sipedon	Mate searching	Male competition
Vipera berus	Mate guarding	Male competition
Turtles		
Glyptemys insculpta	Mate guarding	Male competition
Gopherus agassizii	Mate guarding	Male competition

Sources: Andersson 1994, Halliday and Tejedo 1995, and references cited in text.



for females. Large male wood turtles (*Glyptemys insculpta*) and desert tortoises (*Gopherus agassizii*) dominate smaller males in aggressive interactions and have greater mating success (Kaufmann 1992; Niblick et al. 1994). Large males have greater mating success than do small males in most species of territorial lizards that have been studied (Olsson and Madsen 1998). Large males also are more likely to acquire females in mate-guarding species, such as *Lacerta agilis* (Olsson and Shine 1996), *L. schreiberi* (Marco and Perez-Mellado 1999), and *Plestiodon laticeps* (Cooper and Vitt 1993).

Large males of snakes that fight over females, such as European adders (*Vipera berus*), usually win the most fights (Madsen et al. 1993). Large body size sometimes is advanta-



Figure 14.18 Probability of mating as a function of male body size in three populations of explosive-breeding anurans. In all three species, increased body size is correlated with increased probability of mating. (A after Davies and Halliday 1979; B after Berven 1981; C after Wells 1979.)

geous for species such as the European grass snake (*Natrix*, *natrix*), in which males engage in scramble competition for females but do not fight (Madsen and Shine 1993).

Male traits other than large body size are related to male competitive ability and almost certainly have evolved through sexual selection. Sexual dimorphism in forelimb size is often pronounced in frogs. The arms of males of some species of *Leptodactylus* from South and Central America become greatly enlarged during the breeding season (**Figure 14.19**), and they often have sharp spines on their front feet that are used to jab at opponents in fights (Halliday and Tejedo 1995).

Males of other species of frogs have a variety of weapons used for fighting over females. Males of several species of Asian fanged frogs, *Limnonectes*, are larger than females and have larger heads and stronger jaws. Greatly enlarged fangs inside the lower jaw are used to bite other males during fights (Tsuji and Matsui 2002). Similar fanglike projections are present on the lower jaws of male *Pyxicephalus adspersus*, an African ranid frog. Males engage in violent and sometimes fatal fights during the breeding season (Hayes and Licht 1992).



(B)



Figure 14.19 Sexual dimorphism in *Leptodactylus insularum.* (A) A male with the hypertrophied forelimbs used to wrestle with other males. (B) Female, showing normal forelimb size. (Photographs by Kentwood D. Wells.)



Male lizards generally fight by biting one another. A common pattern in many iguanian lizards, skinks, and lacertids is for males to have larger and more robust heads than females relative to body size (Olsson and Madsen 1998). This pattern of sexual dimorphism is seen both in territorial species, such as the leopard lizard *Gambelia sila* (Lappin and Swinney 1999) and in mate-guarding species such as *Tiliqua rugosa* (Bull and Pamula 1996), *Lacerta agilis*, and *Plestiodon laticeps* (Figure 14.20).

Female choice

The ability of females to compare the qualities of potential mates and select the best ones available was the most controversial part of Darwin's theory of sexual selection, and it also is the major focus of much recent work on sexual selection (Andersson 1994). The easiest kind of female choice to understand is choice based on resources controlled by males, because such resources can have a direct effect on female reproductive success. Howard's (1978b) study of the effect of male territories on survival of eggs laid by female American bullfrogs is a good example, as is Calsbeek and Sinervo's (2002a,b) experimental manipulation of territory quality in the side-blotched lizard (*Uta stansburiana*).

More problematic is female choice of mates based on morphological or behavioral traits of males. One hypothesis to explain such preferences is that once a preference for some type of male trait arises, it can be maintained, and even increased, through a process of **runaway sexual selection**. This phenomenon can occur if there is a genetic correlation between the expression of a trait in males and the preference for that trait in females, so that females choosing males with the trait would pass along genes for the trait to their male offspring; this is known as the **sexy sons hypothesis**. Alternatively, the **good genes hypothesis** proposes that male traits chosen by females are indicators of male genetic quality, so females that choose males with these traits will pass those traits to their offspring.

A third hypothesis is that females choose males with traits that elicit responses from the female's sensory system. For example, if females are particularly good at perceiving



Figure 14.20 Sexual dimorphism in broad-headed skinks (*Plestiodon laticeps*). Males of this species aggressively bite other males in the course of guarding their mates. (A) Mated pair; the male is on the left. (B) Males grow larger overall than do females, and the width of the male head is proportionally even larger. (After Vitt and Cooper 1985; photograph © John Sullivan/ribbitphotography.com.)

red color, then males that evolve displays of red structures might be more successful in obtaining mates than those with display structures of some other color. This model has been called the **sensory exploitation hypothesis** because it assumes that sexual selection favors males that exploit a preexisting sensory bias of females.

Although many studies have demonstrated a correlation between male morphological or behavioral traits and male mating success, it has been much more difficult to distinguish among these models of sexual selection (Andersson 1994). Furthermore, these models of sexual selection are not mutually exclusive. For example, an animal might evolve a signal that exploits the sensory capabilities of conspecific females, but the intensity of the signal or the rate at which it is delivered might be further shaped by sexual selection because these features provide females with reliable information about male quality.

The most common approaches to studying female choice are experimental studies that give females a direct choice between male traits and field studies that correlate variation in male traits with variation in mating success. Frogs and toads are particularly suitable for experimental studies because they communicate mostly with acoustic signals, which are more easily manipulated than visual or chemical signals. The usual method is to give a female a choice of two or more call variants in an arena and measure a preference when the female moves toward or contacts one of the speakers playing the calls. Playback experiments have shown that most female frogs prefer faster, louder, longer, or more complex calls (i.e., those with more notes) (Gerhardt and Huber 2002; Wells 2007). In other words, females are attracted by calls that require more energy to produce, perhaps because these calls provide some indication of differences in the physical condition of males or male quality, or because such calls are more easily detected in a noisy chorus of calling males.

Experiments showing a preference for features of calls that are indicators of male quality suggest that these call features should be under directional selection in natural choruses. It has been surprisingly difficult to document such patterns, however (Friedl 2006). One problem is that only a few studies have examined individual variation in calling behavior in natural choruses. If variation in calling rate, call intensity, or call complexity within an individual is similar to variation among individuals, then these features will not provide females with reliable information about male quality. In fact, several studies have shown that males do differ in their calling behavior, especially in features such as calling rate and call duration (Runkle et al. 1994; Jennions et al. 1995).

Some studies have found a correlation between calling rate and mating success. Variation in calling rate explains only a small proportion of the variation in male mating success, however, because variation in calls is often less important than the amount of time a male spends in the chorus (Wagner and Sullivan 1995). In addition, females often compare only a few males before choosing a mate, so those with the highest calling rates or longest calls are not always evaluated by a female (Murphy and Gerhardt 2002; Murphy 2012). Finally, expression of female preferences can be masked by strong male–male competition (Ursprung et al. 2011) or confounded by alternative mating tactics adopted by some males who intercept females moving toward other males.

Some features of calls exhibit subtle differences among males that can affect female choice. The túngara frog (Physalaemus pustulosus) is a classic example of a species in which call complexity affects female preferences for male calls. When competing with other males in a chorus, male túngara frogs produce a "whine" note that is followed by one or more "chuck" notes (Ryan and Rand 2003). Experiments in which multiple females were presented with choices of calls from several different males showed a strong preference for embellished calls containing chuck notes, but not all males benefitted equally from call embellishment. A key factor was the relative intensity of the chuck note compared with that of the whine note: males with chucks of relatively higher amplitude than the whine were more attractive to females than were males with lower-amplitude chucks (Baugh and Ryan 2011).

Much less is known about traits preferred by females of other amphibians. In general, female salamanders do not show clear evidence of preferring large males to small males, although in some species large males are more successful because of greater competitive ability (Sullivan et al. 1995). However, female great crested newts (*Triturus cristatus*) prefer both large males and those with large, conspicuous crests on their backs and tails (Hedlund 1990). There also is evidence from laboratory experiments that female smooth newts (*Lissotriton vulgaris*) prefer large males and males with large crests (Green 1991).

The criteria used by female reptiles to choose mates are less well understood. Indeed, there is evidence for some reptiles that female choice is of minor importance in determining male mating success. In most studies in which male body size affected mating success, competition among males rather than female choice was the principal mechanism of selection (see Table 14.1). Only a few studies have shown an apparent female preference for large males (Olsson and Madsen 1998; Calsbeek and Sinervo 2002b). Female broad-headed skinks (Plestiodon laticeps) prefer males with large heads (see Figure 14.20) (Cooper and Vitt 1993). Not only did females more frequently associate with such males in the field, they also actively rejected courtship by small males. This species is not territorial, so large male size is not correlated with the quality of defended resources, but it is related to fighting ability. Females did not show a clear preference for the bright orange color that develops on the heads of males in the breeding season, suggesting that color is mainly as an aggressive signal in contests between males. This result is consistent with that of several studies of brightly colored lizards, which produced little evidence that females use color to choose mates (Olsson and Madsen 1995; LeBas and Marshall 2001; Olsson 2001), although there is some evidence for female preference based on ultraviolet signals (Bajer et al. 2010).

Alternative mating tactics

In mating systems in which a few males monopolize most of the available females, less competitive males often adopt alternative mating tactics that enable them to obtain some matings, although usually not as many as those obtained by dominant males. Such tactics can include various forms of sneak matings, male mimicry of female color pattern and behavior, and sexual interference with the mating attempts of other males (Andersson 1994). One common type of alternative mating tactic is for satellite males to associate with dominant or territorial males and attempt to intercept females. This behavior has been reported for many species of frogs, including those that defend resource-based territories, such as green frogs and American bullfrogs (**Figure 14.21**), and those that form choruses or leks (Halliday and Tejedo 1995).

In a study of mating behavior in the natterjack toad (*Bufo calamita*), Anthony Arak (1988) found that small males were more likely to adopt a satellite tactic than were large males He also found that the frequency of satellite behavior increased with increasing chorus density, a pattern also seen in many other species of frogs. A study of *Eleutherodacty-lus johnstonei*, a terrestrial frog from Barbados, found many more satellite males in a high-density population than in a low-density population (Ovaska and Hunte 1992). Some satellite males were small, noncalling males that lacked territories; others were about the same size as the calling

Figure 14.21 Territorial male American bullfrog (*Rana catesbeiana*) with two satellite males. The satellites will attempt to intercept females, an alternative male mating tactic when a few males monopolize most of the available females. (Photograph by Kentwood D. Wells.)

males and switched between calling and satellite tactics. Sometimes groups of satellite males interfered with the mating of territorial males by breaking up their courtship attempts.

Several types of alternative mating tactics and sexual interference have been observed among salamanders (Halliday and Tejedo 1995). Males of

explosive-breeding ambystomatids commonly cover the spermatophores of other males with their own spermatophores (see Figure 14.7). When a female encounters one of these multiple spermatophores, she is most likely to pick up the one on top. Male *Ambystoma tigrinum* court females individually rather than engaging in the sort of scramble competition seen in *A. maculatum* and other explosive breeders. Interfering males sometimes insert themselves between the male and female as the first male leads the female during courtship (**Figure 14.22**). The interfering male mimics the behavior of a female by touching the cloacal region of the courting male to elicit spermatophore deposition. The interfering male then covers the first male's spermatophore with his own.

Male plethodontid salamanders lead females in a tailstraddling walk before depositing a spermatophore. Again, interfering males often insert themselves between the courting male and female and elicit spermatophore deposition. However, in this case the second male does not cover the spermatophore, but he does cause the first male to waste a spermatophore, leaving the female to pick up the second male's spermatophore (Arnold 1976). Similar behavior has been described for several species of newts.

Satellite behavior is common in some territorial and lekking lizards. In collared lizards (*Crotaphytus collaris*), subordinate males live within the territories of older, dominant males. They exhibit low rates of courtship and have low mating success but rapidly increase courtship and mating activities if a territorial male disappears or is removed experimentally (Baird and Timanus 1998). On leks of the green iguana (*Iguana iguana*), small males hang around the periphery of larger males' territories and attempt to copulate with females that pass through. Most of these attempts are resisted by the female and are unsuccessful, but a few are successful. Both territorial and peripheral males sometimes try to force females to copulate rather than engaging in lengthy courtship (Rodda 1992). Forced copulation



has been observed in other lizards as well, including the Lake Eyre dragon (*Ctenophorus maculosus*) from the deserts of southern Australia (Olsson 1995). Forced copulation can be costly to females, both because they may be injured and because it circumvents any attempt to choose particular males as mates. From a male's perspective, it is a way to mate quickly with as many females as possible in the face of intense competition from other males.

In the preceding examples, lizards that adopt satellite or sneaker tactics generally are young individuals that cannot compete successfully for territory ownership with older males. The alternative tactics adopted by these animals are the best tactics they can pursue in the presence of dominant males, but they switch to the preferred territorial tactic as they grow or if dominant males are absent. In some lizards, however, alternative mating tactics are genetically determined and are correlated with permanent differences in breeding coloration. For example, tree lizards (Urosaurus ornatus) from western North America exhibit considerable variation in dewlap color both within and among populations. In one population in Arizona, some males have bright orange dewlaps with a distinct blue or greenish central spot. These males are territorial and typically defend territories that overlap the home ranges of several females. Other males have a yellowish or orange dewlap that lacks a distinct central spot. These males are not territorial but either behave as satellite males or become nomadic and roam over large home ranges. Presumably, orange males obtain mates by sneaking matings in the territories of orange-blue males or by short-term guarding of individual females.

One unusual feature of *U. ornatus* is that subordinate orange males are actually larger than dominant territorial males, although the latter have a stockier build. Phenotypic and behavioral variation appears to be determined by levels of prolactin and testosterone early in development, and the phenotype of a male then remains fixed throughout his life. The behavioral switch between sedentary and no-

(D)

(C)

Figure 14.22 Sexual interference by male tiger salamanders (Ambystoma tigrinum). Panels (A) through (D) depict the animals' forward motion in this sequence of events. (A) The female is following male 1 during courtship. Male 2 inserts himself between the courting male and female. (B) Male 2 then nudges male 1, a behavior normally used by females to elicit spermatophore deposition, and male 1 deposits his spermatophore (blue arrow). (C) Male 2 deposits a spermatophore (red arrow) on top of the spermatophore deposited by male 1. (D) The female moves forward and picks up the spermatophore of male 2; male 1 deposits a second spermatophore after being nudged by male 2. (After Arnold 1976.)



madic behavior of the orange males is more plastic but also hormonally mediated. Under stressful conditions, such as those that lizards encounter during a drought year, high levels of corticosterone suppress testosterone levels and lead to lowered aggression and increased nomadic behavior in orange males. Under more favorable conditions, corticosterone levels are lower and the males become more aggressive and more sedentary (Moore et al. 1998).

A somewhat similar system has been described for sideblotched lizards (*Uta stansburiana*) in California. Males exhibit three distinct color morphs, each of which is associated with a distinct mating tactic (Figure 14.23). Males with dark blue throats establish small territories or guard individual females. Males with orange throats are more aggressive and often usurp the territories of one or more bluethroated males (Calsbeek et al. 2001). Males with yellow throats try to sneak matings in the territories of dominant males. As in Urosaurus, the phenotypes of Uta males are fixed and reflect differences in circulating levels of testosterone (Sinervo et al. 2000). The system is unusually complex because frequencies of the different color morphs fluctuate among years in the same population. This results from a shift in the relative reproductive success of males using the three mating tactics. When orange males predominate, they obtain most of the matings but lose some paternity to yellow sneaker males. The latter subsequently increase in frequency and obtain more matings but lose paternity to blue males that guard individual females and prevent sneaker males from mating. This results in a subsequent increase in blue males. The overall result of this complex interaction among the three morphs is that the least common morph has a relative advantage and subsequently increases in frequency, leading to a regular oscillation in morph frequencies in the population (Zamudio and Sinervo 2000).



Figure 14.23 Color morphs of the side-blotched lizard (*Uta stansburiana*). Male throat coloration is the result of circulating testosterone levels and is associated with distinct mating tactics. Frequencies of the three color morphs, which are genetically determined, shift from year to year as the advantage of each behavioral tactic changes in relation to the others. (A) Males with orange throats are aggressive, defending large territories encompassing the home ranges of several females. (B) Males with blue throats defend small territories or individual females; their territories are often usurped by orange-throated males. (C) Males with yellow throats are not territorial but attempt to sneak matings in the territories of orange-throated males. (Photographs by Barry Sinervo.)

Polyandry and sperm competition

When a female mates with several different males, either simultaneously or sequentially, the mating system is known as **polyandry** (Roberts and Byrne 2011; Byrne and Roberts 2012). For species with internal fertilization, mating with different males can lead to sperm competition, especially if viable sperm are stored in the female's reproductive tract. For amphibians with external fertilization, mating with several males at the same time (simultaneous polyandry) provides opportunities for sperm competition, whereas mating with individual males in succession (sequential polyandry) does not. Simply counting the number of mates obtained by each male may yield an inaccurate estimate of mating success. To determine the relative fitness of each male in a population, genetic studies using DNA fingerprinting or other techniques are needed.

POLYANDRY WITH INTERNAL FERTILIZATION Some female salamanders can store viable sperm for weeks or months (see Chapter 8). Males usually do not guard individual females for long periods of time, so there is ample opportunity for multiple matings by females. Multiple paternity has been documented with genetic studies of salamanders in several families (Jones et al. 2002b; Myers and Zamudio 2004; Chandler and Zamudio 2008; Williams and DeWoody 2009; Caspers et al. 2014). Females of the North American rough-skinned newt (*Taricha granulosa*) sometimes mate with several males, all of which contribute to fertilizing her eggs. Sperm from the first male often fill most of the spermathecae of the female, so subsequent mates have lower fertilization rates (Jones et al. 2002a).

Multiple paternity is common among lizards, snakes, turtles, and crocodylians, and in all of these groups there is the potential for long-term sperm storage (Olsson and Madsen 1998; Davis et al. 2001; Refsnider 2009; Friesen et al. 2014). Even when males closely guard individual females, as in sand lizards (Lacerta agilis), multiple paternity is common (Olsson and Madsen 2001). In Tiliqua rugosa, which has a largely monogamous behavioral mating system, some females mate with more than one male (Bull 2000). Female American alligators (Alligator mississippiensis) exhibit considerable fidelity to particular mates, yet many egg clutches have multiple fathers (Lance et al. 2009). Multiple mating by females could be a relatively low-cost means of avoiding harassment by males searching for mates (Lee and Hays 2004), but it also is possible that females derive some benefit from mating with more than one male. Multiple matings may ensure high rates of fertilization in some salamanders (Caspers et al. 2014). Female sand lizards and European adders (Vipera berus) that mate with several males produce offspring that are more likely to survive than are offspring of females that mate only once. This difference could result from sperm competition, with the sperm of genetically superior males being most likely to fertilize a female's eggs and produce high-quality offspring (Olsson and Madsen 2001).

POLYANDRY WITH EXTERNAL FERTILIZATION Males of most frog species with external fertilization attempt to ensure paternity of a female's eggs by grasping the female in amplexus and releasing sperm while the male holds his cloaca close to that of the female (see Figure 8.5). Nevertheless, simultaneous polyandry and multiple paternity are more common among frogs than once was assumed (Roberts and Byrne 2011). Groups of males of some arboreal frogs that form explosive-breeding aggregations sometimes participate in simultaneous fertilization of the eggs of one or more females (Byrne and Whiting 2011). This behavior has been observed in several rhacophorid frogs that build



Figure 14.24 Group spawning by the African gray treefrog (*Chiromantis xerampelina*). Multiple mated pairs participate in constructing a communal foam nest, while additional unmated males attempt to fertilize eggs. (Photograph by Philip Byrne.)

Multiple males of the Australian myobatrichid frog *Crinia georgiana* are commonly observed in amplexus simultaneously with the same female (**Figure 14.25**), resulting in multiple paternity of egg clutches (Roberts et al. 1999). This type of polyandrous mating is the result of intense competition among males for access to females and

foam nests hanging in trees over rain pools. Once a female begins to lay her eggs, groups of males climb onto her back and participate in beating the mucus around the eggs into a thick foam while fertilizing the eggs. Sometimes large aggregations of paired and unpaired males and females participate in simultaneous group spawning (**Figure 14.24**).

With this type of mating system, one way for a male to enhance his reproductive success is to release enormous numbers of sperm. Foam-nesting rhacophorid frogs that engage in group mating have larger testes relative to body size than do other frogs. The largest testes are found in *Chiromantis xerampelina* and *Rhacophorus arboreus*, species in which multiple males participate in 80–90% of matings (Kusano et al. 1991; Jennions and Passmore 1993).



is a product of a sex ratio heavily skewed toward males in the small breeding pools. As many as four males may contribute to fertilizing a single female's eggs, although often an even larger number are competing for mating opportunities. Multiple mating does not appear to improve the performance of a female's offspring (Byrne and Roberts 2000). In fact, females suffer a cost of polyandrous mating in that fertilization success is reduced, probably because males jostling for position interfere with fertilization (Byrne and Roberts 1999). A comparative study of Australian myobatrachids and hylids showed that *Crinia georgiana* and several other species have unusually large testes, indicating the potential for sperm competition (Byrne et al. 2002).

Genetic studies revealed the occurrence of multiple paternity in the European common frog (*Rana temporaria*) (Laurila and Seppa 1998). This species has an unusual mode of extra-pair fertilization, which has been termed clutch piracy. Unmated males seize egg clutches immediately after they are laid by another pair and release sperm onto the eggs, resulting in some eggs being fertilized by the intruding male (Vieites et al. 2004). Multiple paternity also has been reported for the moor frog (*R. arvalis*), another species with a scramble competition mating system (Knopp and Merilä 2009).

Figure 14.25 Multiple amplexus in the Australian myobatrachid frog Crinia georgiana. Two males are in amplexus with a single female while another male waits nearby. This type of multiple mating often results in multiple paternity of egg clutches. (Photograph by Philip Byrne.)

14.4 Sexual Size Dimorphism

Darwin formulated his theory of sexual selection to account for the evolution of sexual differences in morphology and body size. Several examples of sexually selected male traits have already been mentioned-the tail fins and crests of newts; the enlarged heads, jaws, and teeth of some lizards and salamanders; and the hypertrophied forelimbs and enlarged fangs of frogs. We also have seen that large body size increases male mating success among many amphibians and reptiles. Yet the typical pattern in many lineages of amphibians and reptiles is for females to be larger than males, and sometimes considerably larger. This is true for most frogs and toads, salamanders, turtles, and snakes. Only among crocodylians and lizards do we find a large proportion of species with males as large as or larger than females. To understand these patterns of sexual dimorphism, we need to know something about selective forces acting on body size of both males and females, as well as patterns of age-specific growth.

Most amphibians and reptiles grow rapidly early in life and growth gradually levels off, producing an asymptotic growth curve. In amphibians and reptiles with little or no sexual dimorphism, males and females typically grow at similar rates and reach similar asymptotic sizes (Stamps 1995). In other species the growth rates of males and females diverge early, resulting in different asymptotic sizes (**Figure 14.26**).

In general, the evolution of unusually large body size in males is associated with fighting in frogs (Shine 1979; Howard 1981; Wells 2007), salamanders (Shine 1979), lizards (Stamps 1983), snakes (Shine 1994), and turtles (Berry and Shine 1980). Among frogs, relatively large male body size often is associated with resource-defense mating systems, such as those of American bullfrogs and green frogs. When males defend only calling sites or fight for possession of females, they usually are considerably smaller than



Figure 14.26 Asymptotic growth resulting in sexual dimorphism in body size of amphibians and reptiles. (A) Males of the African bullfrog (*Pyxicephalus adspersus*) grow faster than females after reaching sexual maturity. (B) Male and female American alligators (*Alligator mississippiensis*) grow at similar rates for the first 5 years of life, after which growth of females slows. Dashed lines show the relative sizes of adult

males and females. (C) Males of the Neotropical lizard *Basiliscus basiliscus* grow faster than females after the first year. (D) This pattern is reversed in slider turtles (*Trachemys scripta*). After the first few years of life, females grow faster than males and eventually reach a much larger size. (A after Hayes and Licht 1992; B after Chabreck and Joanen 1979; C after Van Devender 1978; D after Dunham and Gibbons 1990.)
females, even when large males are more likely to mate (Hallidav and Tejedo 1995).

This relationship remains robust among snakes even when differences in phylogeny are taken into account. Males are larger than females in many viperid, colubrid, and elapid snakes with male combat. However, in the European adder (Vipera berus) and the European grass snake (Natrix natrix), males are smaller than females, even though large males win more fights and acquire more mates (Madsen 1988; Madsen and Shine 1993). In New World crotaline snakes, species with large body size are more likely to have male-biased sexual dimorphism than are species with small body size (Hendry et al. 2014).

Females of most aquatic turtles are larger than males, whereas the males of some terrestrial turtles, especially tortoises, are larger than females. Berry and Shine (1980) attributed this relationship to differences in male combat, which is relatively common in male tortoises but rare in most aquatic turtles. In contrast, Gibbons and Lovich (1990) proposed that males of terrestrial species become sexually mature later than males of aquatic turtles, allowing them

including male combat and sexual

Kratochvíl and Frynta 2002.)

the former to put most of their energy into growth and reach a size that protects them from predators.

Phylogenetic analyses provide a way to understand the evolution of sexually dimorphic traits within lineages of closely related species (Kratochvíl and Frynta 2002). Males of most species of eublepharid geckos are highly territorial, and this appears to be the ancestral condition for the family as a whole (Figure 14.27). In territorial species, males consistently have larger heads relative to body size than do females. There is no evidence of male combat in two genera, Goniurosaurus and Holodactylus, suggesting that territorial behavior has been secondarily lost in these lineages. This loss of territorial behavior was associated with a loss of sexual dimorphism in head size and also with a loss of scent glands, which produce pheromones used to mark territories. Sexual dimorphism in body size did not appear to be related to aggressive behavior, however. The ancestral condition for the group is for males to be larger than females, but there were several reversals of this pattern that were not accompanied by loss of territorial behavior in males.



SUMMARY

Most species of amphibians and reptiles are polygynous, with males attempting to acquire multiple mates in a breeding season. Females of some species acquire several mates as well.

Sexual selection generally favors multiple mating by males, because their reproductive success is limited by the number of mates they acquire.

Reproductive success in females usually is limited by the energy reserves needed to produce eggs, but multiple matings may provide some genetic benefits to females.

The type of mating system adopted by males of a species depends on the spatial and temporal distribution of females.

When breeding seasons are short and females are highly aggregated, males often engage in scramble competition for access to females, but often without overt fighting. This type of mating system is common in anurans with explosive breeding seasons, some ambystomatid and hynobiid salamanders, snakes that mate near communal hibernacula in early spring, and some turtles.

When females are widely dispersed but available over a longer breeding season, males usually are forced to find mates by searching over wide areas, and they sometimes guard individual females once they are encountered. This type of mating system occurs in some salamanders, many turtles, and squamates in which females are not spatially aggregated.

The duration of mate guarding is highly variable. Males of some species guard females only until they are ready to mate. Males of other species engage in extended postmating mate guarding, to prevent other males from subsequently mating with the same female.

When females are aggregated in small stable home ranges, males may adopt a strategy of guarding multiple females simultaneously by defending large territories that overlap the home ranges of several females. This is the predominant mating system of small insectivorous lizards.

Defense of food-based territories as a strategy to attract females appears to be uncommon in amphibians and reptiles, but some salamanders and frogs defend resource-based territories around suitable oviposition sites, and males with the best territories often acquire multiple mates.

Some lizards defend resource-based territories, such as piles of rocks, and territory quality can influence female choice of mates.

In some amphibians and reptiles with prolonged breeding seasons, males form aggregations at traditional mating areas and defend small territories where they advertise themselves to prospective mates. Such lek mating systems are found in some large iguanid lizards, possibly some crocodylians, and some newts, while lek-like choruses are common in anurans.

The types of male traits that are favored by sexual selection depend on the nature of the mating system.

Explosive mating aggregations generally favor large body size and other traits correlated with male competitive ability.

Large male body size and conspicuous advertisement signals are often favored in species that defend resource-based territories, situations in which both male– male competition and female choice are important determinants of male mating success.

Sexual selection is responsible for the evolution of loud, complex vocal signals in frogs, for bright coloration and elaborate courtship in newts, and for large body size, bright colors, and conspicuous display structures in many lizards.

Mate searching tends to favor traits related to rapid movement and the ability to detect and locate receptive females, such as responsiveness to pheromonal signals or large home-range size. If males also guard females once they are encountered, large size and conspicuous color may be favored as well.

Sexual selection also can favor the production of large quantities of sperm, especially in those species in which females are likely to mate with more than one male, sometimes leading to direct sperm competition.

Patterns of sexual dimorphism in size are related to patterns of selection.

Large body size often is favored in females because this leads to greater fecundity, and females are larger than males in many amphibians and reptiles.

Fighting among males often selects for large male body size because large males tend to win the most fights.

When the intensity of selection for large body size in males exceeds that acting on females, males may reach larger adult body sizes than females.

Go to the **Herpetology** Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

15 Diets, Foraging, and Interactions with Parasites and Predators

n the first part of this chapter, we describe broad patterns of diet and foraging behavior of amphibians and reptiles. These patterns are associated with morphological, physiological, and behavioral characters that facilitate location, identification, capture, ingestion, and digestion of food items. Next we consider amphibians and reptiles as food resources for other animals, including parasites. Because parasites are so small compared with their hosts, they are usually difficult or impossible to avoid. The response to parasitism is thus largely physiological, and defensive mechanisms involve the host's immune system. In contrast, predators can often be avoided or deterred, and amphibians and reptiles have evolved a range of overt defensive mechanisms. Finally, we discuss an example of coevolution between a snake and its prey.

15.1 Diets

Most amphibians and reptiles are carnivores—that is, they eat other animals. Some are omnivores and eat plant material, at least occasionally, as well as animal material. A very few are strict herbivores. It is easy to appreciate that species differ in the general categories of food eaten. It is conceptually more challenging to integrate all of the interrelated factors that affect diet (**Figure 15.1**). For example, body size affects how large an item can be eaten, but foraging mode affects the kinds of items that can be detected, and foraging mode itself is related to phylogeny. Extrinsic factors such as prey availability and weather influence diet composition from day to day, season to season, and year to year.

Carnivory

The diets of amphibian and reptilian carnivores typically are restricted to general categories of prey: insects and other invertebrates, fish and frogs, squamates, or mammals and birds. Within each general type, carnivores can be categorized by the size of their prey relative to their own size and by specializations for specific prey types (e.g., the snout shapes of crocodylians; see Figure 1.6). Given the small body sizes of most amphibians and lizards, it is not surprising that their diets consist mostly of invertebrates, whereas large reptiles such as snakes and crocodylians eat vertebrates. Exceptions occur, of course. Large frogs, salamanders, and lizards occasionally eat vertebrates, and small species of snakes and juvenile crocodylians eat invertebrates.

The size of feeding structures is often more closely related to the size of prey than to the overall size of the predator. For example, all adult anurans swallow their prev whole, and the size of an anuran's mouth is a key to the sizes and types of prey that it eats (Emerson 1985). Anurans that feed on mites, termites, or ants, or have small heads and narrow mouths, whereas anurans that feed on large prev have broad heads and wide mouths. At one extreme are some frogs whose heads are so large relative to their bodies that they look like hopping mouths (Figure 15.2A). These frogs, including the South American Ceratophrys and Lepidobatrachus and the African bullfrog Pyxicephalus, eat other anurans, including members of their own species. At the other extreme are the Central American rhinophrynid frogs (Rhinophrynus). These fossorial frogs have tiny heads and feed on termites by shooting their tongues through a groove in the small opening of the mouth (Figure 15.2B).

A generalist diet is particularly characteristic of species that feed on invertebrates. For example, a dietary analysis revealed that individuals of the North American salamander *Plethodon cinereus* had eaten representatives of nine classes of invertebrates, including ten orders of insects (Jaeger 1990). The total diversity of prey items must have included hundreds of species.

Even a diet with high species diversity does not represent a random selection of suitably sized prey, however. A comparison of prey items eaten by *P. cinereus* with the availability of those items indicates selectivity based on the



Figure 15.1 Major sources of variation in the diets of amphibians and reptiles. The sources of variation shown at the left are complexly interrelated with one another and, except for resource availability, are influenced by phylogeny and other historical factors. (After Vitt and Pianka 2007.)

digestibility of different kinds of prey (Jaeger 1990). During wet nights when salamanders are able to forage in the leaf litter of the forest floor, they eat many small and softbodied prey that can be digested rapidly. On dry nights, when foraging activity is limited by the risk of dehydration and fewer prey are available, individuals eat relatively more hard-bodied (heavily chitinized) prey, which take longer to digest. Salamanders thus preferentially select soft-bodied prey on wet nights, but eat indiscriminately on dry nights when the number of accessible prey is relatively low.

While the potential prey diversity of predators that eat vertebrates will obviously be lower than that of species that eat invertebrates, dietary diversity can still be impressive. For example, stomachs of 580 horned adders (*Bitis caudalis*) from southern Africa contained several species of amphibians, more than 27 species of lizards, 1 snake, and at least 6 species of birds and mammals (Shine et al. 1998).

In contrast to the many amphibians and reptiles that display dietary diversity, a few are dietary specialists. Species with specialized diets often exhibit morphological, physiological, and behavioral specializations for feeding on a particular kind of food item. For example, North American horned lizards (*Phrynosoma*) and the Australian thorny devil (*Moloch horridus*) (see Figure 12.13) are specialists on ants. Their peglike teeth, spiny tanklike bodies, and cryptic coloration may be associated with their diet. That is, the tanklike bodies may be needed to accommodate the large volumes of small prey these lizards eat, and this body form may make rapid locomotion impossible. Cryptic coloration and limited activity may make these lizards relatively inconspicuous to predators, and sharp spines are a good defense if crypsis fails.

While this hypothesis is plausible, a lizard does not have to be stout and spiny to be an ant specialist. *Sceloporus magister* in North America and *Liolaemus monticola* in Chile subsist largely on ants. While these species have dental specializations similar to those of horned lizards and thorny devils, they do not have the other morphological specializations (Greene 1982).

The evolution of snakelike shapes by lizards is associated with dietary specialization on ants and termites. Like snakes, snake-shaped lizards must feed a large body through a small mouth. This constraint is especially severe for lizards, which have far less **skull kinesis** than do snakes. Termites and ants are small and abundant in many habitats, and they are common items in the diets of snake-shaped lizards. For example, the fossorial *Typhlosaurus* skinks in the Kalahari Desert of Africa feed largely on termites, even specializing on particular castes within a species of termite (Huey et al. 1974). Pygopodid lizards in the genus *Aprasia* are specialists on ant larvae and pupae (Webb and Shine 1994).

Marine snakes are particularly prone to dietary specialization. Only 1 of 16 sea snake species collected from the coast of the Malay Peninsula is a prey generalist (Glodek and Voris 1982). The diets of the others fall into one of five categories: eels, gobies, burrowing gobies, catfish, or fish eggs. Each of these dietary specializations is associated with sensory, behavioral, and morphological adaptations for locating and capturing prey. For example, egg specialists in the genus *Emydocephalus* (Figure 15.3) lack teeth except

Figure 15.2 Body forms reflect the diet

of anurans. In general, frogs that eat large prey items have large heads and wide mouths; frogs that eat small prey items have small heads and narrow mouths. Contrast the relative head and mouth size of the South American bullfrog *Ceratophrys ornata* (A), which eats large prey (including vertebrates), with that of the Mexican burrowing frog *Rhinophrynus dorsalis* (B), which eats termites. Frogs are not drawn to scale. (After Cogger and Zweifel 1992.)





Figure 15.3 Turtle-headed sea snakes (*Emydocephalus*) are specialists on fish eggs. The *Emydocephalus annulatus* shown here has inserted its head into a hole in a reef, where it is eating eggs in the nest of a blenny (*Salarias alboguttatus*). The male blenny (center) is attempting to repel the snake. (Photograph by Claire Goiran.)

for medially facing fangs on the maxilla (Voris 1966). Eggs are scraped from the nest substrate with enlarged surpralabial scales (Guinea 1996).

Like mammalian and avian predators, many carnivorous amphibians and reptiles feed on carrion when it is available. Pit vipers and piscivores are the snakes most commonly reported to eat carrion (DeVault and Krochmal 2002). Komodo dragons (*Varanus komodoensis*) are notorious scavengers (**Figure 15.4**). Reports of scavenging by aquatic turtles are common, and many lizards, including Australian bluetongued and shingle-backed skinks (genus *Tiliqua*), feed on carrion. Even amphibians feed on nonliving items: tadpoles eat dead conspecifics, and cane toads (*Rhinella marina*, formerly *Bufo marinus*) eat pet food put out for dogs.

Cannibalism

Cannibalism is usually opportunistic, and individuals attack and eat a conspecific just as they would any other prey item. Nonetheless, cannibalism occurs regularly in ephemeral breeding ponds where many amphibian larvae are crowded together and resources are limited (Crump 1992). Some larvae in populations of tiger salamanders (Ambystoma tigrinum) and spadefoot toads (Scaphiopus, Spea) develop enlarged mouths and jaw muscles and capture and consume other larvae (Figure 15.5). The developmental processes that produce these morphological changes are triggered by environmental cues and do not occur in all populations (Pfennig 1997). For Ambystoma, the environmental cue is crowding of larvae; for Spea, the cue is chance consumption of another tadpole or a freshwater shrimp. Not all individuals become cannibals, even when environmental conditions favor it; cannibalism is thus controlled by a combination of genetic and environmental factors.

Biologists find such cannibalism puzzling, because eating a relative incurs a substantial cost in terms of the shared genes of any cannibalized relative. Hence, an individual acts against its **inclusive fitness**—the genetic contribution of an individual to future generations plus that of its relatives—if it kills a sibling. Several researchers have conducted experiments to determine if cannibals can recognize their kin and thus avoid them. The results are mixed, apparently because avoiding relatives is favored by selection in some situations but not others. When cannibalistic morphs of *A. tigrinum* and *Spea* are given a choice between siblings and distantly related individuals, they eat fewer siblings than nonrelated individuals (Pfennig 1997). In contrast, larvae of the marbled salamander (*Ambystoma*



Figure 15.4 Komodo dragons (Varanus komodoensis) feeding on carrion. Well known as aggressive predators, the diets of these largest extant lizards also include the carcasses of deer and water buffalo that have died of septic wounds inflicted in earlier Komodo attacks. (Photograph © kkaplin/Alamy.)



Figure 15.5 Normal and cannibalistic morphs of the tiger salamander (*Ambystoma tigrinum*). In the face of ephemeral breeding ponds and limited resources, some larvae will develop enlarged mouths and jaw muscles, allowing them to consume other larvae. (A) Normal morph. (B) Cannibalistic morph.

opacum) do the opposite, preferring to eat their own kin (Walls and Blaustein 1995). Walls and Blaustein suggested that cannibalism might greatly increase the individual's **direct fitness**—its own genetic contribution to future generations—without decreasing the individual's inclusive fitness if it ate smaller relatives that would not metamorphose before the pond dried (and thus would die anyway).

For tadpoles of the invasive cane toad (*Rhinella marina*) in Australia, the selective cost of cannibalism appears negligible. Tadpoles avidly eat the eggs of conspecifics but metamorphose before their mother produces a subsequent clutch. As a consequence, tadpoles do not encounter eggs of close kin. Cannibalism reduces larval density overall, and survivors benefit because they grow faster by eating younger tadpoles, and as a result, also reduce competition for food (Crossland et al. 2011). Cannibalism provides benefits for adult males of the Puerto Rican frog *Eleutherodactylus coqui*. Parental male frogs guard their egg clutches, and other males opportunistically raid the nests and consume the eggs if the parental male is not present or is unable to defend its nest successfully (**Figure 15.6**). This behavior increases the fitness of the cannibal by reducing the reproductive success of a competitor as well as by supplying a meal.

Cannibalism is also common among many dendrobatid frogs. A parent carries tadpoles to small pools of rainwater-phytotelmata-that form in holes in trees and vines, the leaf axils of bromeliads, empty nutshells, and similar sites (Caldwell and Araújo 2004; Summers and McKeon 2004). The tadpoles of species that develop in relatively large phytotelmata feed on aquatic insects and other small organisms. Cannibalism occurs if multiple tadpoles are placed in a pool; larger tadpoles consume smaller conspecifics until only one is left. Males of some species select phytotelmata that are not occupied by other tadpoles, whereas other species deposit their tadpoles indiscriminately (Summers and McKeon 2004). Paradoxically, males of the French Guianan frog Dendrobates tinctorius seem to increase the risk of cannibalism by placing their tadpoles in phytotelmata already occupied by a large resident tadpole and avoiding phytotelmata with a small resident (Rojas 2014).

Cannibalism is far less common in reptiles than in amphibians, perhaps because offspring are often produced within the adult home range and the chance of an adult eating its own offspring is thus high (Polis and Myers 1985; Mitchell 1986). Limited information available suggests that adults may avoid eating smaller conspecifics.

Some individual adult curly tailed lizards (*Leiocephalus schreibersi*) in the Dominican Republic do not eat juveniles, even though cannibalism by adults appears to be a major cause of juvenile mortality overall. When presented with juvenile *Leiocephalis* and *Anolis* of the same body size, two-





Figure 15.6 Male *Eleutherodactylus coqui* **defend their eggs from cannibalistic males.** These small frogs (SVL 3–4 cm) often nest within the shelter of decaying palm fronds, where parental males guard egg clutches laid by the females.



(A) A male attending an egg clutch. (B) A parental male (right) blocks a nest intruder, attacking and biting the conspecific male threatening to cannibalize the eggs. (A, photograph by Margaret Stewart; B after Townsend et al. 1984.)

thirds of the adult *Leiocephalis* ate the *Anolis*, while only one-third ate juvenile *Leiocephalis* (Jenssen et al. 1989). All but 3 of the 24 resident juveniles in the study area had home ranges that were completely within the home ranges of a non-cannibal male and a non-cannibal female. Adults actively defend their home ranges from intruding adults, so juveniles within the territory of a non-cannibalistic pair would gain protection. Whether non-cannibalistic adults were protecting their own young, however, is not known.

Herbivory and omnivory

Among amphibians, only the larvae of anurans feed on plants; tadpoles feed on algae, bacteria, and detritus by scraping attached materials from the substrate or by filter feeding in the water column or at the surface (see Chapter 11). The strictly herbivorous reptiles are land tortoises (Testudinidae), the green sea turtle (Chelonia mydas), all members of the lizard family Iguanidae, the agamid lizards Uromastyx and Hydrosaurus, and the scincid lizard Corucia. These species are herbivorous throughout life, and their diets are made up largely of leaves (Iverson 1982; Rand et al. 1990). Herbivorous reptiles and tadpoles, like other vertebrates, lack cellulases and consequently cannot digest cellulose, the polysaccharide that makes up the cell wall of vascular plants and some algae. Digestion of plant material is facilitated by mutualistic intestinal symbionts (bacteria, protozoans, and nematodes) that break down cellulose into simple compounds, such as short-chain fatty acids, that are absorbed across the wall of the intestine.

Digestion of plant material by some tadpoles is enhanced by nematode symbionts (Pryor and Bjorndal 2005). American bullfrog (*Rana catesbeiana*) tadpoles with their normal complement of microbial symbionts were divided into two groups, one with *Gyrinicola batrachiensis* nematodes and one without nematodes. Tadpoles with nematodes metamorphosed 16 days earlier than tadpoles without nematodes (191 vs. 207 days, respectively). This striking difference in the rate of development is attributable to the greater total production of short-chain fatty acids in the guts of infected tadpoles—20% of total daily energy requirements compared with 9% for tadpoles with only microbial symbionts

In reptiles, microbial digestion takes place in an elongated and enlarged colon. The colon is partitioned by a series of valves or ridges that slow the passage rate of the digesta and increase the surface area for absorption of nutrients. As a consequence, the digestive efficiencies of herbivorous turtles and lizards are similar to those of mammalian hindgut fermenters such as horses and rabbits (Bjorndal 1985). For example, individuals of the green iguana (*Iguana iguana*) of Central America digest 54% of their plant diet, and microbial fermentation provides at least 38% of their caloric intake (McBee and McBee 1982; Troyer 1984).

The offspring of mammalian herbivores are inoculated with intestinal symbionts during birth and subsequently by mutual licking of mother and young. In contrast, herbivorous reptiles do not exhibit parental care, and the gut symbionts needed to digest food are not passed directly from parents to their offspring. How, then, do hatchlings acquire their gut microbes? Katherine Troyer's (1982) observations of the green iguana in Panama suggest that transferring gut symbionts between generations is the function of a specialized social interaction that occurs soon after hatching.

Green iguanas nest communally, and many clutches are deposited in close proximity. Hatchlings swallow soil from the nest chamber and from the nesting area during the first week after hatching. Soil bacteria form a simple fermentation system in the gut that facilitates digestion of plant material during the second week of life. Hatchlings then disperse as family groups (Burghardt et al. 1977) into the forest canopy, where they associate with adults and acquire their microbial symbionts by seeking out and eating feces of adults (Troyer 1982). This brief association with adults is necessary because the symbionts are obligate anaerobes and do not live long when exposed to oxygen outside a lizard's gut. After inoculation with gut microbes, juvenile iguanas return to the forest-edge vegetation, where they remain for several years while they grow to adult size.

In general, herbivorous reptiles are large and live in warm climates (Pough 1973; Cooper and Vitt 2002; Espinoza et al. 2004). Reptilian herbivores may need to be large to fill their energy and nutrient demands on a strictly plant diet; large animals have low mass-specific energy requirements and can thus support the relatively large guts needed for large volumes of plant material. They may need to live in warm environments to have the high body temperatures needed for effective fermentation of plant material. Nonetheless, herbivory has evolved multiple times in the lizard family Liolaemidae, and herbivorous species are not only small, but their distributions are concentrated in cool climates (Espinoza et al. 2004). The secret to their success as herbivores is that they are able to attain body temperatures as high as those that characterize the large herbivores that live in warm climates. Small body size allows these lizards to heat rapidly in climates where thermal opportunities are unpredictable and brief.

While few reptiles are herbivorous, many reptiles consume plant materials, at least occasionally. Cooper and Vitt (2002) estimate that only 1% of lizard species are herbivores (90% or more plant volume in diet) while 12% are omnivores or herbivores (10% or more plant volume in diet). Fruit and flowers are particularly common food items for omnivorous species because these structures have large energy-rich cells that are easily ruptured so that their energy and nutrients are readily accessible (Schall and Ressel 1991). Fruit and flowers tend to be available seasonally, and omnivores thus opportunistically utilize these plant parts when available. For example, the diet of the North American fringe-toed lizard *Uma inornata* included 59% plant material (flowers of two species of shrubs) in May and 38% plant material in July (Durtsche 1995). Arthropods (A)





Figure 15.7 Nectivorous lizards may act as pollinators in island ecosystems On some islands, a low density of bird pollinators may contribute to the feeding habits of some lizards. In the Canary Islands, Gallotia galloti (Lacertidae) feeds on the nectars of (A) foxglove (Isoplexis canariensis) and (B) tower of jewels (Echium wildpretii). (Photographs by José Juan Hernández.)

were most abundant in the habitat in May, suggesting that the lizards were feeding selectively on flowers at this time.

Omnivorous lizards share some or all of the important adaptations of herbivorous lizards. These include a long, partitioned colon, large body size, high bite force relative to body size, and teeth that are robust and bladelike (Herrel 2007). The latter two traits allow herbivores to reduce tough fibrous plant materials into bite-size pieces. Omnivorous diets thus provide an evolutionary transition to herbivory.

Adaption to the consumption of plant material can emerge surprisingly quickly. In 1971, five pairs of the lizard Podarcis sicula were taken from a small island in the Adriatic Sea and introduced to a nearby island (Herrel et al. 2008). The introduced population not only flourished, but 36 years later exhibited adaptive evolution to its new environment. A shift from insectivory (<10% dietary plant mass) to omnivory (roughly 50% dietary plant mass) was associated with an increase in body and head size, changes in head shape, and an increase in bite force relative to the source population. Individuals in the introduced population even exhibited colonic valves similar to those of specialized herbivorous lizards.

Omnivorous lizards also feed on nectar. Nectivory, however, is an island phenomenon; 35 of 37 reports of nectar feeding by lizards are from islands (Olesen and Valido 2003). Lizards that feed on nectar may be important pollinators in island ecosystems because of the low abundance and diversity of nectivorous birds. On the Canary Islands, the most frequent visitors to flowers of the foxglove Isoplexis carnariensis are the lacertid lizard Gallotia

galloti (Figure 15.7) and a bird, the Canary Islands chiffchaff (Phylloscopus canariensis); both species feed opportunistically on nectar (Rodríguez-Rodríguez et al. 2013). While the lizards produce a higher seed set per visit, the warblers are the more effective pollinators overall because they make so many more visits to flowers than lizards. Pollination by lizards is thus somewhat complementary to pollination by the more active endothermic warblers. In contrast, day geckos (Phelsuma) on the island of Mauritius are the most important pollinators of Trochetia boutoniana and T. blackburniana. These plant species produce red and vellow nectar, respectively. Colored nectar is a visual signal that is much more attractive to geckos than clear nectar, and thus presumably increases the efficiency of gecko pollinators (Hansen et al. 2006).

Ontogenetic and sexual variation in diet

Many young birds and mammals are fed by their parents and do not begin to forage for themselves until they have reached adult body size. In contrast, young amphibians and reptiles are on their own, and populations of amphibians and reptiles are made up of individuals that vary widely in body size. Changes in the diets of carnivores during ontogeny reflect an increasing ability to capture, subdue, and swallow large prey. Both maximum prey size and the range of prey sizes eaten typically increase as individuals grow because large individuals continue to eat small prey while they add large prey to their diets. The types of prey eaten may change as well. For example, adults of the water snake Nerodia erythrogaster are anuran specialists, but juveniles eat small fish (Mushinsky et al. 1982). Diets shift to frogs and toads when individuals reach body lengths between 50 and 70 cm (Figure 15.8). Similarly, the occurrence of insects gradually decreases and the occurrence of crabs increases during ontogeny in the diet of Crocodylus acutus (Platt et al. 2013).

A few species of reptiles shift from a largely carnivorous diet as juveniles to a largely omnivorous diet as adults. For example, juvenile slider turtles Trachemys scripta eat small

(B)



fish and invertebrates as well as plant material, whereas adults eat mostly plant material. A shift from largely carnivorous juveniles to largely omnivorous adults is also exhibited by the Central American lizard *Basiliscus basiliscus* and the South American lizard *Tropidurus torquatus*. For *T. torquatus*, the proportion of plant material in the diet increased from 5–23% in the two smallest size classes to 62% in the largest size class (Fialho et al. 2000). The carnivorous diets of juveniles provide more energy and nutrients (especially nitrogen) for growth than do the herbivorous diets of adults. Juveniles may also be able to capture moving prey more readily than adults because they are more agile.

As individuals reach adult size, the diets of males and females may diverge as the result of differences in body or head size or both. For example, females of the file snake *Acrochordus arafurae* in northern Australia have much larger bodies and heads than do males. Females forage in deep water and eat large fish, whereas males forage in shallow water and eat small fish (Shine 1986).

Male lizards typically have relatively larger heads than females, and conversely, females have relatively larger abdomens than males (Scharf and Meiri 2013). Such sexual dimorphism should favor larger prey sizes for males even at the same overall body mass or snout-vent length. For example, adult males of the lizard *Anolis conspersus* are considerably larger than adult females. Not only do adult males eat larger insects than do adult females, but males eat larger insects than females even when both sexes are the same snout-vent length (Schoener 1967).

Temporal and spatial variation in diet

Diet composition is far from static. Diets vary from season to season, from year to year, and from place to place. For example, year-to-year variation occurs in the diet of lakeshore populations of the western garter snake (*Thamnophis elegans*) at Eagle Lake in California (**Figure 15.9**). Annual variation Figure 15.8 Ontogenetic changes in the diet of a water snake (Nerodia erythrogaster). The index of relative importance is a measure of the relative contributions of fish and amphibians to the diets of each size class (determined by snout-vent length) of the snake. Nerodia erythrogaster eat fish when they are small and switch to amphibians as they grow larger. (After Mushinsky et al. 1982; photograph by Robin Andrews.)

in rainfall determines water level, and hence whether the toad *Bufo boreas* is able to breed. In wet years, snakes eat newly metamorphosed toads, whereas in dry years they eat fish and leeches, which are always available in the shallow water of the lake (Kephart and Ar-

nold 1982). As we discussed in Chapter 9, *Thamnophis elegans* also exhibits geographic variation in diet (Bronikowski and Vleck 2010): individuals in lakeside populations eat fish, whereas individuals in meadow populations eat frogs (*Pseudacris regilla*).



Figure 15.9 Annual variation in the diet of *Thamnophis* **elegans.** The histograms show the proportion of amphibians, leeches, and fish in the diet of *T. elegans* at Eagle Lake, California in each of 7 years. Although fish and leeches are always available and are the most dependable prey for this snake population, they are eaten less frequently in years when toads (*Bufo boreas*) are available. (After Kephart and Arnold 1982.)

15.2 Amphibians and Reptiles as Consumers

Searching for, seizing, and ingesting food items are important aspects of the lives of all individuals. These behaviors are a sequence of events that individuals repeat many times throughout their lives no matter whether their diet consists of arthropods, foliage, lizards, frog eggs, or nectar. The nature of the search, what items are selected, and the mechanisms used to seize and process them vary among clades. While the behaviors used during a feeding cycle may appear instinctive, recent laboratory studies demonstrate that amphibians and reptiles are surprisingly quick learners and use cognitive skills to find food and to avoid inedible items.

Innate and learned responses to prey

The characteristics of prey that stimulate a feeding response are, in part, genetically based (innate) and differ among species with different foraging modes (Roth 1986). Frogs and salamanders that actively search for prey respond to elongate items that move continuously. In contrast, frogs and salamanders that sit and wait for prey to come into range prefer small compact items with jerky movements. Innate responses may vary among individuals as well. Each *Anolis lineatopus* lizard in Jamaica has its own menu of acceptable and unacceptable prey types at hatching (von Brockhusen 1977). Some hatchlings readily eat crickets, whereas others will not attack crickets unless they have been starved.

Individual preferences change slowly as individuals gain experience through learning; individuals eat a greater diversity of prey types as adults than they did as hatchlings.

The contribution of learning to the foraging behaviors exhibited by amphibians and reptiles is greatly underappreciated. Studies of amphibians and reptiles have not demonstrated effective learning skills because the animals typically are not provided with biologically relevant physical and social conditions before and during testing (Burghardt 2013). When appropriate conditions are provided, amphibians and reptiles can respond effectively to novel situations. For example, juvenile black-throated monitor lizards (Varanus albig*ularis*) required only a single trial to learn to open a hinged door and extract a mouse from a transparent plastic tube. In the first trial, the lizards took an average of 5.5 minutes to get the door open and catch a mouse, but they did this in only 1 minute in the second and third trials (Manrod et al. 2008).

Incubation temperature affects cognitive abilities as well as other aspects of the phenotype (see Chapter 9). Hatchlings of the scincid lizard *Bassiana duperreyi* exhibit enhanced learning performance both with regard to escaping from simulated attacks of predators and finding food if they hatch from eggs incubated at higher rather than lower temperatures (**Figure 15.10**) (Amiel and Shine 2012; Amiel et al. 2013).

One of the skills putatively limited to social species is the ability to learn from the behaviors of other individuals. Tortoises are not social animals. Nonetheless, while four juvenile red-footed tortoises (*Geochelone carbonaria*) were baffled by a fence that kept them from feeding on strawberries placed on the opposite side, four other individuals learned to walk around this barrier after they watched a trained tortoise complete the detour and eat the strawberries. None of the four non-observers succeeded in reaching the strawberries, whereas all of the observer tortoises were successful (Wilkinson et al. 2010). Learning was socially mediated, albeit some of the four individuals were better learners than others.

Not all potential prey items are edible, and some are dangerous. For some amphibians and reptiles, avoidance of noxious or dangerous prey is learned. If a predator associates prey features such as conspicuous coloration or distinctive



Figure 15.10 The effect of incubation temperature on learning in a scincid lizard (**Bassiana duperreyi**). Hatchlings from eggs incubated at $24 \pm 5^{\circ}$ C (warm) and at $18 \pm 5^{\circ}$ C (cold) were tested to determine if their ability to locate a food reward improved over time. The lizards were offered crickets, which were consistently placed in one of two distinctly colored and patterned arms of a Y-maze. Both groups of hatchlings improved their performance over time, but hatchlings from the warm incubation group found the reward faster and made fewer errors. (A) Mean number of successful outcomes per trial for warm and cold incubation treatments. (B) Mean log-time to complete trials for each treatment. (After Amiel et al. 2013.)

behavior with an unpleasant experience, it can subsequently avoid similar prey. In Australia, for example, hatchling freshwater crocodiles (*Crocodylus johnstoni*) learn to avoid newly metamorphosed cane toads (*Rhinella marina*) (Somaweera et al. 2011). Naive individuals initially ate toads, and apparently suffered no long-term ill effects from the toad's bufadienolide toxin. Nonetheless, after exposure to one or two toads, the majority of crocodiles did not attack toads again. If hatchlings continue to avoid toads as they grow to adult size, freshwater crocodile populations will eventually consist of toad avoiders. The potential for such learned avoidance is important for crocodile conservation, because adult toads contain enough toxin to kill adult crocodylians.

Predators will not be able to learn from experience if the consequences of attacking dangerous prey are always fatal. When cane toads were introduced to Australia, for example, populations of the black snake *Pseudechis porphryiacus* declined precipitously because most snakes that ate toads died. In this situation, selection should favor individuals that exhibit genetically based (innate) characters that reduce the probability that a snake will eat a toad, or that make a snake less likely to die if it does so.

Phillips and Shine (2006) tested these predictions by comparing snakes from areas where cane toads had been established for 40 to 60 years (about 23 snake generations) with naive snakes from areas that had not yet been invaded by toads. Naive snakes readily ate freshly killed cane toads (with toxin-filled parotoid glands removed), whereas snakes from areas of long-term sympatry did not eat any of the cane toads offered. To determine if naive snakes were less resistant to cane toad toxin than snakes from the toadexposed population, the researchers dosed snakes from both populations with an amount of toxin previously determined to be nonlethal (80 µg of toad skin per gram of



snake body mass) using a feeding tube. Naive snakes were less resistant than toad-exposed snakes; the toxin reduced the swimming speed of naive snakes by 30% compared with an 18% reduction in snakes from toad-exposed populations. These differences between naive and toad-exposed snakes appear to be innate. Naive snakes did not learn to avoid freshly killed mice or lizards after they had eaten one that had been laced with a large but nonlethal amount of toad toxin. Moreover, resistance was not induced when naive snakes were dosed with a series of small but nonlethal doses of toxin over several weeks.

Sensory modalities

Amphibians and reptiles use a diversity of sensory modalities while they search for, attack, and consume prey items. The best studied are visual (photoreception) and chemical (chemoreception). We can relate to visual capabilities intuitively because humans are highly visual animals, but we have relatively poor chemosensory abilities. It will therefore be helpful to explain what we mean when we talk about the use of chemosensation for prey detection.

Olfaction is the detection of airborne volatile molecules by receptors in the olfactory epithelium of the nasal cavity, and gustation is the detection of chemicals dissolved in water by taste buds (receptor cells) on the tongue or the epithelium inside the mouth. The roles of olfaction and gustation in squamate feeding are not well understood, but they appear to be used to detect highly odoriferous foods (e.g., flowers, carrion) and to make feeding decisions about food once it is in the mouth, respectively.

Vomerolfaction, on the other hand, is an important sensory modality of squamates, and its function in prey detection is well known. Vomerolfaction is the detection of nonvolatile molecules sampled by the ventral surfaces

of the tongue as it is flicked out of the mouth and contacts the substrate. The tongue is curled as it is drawn back into the mouth, so that its ventral surface transfers odor molecules to the passageways that lead to paired vomeronasal organs (also known as Jacobson's organs) located above the roof of the mouth (**Figure 15.11**).

In squamates, the rate of tongue flicking is a behavioral assay of the stimulation of the chemical receptors that stimulate feeding responses. Burghardt (1967) pioneered the technique that is still used to study feeding responses. Newly hatched snakes flick their tongues and strike at cot-

Figure 15.11 Vomerolfactory system of a squamate. (A) The paired vomeronasal organs (only the left side is shown here) detect odor molecules on the substrate contacted by the animal's flicking tongue. (B) The ventral (lower) surface of the tongue curls back, transferring the chemical signals to the vomeronasal organs via openings in the roof of the mouth. ton swabs that have been dipped in water extracts of potential prey and respond selectively to different kinds of prey. They respond most strongly to odors of the prey normally eaten by members of their own population. For example, adult smooth green snakes (*Opheodrys vernalis*) eat insects and newly hatched green snakes respond most strongly to insect extracts, whereas adult brown snakes (*Storeria dekayi*) eat earthworms and hatchling brown snakes respond most strongly to earthworm extracts (Burghardt 1967). Selectivity in these studies was exhibited before individuals had any previous exposure to prey. The specialization thus seen in their diets is produced by innate responses to the chemical cues of particular prey types.

Sensory modalities used by amphibians and reptiles during a feeding cycle also include infrared reception, mechanoreception, and electroreception. While we know far less about these modalities than we do about vision and chemoreception, they can be the primary sensory modality for a species or can be integrated synchronously or sequentially with other sensory modalities. and predator avoidance in some species (Wilkens and Hofmann 2005). The expression of these two types of organs within the three major amphibian lineages is highly variable (Fritzsch and Wake 1986). Salamanders and caecilians, but not anurans, have electroreceptors, and ecology may be more important than phylogeny in determining the functional components of the lateral line system.

Tympanic hearing of airborne and substrate-born vibrations is an important sensory modality for the socially vocal frogs and crocodylians. Crocodylians are capable of locating sounds produced both above and below water (Dinets 2013; Bierman et al. 2014). The extent to which these and other taxa use hearing to detect prey, however, is known only for a few taxa. Fossorial lizards—for example, *Scincus scincus* (Hetherington 1989) and other sand-swimming skinks (e.g., *Chalcides*)—can detect insects moving on or under the sand surface using vibratory cues. In response, the skinks swim through the sand and emerge when they are near enough to capture the insect with a quick snap of their jaws.

F : 1.a

Pit vipers, boas, and pythons have pit organs that sense infrared radiation; thermal cues are used to identify and orient the snake toward endothermic prey (see Figure 4.5). A pit viper uses the heat radiated from a mouse, for example, to detect its prev. After the strike, the envenomated prey is quickly released. Release reduces the chance a snake will be injured if the prey struggles, but also allows the prey to dash away from the snake before it dies. The bite, however, sets in motion chemical changes in the envenomated prey, and snakes use this information to follow the prey's odor trail (Kardong and Smith 2002; Smith et al. 2005).

Aquatic amphibians have lateral line systems that are used to detect prey (and predators). These systems consist of mechanoreceptors (neuromasts) and electroreceptors (ampullary organs) arranged singly or in rows on the head and body (Duellman and Trueb 1994). Neuromasts are hair cells that respond to directional changes in water currents at the skin surface. For example, African clawed frogs (Xenopus) can detect the movements of insects swimming nearby and use this information to capture them. Ampullary organs are modified neuromasts that sense weak, low-frequency electric stimuli. They appear to facilitate prey capture

Character	Foraging mode		
	Active	Sit-and-wait	
Percent of time moving	High	Low	
Movements/time	High	Low	
Feeding rate	High	Low	
Sensory mode	Vision and vomerolfaction	Vision	
Tongue morphology, function	Narrow and bifurcated, vomerolfaction	Fleshy, prey capture	
Prey movement, distribution	Hidden and mobile, clumped	Mobile	
Body form	Slim	Stout	
Relative clutch mass	Low	High	
Types of predators	Vulnerable to both sit- and-wait and actively foraging predators	Vulnerable to actively foraging predators	
Predation risk	High	Low	
Primary mode of escape	Flight	Crypsis	
Endurance	High	Low	
Sprint speed	Low	High	
Aerobic capacity	High	Low	
Anaerobic capacity	Low	High	
Metabolic rate	High	Low	
Daily energy intake	High	Low	
Learning ability	High	Low	
Predation risk Primary mode of escape Endurance Sprint speed Aerobic capacity Anaerobic capacity Metabolic rate Daily energy intake Learning ability	foraging predators High Flight Low High Low High High High	Low Crypsis Low High Low High Low Low	

Data from Huey and Pianka 1981; Pough et al. 2004; Cooper 2007.

^aCorrelates of each feeding mode are directly applicable to lizards but have been applied with modification to frogs (Toft 1981) and snakes (Beaupre and Montgomery 2007).

TABLE 15.1 Correlates of active and sit-and-wait foraging modes

Foraging modes

(A)

The behaviors that amphibians and reptiles use to search for prey appear dichotomous. If you were to sit quietly in the understory of a Central American rain forest, for example, your attention would probably be drawn first to a foraging Holcosus (Teiidae, formerly Ameiva) lizard. These terrestrial lizards move continuously and conspicuously while searching for prey. Individuals push their snouts into piles of leaves, scratch into heaps of decaying bark, and dig under logs. A dramatically patterned chartreuse and black dendrobatid frog might also attract your attention. It, too, moves constantly while foraging, albeit on a smaller geographic scale than the much larger Holcosus. If you are really attentive, you might see a small slender lizard perched motionlessly on a low branch or tree trunk. It is an Anolis, and it is also foraging, but the only evidence of this behavior is subtle movement of its eyes and head as it scans the ground below. If you watch long enough, you will see it leap down suddenly to capture an insect, and then run back up the tree. You are unlikely to see a Craugastor (formerly Eleutherodactylus) frog, which is the anuran counterpart of the Anolis lizard. Like Anolis, a Craugastor is cryptically colored and patterned. It is even less conspicuous than the Anolis, however, because it hides in the leaf litter and feeds infrequently.

The dichotomous behaviors in the scenario above are called active foraging (the *Holcosus* lizard and dendrobatid frog) and sit-and-wait foraging (the *Anolis* lizard and *Craugastor* frog). In general, active foragers move frequently and relatively rapidly, and search large areas. Actively foraging lizards tongue flick frequently, using vomerolfaction to detect concealed prey. Prey items are usually captured with little or no pursuit. In contrast, sit-and-wait foragers search

visually for prey from a fixed perch site. Capture may follow a brief pursuit, or the individual may wait until the prey can be ambushed.

Some sit-and-wait predators lure prey within striking range by twitching body parts (**Figure 15.12**) (Murphy 1976; Sazima 1991; Hagman and Shine 2008; Hagman et al. 2009). Alligator snapping turtles (*Macroclemys temminckii*) display a wormlike appendage on their tongue to attract fish. Some snakes and the pygopodid lizard *Lialis burtonis* in Australia attract small frogs and lizards by undulating their tails. Tail tips are often lighter in color than the rest of the body, a feature that makes the lure more conspicuous. Cane toads (*Rhinella marina*) and horned frogs (*Ceratophrys*) twitch their toes to attract small frogs.

Since Huey and Pianka (1981) first characterized active foraging versus sit-and-wait foraging modes, this dichotomy has become an organizing principle for many groups of organisms (Cooper 2005), and especially for lizards (Reilly et al. 2007). The reason is that foraging modes are broadly integrated with a wide range of biological traits that are functionally related to the acquisition of food (**Table 15.1**). The most fundamental integration is between foraging mode and sensory modality; all active foragers use vomerolfaction to detect prey and have elongate forked tongues that function as sensory structures. In contrast, sitand-wait foragers use vision to detect prey and have fleshy tongues that they use to capture prey (**Figure 15.13**).

In the following sections we discuss some of the other correlates of foraging mode. We focus on lizards, but amphibians (Toft 1981) and snakes (Beaupre and Montgomery 2007) can be viewed in this context as well.

DIET We pointed out that knowing the qualitative and quantitative distribution of foods in the environment can only tell us what a predator *could* eat, not what it *does* eat. The foraging mode paradigm offers a clear example of how diets are profoundly influenced by how organisms



Figure 15.12 Examples of luring.

(A) An alligator snapping turtle (Macroclemys temminckii) displaying the wormlike appendage on its tongue. (B) Toe twitching by a cane toad (Rhinella marina). The photograph is a composite of four frames from a video recording; the blurred toe on the hind foot is the result of the foot's rapid vertical motion, which attracts smaller toads. (C) Frames from a video sequence show caudal luring by the Australian death adder (Acanthophis praelongus). Note responses of the caged cane toad to the tail movements. (A, photograph by Harvey Pough; B,C from Hagman et al. 2009 and Hagman and Shine 2008, courtesy of Mattias Hagman.)

(A)



Figure 15.13 Tongues of squamates. (A) Elongate forked tongue of the elapid snake *Hoplocephalus bungaroides*, found in Australia. (B) Fleshy tongue of the iguanian lizard *Phrynosoma solare*. (A, photograph by Sylvain Dubey; B, photograph © BBC Hidden Kingdoms Program.)

search the environment. Active foragers encounter more hidden prey than do sit-and-wait foragers, and they can discriminate between prey with chemical defenses and those without. These two factors alone may account for the observation that termites (tasty) are characteristic items in the diets of active foragers that search for hidden prey using vomerolfaction, whereas ants (chemically defended) are characteristic items in the diets of sit-and-wait foragers that search visually for prey (Vitt and Pianka 2007).

Prey size does not appear to be related to foraging mode. While Vitt and Pianka (2007) suggest that large prey are best captured in the jaws and small prey with the tongue, the fact is that both active foragers and sit-and-wait foragers eat a wide range of prey sizes. We just noted that actively foraging and sit-and-wait foraging species of lizards commonly eat termites and ants, respectively. At the other extreme, some active foragers and some sit-and-wait foragers eat relatively large prey. For example, actively foraging varanid lizards consume mammals, and the pygopodid *Lialis burtonis* eats other lizards, while an extreme sit-and-wait forager, the Central American casque-headed lizard *Corytophanes cristatus*, feeds once a day or less, and eats insects that average half its body length (**Figure 15.14**).

MORPHOLOGY The body forms of active foragers match their lifestyle. They have slim bodies, long tails, and relatively long legs. In contrast, sit-and-wait foraging lizards and snakes tend to have stout bodies, short tails, and relatively short limbs (**Figure 15.15**). As a result, foraging mode constrains the mass of eggs or embryos that a female can carry (Vitt and Price 1982). The slim, streamlined bodies of active foragers are associated with low relative clutch masses (i.e., the mass of the clutch divided by the mass of the female). In contrast, the stout bodies of sit-and-wait foragers are associated with high relative clutch masses.

These associations presumably reflect both morphological constraints (space within the abdomen) and performance constraints (a large clutch mass would be a greater handicap to females of active foragers than of sit-and-wait foragers). These observations do not mean that body shape reduces

(A)



(B)



the annual reproductive output of active foragers, however, because active foragers may produce several small clutches per season, whereas sit-and-wait foragers usually produce just one or two large clutches.

PREDATORS Predation on active and on sit-and-wait foragers is likely to differ qualitatively and quantita-

Figure 15.14 Prey items of the Central American lizard Corytophanes cristatus are large relative to its body size. (A) Adult *C. cristatus*. This species is a sit-and-wait forager that feeds infrequently on large insects. (B) A juvenile with a head-and-body length of 53 mm had a 28-mm-long beetle larva removed from its stomach. (From Andrews 1979; photographs by Robin Andrews.)



Figure 15.15 Morphology of active foragers versus sit-andwait foragers. (A) *Aspidoscelis exsanguis*, an actively foraging lizard, has a sleek, slim body. (B) The sit-and-wait forager *Sceloporus undulatus* is stout. (Photographs: A, Robin Andrews; B, © Brian Barnes/Alamy.)

tively. Foraging mode and vulnerability to predators alternate in successive levels of a food web: active foragers are vulnerable to both sit-and-wail and actively foraging predators whereas sit-and-wait foragers are vulnerable to actively foraging predators (Huey and Pianka 1981).

Active foragers often have patterns and colors that are conspicuous, at least to a human observer. Because their frequent movements make them conspicuous, being cryptic would have little value, and other selective forces act on color and pattern. In contrast, sit-and-wait foragers usually match their background, and crypsis is enhanced by low rates of movement.

An outcome of the extensive and frequent foraging movements of active foragers is that they should be subject to a greater risk of predation than sit-and-wait foragers. This prediction is supported by observations of snakes. Predation on the actively foraging colubrid *Coluber* (formerly *Masticophis*) *flagellum* (16%) was twice that on the sit-andwait foraging viparid *Crotalus cerastes* (8%) over 3 years at a study site in California's Mohave Desert (Secor 1995). Similarly, the predation rate (car, human, and natural) on two species of actively foraging snakes in France was greater than the predation rate on four species of sit-and-wait foraging snakes (Bonnet et al. 1999). Cars, like natural predators, are more likely to intercept an active forager than a sit-and-wait forager.

PHYSIOLOGY Do animals that spend long periods in continuous motion while foraging differ in metabolic capacity and energy balance from animals that rely on brief but intense bursts of speed to capture prey but are otherwise inactive? The answer to this question is clearly yes (Beaupre and Montgomery 2007; Brown and Nagy 2007). Active and sit-and-wait foragers differ in the extent that they use aerobic and anaerobic metabolic pathways. Active foragers use high aerobic capacity to support long periods of activity; they have high endurance but low sprint speed. Sit-andwait foragers use their high anaerobic capacity to support high-speed attacks on prey; they have high sprint speed but low endurance. In accord with their high oxygen requirements, active foragers have larger hearts and more red blood cells per unit of plasma (i.e., a higher hematocrit) than do sit-andwait foragers. These characteristics provide relatively high levels of oxygen to the tissues of active foragers. Active foragers capture more prey while foraging than sit-and-wait foragers do but have higher energy requirements as well because of the cost of foraging. On a daily basis, however, active foraging appears to produce a greater net energy gain than does sit-and-wait foraging. For two species of lacertid lizard at one Kalahari Desert site, the actively foraging *Heliobolus* (formerly *Eremias*) *lugubris* had a net daily energy gain greater than that of the sit-and-wait forager *Pedioplanis* (formerly *Eremias*) *lineoocellata* and consequently grew almost twice as fast (Nagy et al. 1984).

In accord with their high activity levels, active foragers maintain higher body temperatures while foraging (e.g., Aspidoscelis, 40°C; varanids, 35–36°C) than do sit-andwait foragers (e.g., Anolis, 26-30°C; Sceloporus, 34-35°C). Because active foraging can be interspersed with thermoregulatory behaviors, active foragers have greater scope for thermoregulation than do sit-and-wait foragers. For the latter, thermoregulation is constrained to the microclimate around a fixed perch by the importance of limiting movements that would attract the attention of predators. Because enzyme kinetics are temperature-dependent, an active forager at a high body temperature can support higher levels of aerobic activity than can a sit-and-wait forager at a lower body temperature. The occasional sprints of sit-and-wait foragers are supported by anaerobic metabolism that is less sensitive to temperature.

Foraging modes that don't fit the paradigm

Viewing foraging behavior as a dichotomy has provided useful insights into the evolution of complex adaptations. Nonetheless, many taxa cannot be pigeonholed neatly into this dichotomy (Reilly et al. 2007). For example, many reptiles are better characterized as cruise foragers because they alternate foraging movements with pauses at sites where they sit and wait for prey. The chameleon *Bradypodion pumi*- (B)

(A)



Figure 15.16 Gekkotan lizards exhibit a diversity of foraging modes. Gekkotans are nocturnal and have a highly developed olfactory sense, distinguishing them from diurnal lizards that rely on vision and vomerolfaction to locate prey. (A) Active forager *Coleonxy variegatus* (North America). (B) Sitand-wait forager *Thecadactulus rapicauda* (Central and South America). (C) *Diplodactylus vittatus* (Australia), a presumed mixed forager. (Photographs: A, © blickwinkel/Alamy; B, © R. M. Bolton/Alamy; C, © Chris Mattison/Alamy.)





lum provides an example. This lizard spends relatively more time moving than sit-and-wait foragers do, but it makes fewer moves per minute than active foragers do (Butler 2005). Several snakes exhibit flexible foraging in which they mix active and sit-and-wait foraging either seasonally or on a daily basis (Beaupre and Montgomery 2007). Foraging behavior also varies among closely related species. For example, while all *Anolis* fall within the general category of sit-and-wait foragers, rates of movement during foraging differ among **ecomorphs** (Johnson et al. 2008).

Identifying foraging modes that don't fit the active foraging versus sit-and-wait foraging paradigm is difficult because observations of foraging behavior have often been forced into one or the other of the two paradigmatic modes. Nonetheless, it is clear that while members of some species or clades are either active foragers or sit-and-wait foragers, others exhibit intermediate behaviors and still others combine behaviors characteristic of active and sit-and-wait foraging.

Observations of gekkotan lizards provide insights into the factors responsible for the diversity of foraging modes. Bauer (2007) considers that gekkotans generally exhibit mixed foraging modes in which movement patterns are intermediate between those of active and sit-and-wait foraging and range from cruise foraging (slow, continuous movements) to serial ambushing (movement between ambush sites). The mixed foraging modes of gekkotans may reflect two features that characterize this taxon: nocturnality and highly developed olfactory senses that are used for detection of food (Schwenk 1993). Fundamental components of gekkotan physiology, morphology, and ecology thus differ from those exhibited by lizards that are diurnal and that use either vomerolfaction (active foragers) or vision (sitand-wait foragers) to detect food. As a result, gekkotans exhibit suites of characters associated with foraging modes that extend the range from paradigmatic active foragers (eublepharids, pygopodids), to mixed foragers, to sit-andwait foragers (*Phelsuma*, sphaerodactylids) (**Figure 15.16**).

Phylogeny and foraging modes

A fundamental assumption of the foraging mode paradigm is that the association between foraging mode and ecological, morphological, and physiological traits (see Table 15.1) is the result of adaptive evolution. A problem with this interpretation is that foraging mode is strongly associated with phylogeny. For example, most varanid, scincid, teiid, and lacertid lizards are active foragers, and most iguanid lizards are sit-and-wait foragers. Hence, the link between foraging mode and other traits could be the result of phylogenetic history rather than adaptive evolution. Fortunately, phylogenetic relationship provides a conceptual framework to distinguish between these possibilities.

Herbivory, for example, has evolved in many different lizard clades (**Figure 15.17**). Herbivores are active foragers by definition because waiting motionless for plants to pass by is not a successful evolutionary strategy (Herrel 2007). Nonetheless, most herbivorous lizards belong to the Iguanidae. Unlike their sit-and-wait ancestors, iguanid herbivores are not only active foragers, they also use vomerolfaction to detect food. Herbivores in clades that were ancestrally active foragers also exhibit character reversals: they have stout bodies and large heads, characters that are typically associated with the sit-and-wait foraging mode. Herbivorous lizards also share sets of unique characters related to a diet of plant material: high bite forces, mediolaterally flattened and bladelike teeth, tall heads, long guts, and partitioned colons (Herrel 2007). Both character reversals and the evolution of **Figure 15.17 Herbivorous lizards are phylogenetically diverse.** Herbivores are by definition active predators, since plant prey cannot come to them. Most herbivorous lizard species belong to the Iguanidae, represented here by (A) *Cyclura nubila*. Herbivores are also found among other taxa, including (B) Scincidae (e.g., *Corucia zebrata*) and (C) Agamidae (e.g., *Uromastix aegyptius*). (Photographs: A,B, Harvey Pough; C, Christopher R. Tracy.)



(B)

unique characters provide evidence of adaptive evolution associated with a dietary shift to herbivory, irrespective of phylogenetic relationship.

15.3 Parasites

We separate the discussions of parasitism and predation because different groups of organisms act as parasites and as predators, and the two kinds of interactions have distinctive features and outcomes.

- Predators are usually at least as large as their prey, whereas parasites are always smaller than their hosts.
- The interaction between parasite and host is prolonged, with the host providing nutrition (and often a home) for the parasite, whereas the interaction between predator and prey is short and violent.
- Parasites must keep their host alive, at least until the parasite or its offspring can reach a new host, whereas predators must kill their prey to ensure their own survival and reproduction.

The line between predation and parasitism can be fuzzy because some organisms that act like parasites in the short term are functionally predators. For example, larvae of sarcophagid flesh flies that feed on bufonid harlequin frogs (*Atelopus*) and dendrobatid frogs do not kill their hosts outright, but the frogs die within a few days (Crump and Pounds 1985; Hagman et al. 2005).

Amphibians and reptiles are parasitized by the same types of organisms that plague other vertebrates. The biology of parasite-host relationships is best known for humans because of the social and economic impacts of diseases such as malaria (*Plasmodium*, a protozoan), schistosomiasis (*Schistosoma*, a trematode), and onchocerciasis (*Onchocerca*, a nematode). There is every reason to suspect, however, that the interactions between parasites and their amphibian and reptile hosts are similar to those between parasites and human hosts.

Internal parasites

(C)

Internal parasites of amphibians and reptiles include both single-celled (protozoan) and multicellular (metazoan) animals. Transmission to a new host is a critical part of the life cycle of parasites. For some parasites, infective stages are transmitted directly from one host to another. Others have complex life cycles that involve one or more intermediate hosts before the parasite is transmitted to the definitive host in which it reproduces sexually.

PROTOZOAN PARASITES Sarcocystis, a protozoan found in the muscles of the giant lacertid lizard *Gallotia stehlini* on the island of Gran Canaria (Matuschka and Bannert 1989), is transmitted when males break off their opponent's tail during a fight; transmission occurs if a male eats the tail of an infected individual. *Opalina ranarum*, the most abundant and widespread of the intestinal protozoans in amphibians, also exhibits direct transmission. Infective *Opalina* cysts are released along with feces when adult frogs enter water to breed, and tadpoles are infected when they consume the cysts. Reproductive hormones of the frog are used by *Opalina* to synchronize its own reproductive cycles with that of its host, and hence facilitate transmission (Lawrence 1991).

Other protozoans have complex life cycles. Phlebotomine sand flies, for example, are the intermediate host and the transmission vector for malarial parasites of the western fence lizard (*Sceloporus occidentalis*) (Schall and Marghoob 1995). A sand fly becomes infected when it feeds on the blood of an infected lizard. The malarial parasite goes though a series of developmental stages in a sand fly, and only then can the bite of an infected sand fly transfer the parasite to another lizard.

METAZOAN PARASITES Metazoan parasites are largely wormlike animals, including nematodes (Nematoda), tongue worms (Pentastomida), and flukes and tapeworms (Platyhelminthes). When cane toads were introduced to Australia, they arrived with a host-specific parasite, the nematode *Rhabdias pseudosphaerocephala*. Because this parasite exhibits direct transmission, it does not depend on other Australian animals to maintain its association with the cane toad. Adult parasites live in the lungs, where they feed on blood. Eggs are coughed up into the digestive tract where they hatch; larvae exit with feces. After one free-living generation, infective larvae find a new toad host, bore through its skin, and make their way into the lungs.

Cane toads illustrate the importance of transmission rate for the continued association of parasites and their hosts. Cane toads are still rapidly extending their range in the Northern Territory, and toads at the range front do not have *Rhabdias* parasites, presumably because of radically reduced transmission rates where host density is low (Kelehear et al. 2012). Escaping their nematode parasites may even enhance the rate of expansion of toads because uninfected toads at the invasion front have greater endurance than infected toads (Llewelyn et al. 2010; Pizzatto and Shine 2012). Escape is temporary, however, as the parasites are only about 2 years behind the toads, and most toads in the population are infected after another 2 to 3 years.

A nematode parasite of horned lizards has a single intermediate host (Sherbrooke 2003). The nematodes live in the stomach of the lizard. When females mature and contain eggs, the nematodes release their hold on the stomach wall and pass through the gut onto the desert floor with the feces. The female quickly desiccates and dies, but her eggs can resist desiccation for 2 years or more. If a harvester ant encounters the dry body of the nematode, the ant carries it back to the nest, where it is fed to ant larvae. The nematode eggs hatch and grow inside the ant larva without harming it. When the infected ant larva metamorphoses into a foraging worker, it may be eaten by a horned lizard, thus completing the transmission cycle (**Figure 15.18**).

The trematode fluke Ribeiroia ondatrae has an even more complex life cycle. Birds and mammals associated with freshwater habitats are the definitive hosts for this fluke (Johnson et al. 2004). When the definitive host defecates, fluke eggs are shed into the water where they hatch into ciliated larvae, or miracidia, that infect the first intermediate hosts, planorbid snails. Several cycles of asexual reproduction take place in snails such that many more freeswimming cercariae larvae exit the snail than the number of miracidia in the initial infection. When cercariae encounter a tadpole-the second intermediate host-they encyst around the developing limbs and may cause malformations. Frog limbs can be truncated or missing, or frogs may express extra limbs (Figure 15.19). These malformations make the frogs more vulnerable to predation by birds or mammals, thus increasing the probability that the parasite will encounter its definitive host.

External parasites

External parasites of amphibians and reptiles include leeches (annelid worms), mites, ticks, and mosquitoes and other blood-sucking flies. Most external parasites complete at least part of their life cycle in the environment and exhibit direct transmission. The most important external parasites of aquatic amphibians and reptiles are leeches. Turtles sampled from ponds in Illinois during one summer were host to four species of *Placobdella* leeches (Readel et al. 2008). Painted turtles (*Chrysemys picta*) and snapping turtles (*Chelydra serpentina*) were the most heavily infested (43% and 48% of individuals, respectively); sliders (*Trachemys scripta*)

Figure 15.18 The nematode *Physaloptera phrynosoma* is a parasite of horned lizards. (A) The dissected stomach of a lizard (*Phrynosoma solare*) contains a black mass of consumed ants and numerous whitish, transparent nematodes (arrow). (B) Female nematode (arrow) discharged with a fecal pellet of *P. modestum*. (C) Nematode larvae emerging from ants that were eaten by *P. solare*. (Photographs by Wade Sherbrooke.)









(C)





and common musk turtles (*Sternotherus odoratus*) were the least infested (18% and 19% of individuals, respectively). Given that leeches drop off their host after feeding, these infestation rates are probably underestimates.

Ticks are common parasites of reptiles, and mites parasitize both reptiles and amphibians. Ticks alternate feeding **Figure 15.19 Trematode parasitism causes limb abnormalities of amphibians.** Encystment of the trematode *Ribeiroia ondatrae* cercaria around the developing limbs of tadpoles causes missing (A) and extra (B) limbs in northern leopard frogs (*Rana pipiens*) and other amphibians. (Photographs by Pieter Johnson.)

on their host and living in the environment, and all life stages are parasitic. Chiggers are the larval stages of trombiculid mites; when the larvae finish feeding they drop off their hosts and metamorphose into independent predatory adults. Chigger mites tend not be host-specific, and some species that attack lizards also attack birds and mammals. Hannemania dunni chiggers parasitize various species of plethodontid salamanders in the southeastern United States (Westfall et al. 2008). In contrast, pterygosomatid mites are lifelong residents on their hosts, and each mite species is associated with a very limited number of lizard species (Bochkov and Mironov 2000; Bertrand and Modry 2004). One of the more surprising locations for mite infestation is in the cloaca of aquatic turtles (Camin et al. 1967; Bochkov 2002). Cloacarinae mites are presumably transmitted directly to a new adult host when turtles copulate.

Feeding by ticks and mites would seem to be detrimental to their hosts. Nonetheless, many species of iguanid, chamaeleonid, gekkonid, lacertid, and scincid lizards have morphological structures called acarodomatia, or mite pockets, where mites and tick attach and feed (**Figure 15.20**) (Arnold 1986). Mite pockets consist of invaginations





(D)

(B)



Figure 15.20 External parasites (A) The five most common sites of mite pockets in lizards. (B) Engorged tick attached to the neck of the Australian skink *Tiliqua rugosa*. (C) Chigger mites (red patches) in and near a mite pocket and around the eye of *Phrynosoma cornutum*. (D) Chigger mites in a mite pocket of *Phrynosoma solare*. (A from Arnold 1986. Photographs: B, Brent Opell; C,D, Wade Sherbrooke.)

(C)



that are thinly scaled internally, and in response to feeding by mites and ticks they become highly vascularized, with dense masses of lymphocytes. While acarodomatia clearly benefit the parasites, the benefit to the lizards is not obvious. Observations of the European lacertid *Psammodromus algirus* support the idea that the presence of the pockets reduces attachment by ticks at locations that affect functions such as hearing (in the ears) or locomotion (around the legs) (Salvador et al. 1999). Individuals with low tick infestation had more ticks in pockets than did individuals with high infestation, suggesting that ticks prefer to be in pockets. Moreover, male lizards with pockets occluded (thus forcing ticks to attach elsewhere on the body), disappeared (presumably as the result of death) from the study area at a higher rate than males with normal pockets.

15.4 Predators

Most amphibians and reptiles are small and tasty. As a consequence, a wide diversity of animals feed on them. Even crocodylians, a relatively small taxon of seemingly well defended individuals, are eaten by an impressive array of invertebrates as well as vertebrate predators (Somaweera et al. 2013).

Predation on eggs

Eggs are the most vulnerable stage in the life cycle. They are highly nutritious and generally palatable (Orians and Janzen 1974; Gunzburger and Travis 2005); they are stuck in the nest selected by the parent until they hatch; and in most species, they are not defended by parents. As a result, mortality rates are typically higher than at any other life stage. Defensive mechanisms are not usual because selection favors energy allocation to rapid development (and thus a rapid transition to less vulnerable stages) rather than allocation to defensive mechanisms.

Eggs of aquatic-breeding amphibians are particularly at risk of predation because they are concentrated in aquatic habitats. Invertebrates are important predators, especially in ponds where fish are absent. Invertebrate predators include caddisfly, beetle, and dragonfly larvae, crayfish, and leeches. Fish and turtles eat amphibian eggs, as do other amphibians (see also the earlier discussion of cannibalism). Selection of oviposition sites by females may be based on the presence or absence of predators. Females of some frogs, for example, deposit eggs in ponds without fish or in water that is too shallow for fish to reach (Holomuzki 1995). Female Hyla chrysoscelis avoid ovipositing in cattle tanks containing species of fish that eat eggs but are indifferent to the presence of species that do not (Binckley and Resetarits 2003). Female frogs may also avoid ponds with predatory tadpoles, including conspecifics (Wells 2007).

The eggs of terrestrial-breeding amphibians (see Chapter 8) have their own sets of predators. Eggs of red-eyed treefrogs (*Agalychnis callidryas*), for example, are deposited on leaves overhanging streams or ponds; they are attacked by fungi, collected by social wasps to feed to their brood (**Figure 15.21A**), and eaten by fly larvae and by the cat-eyed



(C)





(A)



Figure 15.21 Predators of amphibian and reptile eggs. (A) A *Polybia* wasp drags an egg of the frog *Agalychnis callidryas* away from the clutch (left) and grasps the egg just prior to flying back to her nest (right). (B) The cat-eyed snake *Leptodeira septentrionalis* is another predator on eggs of *A. callidryas*. (C) A dingo digging up *Crocodylus johnstoni* eggs. (Photographs: A, C. Ziegler/Minden/ Corbis and Karen Warkentin; B, Michael and Patricia Fogden/Corbis; C, from Somaweera et al. 2013.)

snake Leptodeira septentrionalis (Figure 15.21B). Frog embryos can escape these predators once they reach a critical size; in response to chemical or vibratory cues, they hatch prematurely and drop into the water below (Warkentin 2005; Warkentin et al. 2006; Wells 2007). While these early hatchlings then take their chances with aquatic predators, they certainly would die if they remained in the egg capsule. Parental care of eggs and larvae is common for terrestrialbreeding amphibians; presence of a parent reduces the risk of microbial infection and predation.

Numerous kinds of animals eat reptile eggs. Ants in the genus Solenopsis, for example, are the most important source of mortality for eggs of the lizard Anolis apletophallus (formerly Anolis limifrons) in Panama (Andrews 1988). Some snakes are specialists on reptile eggs (Scanlon and Shine 1988). These include Oligodon in Asia (discussed in Section 9.4), the scarlet snake (Cemophora coccinea) in North America, a clade in the genus Simoselaps in Australia, and shovel-snout snakes (Prosymna) in Africa. In Australia, dingos and varanid lizards dig up and eat crocodylian eggs (Figure 15.21C)

Nesting by lizards, snakes, and terrestrial turtles tends to be a solitary endeavor; predation on any one nest is thus largely independent of that on other nests. For some species, however, nests are aggregated because suitable sites are limited. Aquatic turtles, for example, nest at near-shore habitats that allow females to lay their eggs and then return quickly to the water (see Figure 12.15). Such aggregations of nests, especially when newly constructed, attract predators. Nests of Blandings turtles (Emydoidea blandingi) and painted turtles (Chrysemys picta) in Michigan, for example, are most likely to be found by predators within 1 to 2 days of oviposition. Raccoons, foxes, and coyotes presumably find fresh nests using odors left by females as they move to and from nesting sites (Tinkle et al. 1981; Congdon et al. 1983).

Predation on the eggs of sea turtles is particularly intense. In fact, the highly synchronized nesting of some species may be an evolutionary response to high nest predation (Eckrich and Owens 1995). A lone female nesting on an exposed beach is conspicuous, and her entire clutch would probably be lost to predators. In contrast, predators will not find all the nests in the concentrated melee that results when hundreds or thousands of females nest together. Nonetheless, crabs, wild pigs, raccoons, vultures, and other animals often destroy the majority of the eggs laid by Kemp's and olive Ridley sea turtles (Lepidochelys) during their massive arribadas on beaches in Central America (Burger and Gochfeld 2014).

Predation on amphibian larvae

The predators of amphibian larvae are largely the same as those that feed on eggs, the most important being invertebrates and other amphibian larvae. Larvae exhibit a diversity of defensive mechanisms, including cryptic coloration, rapid locomotion once detected, phenotypically plastic responses to specific predators, and being distasteful or toxic (Wells 2007). In general, however, amphibian larvae are highly palatable food items for at least some predators in any given community (Gunzburger and Travis 2005; Wells 2007). In a few taxa, however, highly toxic adults sequester chemical toxins in eggs and larvae, thus protecting them from all but specialized predators (discussed in Section 15.5).

Predation on postnatal amphibians and reptiles

Generally, small species of amphibians and reptiles are vulnerable to invertebrate and small vertebrate predators, whereas larger species are vulnerable only to larger vertebrate predators (Figure 15.22). Spiders are important predators of small frogs and lizards, whereas snakes, birds, and mammals prey on medium-size to large amphibians and

Figure 15.22 Predators on postnatal amphibians and reptiles. (A) Frog-eating bat about to seize a robber frog (Craugastor fitzingeri). (B) Australian kookaburra eating a Lerista skink. These lizards have only vestigial legs. (C) Belostomatid water bug eating a túngara frog (Engystomops pustulosus). (Photographs: A, Merlin Tuttle/Bat Conservation International/Science Source; B, John Cancalosi/Alamy; C, Kristiina Hurme.)

(A)



(B)





reptiles. The secretary bird (*Sagittarius serpentarius*) of Africa is renowned for feeding on snakes, including venomous cobras and adders, and the laughing falcon (*Herpetotheres cachinnans*) of South America is a specialized snake feeder. Jaguars are important predators of crocodylians in the Brazilian Amazon (Da Silveira et al. 2010). Killer whales attack leatherback sea turtles, and dead turtles have been found with missing parts that match the gapes of white sharks (Long 1996).

15.5 Defensive Mechanisms

Defensive mechanisms are part of the evolutionary history of a lineage, and related species tend to share patterns of defense. All amphibians, for example, have both mucus and granular (poison) glands in their skin, and both types of glands are used for defense. Mucus glands, which normally serve to keep the skin moist, may secrete adhesive materials that hinder a predator. Poison glands are commonly used for defense, and specific defensive chemicals characterize many lineages of amphibians.

Crypsis, sprinting away, struggling, hissing, screaming, biting, urinating, defecating, and discharging anal glands are common defensive mechanisms of amphibians and reptiles (Greene 1988; Wells 2007; Toledo et al. 2011). Anurans often empty their bladders when they are attacked. In addition to startling the predator and causing it to hesitate in its attack or even release its hold, emptying the bladder makes a frog lighter and increases the distance it can jump (Buchanan and Taylor 1996). Most turtles are able to pull the head, legs, and tail into the shell, and a few lineages have added hinges to the shell that provide extra protection. Hinges that allow the plastron to be raised give the North American mud turtles their generic name (Kinosternon, "movable breastplate") and the North American and Asian box turtles (Terrapene and Curora, respectively) their common name. The African hinged-back tortoises get their generic name (Kinixys, "moveable box") from the flexible hinge that joins the bones and scutes at the rear of the carapace.

Keep in mind that no individual can rely on a single defense. Defenses employed by an individual when it is young and small may not be effective when it is older and larger. Moreover, predators come in many sizes and employ a wide range of predatory tactics. Amphibians and reptiles thus have suites of defenses that are employed during their lifetime, or even during a single encounter with a predator. Defenses are usually employed in a hierarchical fashion. The horned lizard Phrynosoma cornutum, for example, relies on its cryptic coloration as its first line of defense. Once discovered, however, individuals exhibit responses that are specific to particular predators. If a rattlesnake approaches, a lizard runs to a new location and freezes, thus avoiding capture by a relatively slow-moving species of snake (Sherbrooke 2008). If a lizard is approached by a coachwhip (Coluber, formerly Masticophis), a visual predator that the lizard cannot outrun, the lizard remains stationary but displays its cranial horns and tilts its body to increases its apparent size to the predator (Figure 15.23A). When dogs, foxes, or bobcats threaten a horned lizard, it squirts blood from its eyes (Figure 15.23B); blood squirting does not occur in response to birds or rodents (Middendorf and Sherbrooke 1992). The response of canids and felids to blood squirted in their mouths indicates that they find the chemical-laden blood noxious (Figure 15.23C) (Schmidt et al. 1989; Sherbrooke et al. 2012). Chemicals in the blood are presumably obtained from the harvester ants (*Pogonomyrmex*) eaten by *Phrynosoma* individuals (see Table 15.2).

The nature of defense may also vary as a function of an individual's physiological state. When ambient temperature is low, *Anolis lineatopus* flee at greater distances when approached than when ambient temperature is high. Because running speed is greater at high than at low body temperatures, the lizards presumably gauge their probability of escape by their body temperature (Rand 1964). The agamid lizards *Trapelus* (formerly *Agama*) *savignyii* and *T. mutabilis* (formerly *A. pallida*) either flee or fight when threatened. At body temperatures of 34°C to 42°C, running away is the most common response to simulated predation. At a body temperature of 20°C, when the lizards cannot run well, all individuals fight, and their defensive repertoire includes gaping, lunging, and attempting to bite (Hertz et al. 1982).

Other factors, such as reproductive status, energy levels, and distance to hiding places, also affect what defensive mechanisms are employed. For example, female squamates that are temporarily handicapped by the mass of eggs and embryos alter their behavior in ways that may reduce their vulnerability to predation (Schwartzkopf and Andrews 2012). Gravid females may remain close to refugia where they can easily escape predators (Bauwens and Thoen 1981; Andrews et al. 1997); they may also exhibit reduced movements and social display (Johnson et al. 2010).

In the following sections we discuss specific defensive mechanisms in roughly the order that these defenses are exhibited. This order thus parallels the sequence by which predators find, identify, approach, capture, and ingest prey. For comprehensive reviews of this topic, see Brodie 1983, Greene 1988, Pough 1988, Wells 2007, and Toledo et al. 2011.

Avoiding detection

The first line of defense for many species is avoiding detection. Individuals may do so through **crypsis** (**Figure 15.24**). Crypsis can involve general or specific resemblance to some feature of the environment. Familiar examples of general resemblance are the brown color of small lizards and frogs that rest on tree trunks or the ground and the green color of small lizards and frogs that rest on leaves. General resemblance may be enhanced by disruptive patterns or structures that break up or obscure the outline of the body. For example, fleshy protuberances above the eyes, on the snouts, and on the ankles of some frogs may increase crypsis by disrupting the body outline of the animal.



Figure 15.23 Interactions between horned lizards (*Phrynosoma cornutum***) and their predators.** (A) Once detected by a predator it cannot outrun (here a greater roadrunner, *Geococyx californianus***)**, a horned lizard increases its apparent size by flattening its body and tilting it perpendicularly toward the approaching predator. (B) Projection of blood from the eye of a horned lizard is elicited by attacks by canids and felids. (C) Bobcat reacting to horned lizard blood by shaking its head, extruding its tongue, and drooling copiously. (Photographs: A, Wade Sherbrooke; B, Raymond Mendez; C, © National Geographic Television.)

Alternatively, an animal may resemble a specific inedible object in the environment. Many small brown lizards and frogs have a light line running down their backs that resembles the midrib of a leaf (see Figure 15.6), making them look even more like a dead leaf as they rest on the forest floor. The smallest species of horned lizard in North America, *Phrynosoma modestum*, looks like a pebble in its desert environment (Sherbrooke and Montanucci 1988). What appears to be a bird dropping on a leaf may, on close inspec-





tion, turn out to be a small black-and-white frog (Toledo and Haddad 2009). Fecal mimicry is common among insects but less so in vertebrates, probably because vertebrates are generally too large to make the resemblance credible.

Fitness, in the evolutionary sense, requires that individuals not only survive but grow to adult size and reproduce, and do so in a timely fashion. Observations of the túngara frog (Engystomops pustulosus) in Panama provide an example of how predator avoidance compromises reproductive success (Ryan 1985). By vocalizing, males increase their attractiveness to females, but the particular calls that are most attractive to females are also the calls that are the most attractive to the bats that eat frogs. Ryan and his colleagues tested the responses of calling frogs to bats by using models of bats. Their results suggested that frogs detect bats visually. The intensity of calling was reduced when bat models were flown overhead on nights with a full moon, whereas frogs continued to call in the presence of bat models on nights that were completely dark. Moreover, when the models of bats were close to the frogs, the frogs deflated their

Figure 15.24 Crypsis: Background mimicry. Background mimicry by a Brazilian frog (*Bokermannohyla alvarengai*). This species spends the day resting on boulders where its dorsal pattern blends well with lichens. (Photograph by Denis V. Andrade and Glenn J. Tattersall.)

vocal sacs, dived under the water, and swam away. In contrast, when the models of bats were high over the pond, the frogs stopped calling but kept their vocal sacs inflated and thus were able to resume calling quickly. These behaviors suggested that male frogs were adjusting calling behavior to the perceived risk of predation. An additional twist to this story is that male frogs that stopped calling still advertised their presence to bats from the ripples that continued to move across the water surface (Halfwerk et al. 2014).

Signaling inedibility

Once it has detected a potential prey item, the predator must identify it as edible or inedible. A prey item can be inedible because it is unpalatable (bad tasting), toxic, venomous, or dangerous for other reasons such as spines or large body size. Because the predator, the prey, or both could be harmed during an attack on an inedible prey item, selection favors prey that signal inedibility and predators that recognize that signal.

The spread hood of a cobra is one example of a signal that truthfully advertises a dangerous prey. Some venomous snakes use auditory signals of inedibility, includ-

Figure 15.25 Aposematic coloration of amphibians.

(A) The cryptic pattern of *Allobates talamancae* represents the ancestral condition of South and Central American dendrobatid frogs. Derived species such as (B) *Dendrobates auratus* sequester toxic alkaloids from prey and have evolved aposematic patterns and colors to warn predators of their unpalatibility. Similar aposematic patterns are found in other frogs, including (C) the mantellid *Mantella baroni* from Madagascar and (D) the bufonid

ing the rattling of rattlesnakes in North America and the buzzing sound of the African vipers *Echis* and *Cerastes* that is made by rubbing specially modified scales on adjacent coils against each other. The formidable spines of the lizard *Moloch horridus* in Australia, many species of *Phrynosoma* in North America, and *Smaug* (formerly *Cordylus*) giganteus in South Africa (see Figure 15.32A) also signal real danger to a predator. The spines can puncture the inside of the predator's mouth; it is not uncommon to find snakes that have died with a horned lizard wedged in their throats, the spines projecting through the snake's neck (Sherbrooke 2003).

APOSEMATISM A few lineages of amphibians are characterized by potent chemical defenses (Daly 2003; Hanifin 2010; Savitzky et al. 2012). Toxic chemicals are synthesized in granular glands. These include the cardiotonic bufadienoloides of bufonids and the neurotoxic tetrodotoxins (TTX) of salamandrids and *Atelopus* frogs (Clarke 1997). Toxins also can have an environmental source: the alkaloids sequestered in the granular glands of dendrobatid frogs are obtained directly from arthropod prey.

Atelopus spumarius from Peru. (E) The aposematic coloration of the European fire-bellied toad (*Bombina orientalis*) is usually concealed; its vivid red ventrum is displayed when it arches its back and exposes its sides and the palms of its feet (the unken reflex). (F) The European fire salamander (*Salamandra salamandra*) is not only aposematic, but it sprays toxic secretions from dermal glands when it is attacked. (Photographs: A–E, Martha L. Crump; F, Edmund Brodie, Jr.)





(B)





(D)







(F)



Toxins	Prey source	Taxa known to sequester toxins	Taxa that may sequester toxins
Lipophilic alkaloids	Ants (several families), oribatid mites, coccinellid and choresine beetles, siphonotid millipedes	Dendrobatidae, Mantellidae, Melanophryniscus, Pseudophryne, Eleutherodactylus	Hemisus, Myobatrachus, Rhinophrynus, Hemidactylium, Phrynosoma, Moloch, Scolecophidia, Erythrolamprus
Tetrodotoxin (TTX)	Salamandridae, Atelopus	Thamnophis	Erythrolamprus (formerly Liophis)
Bufadienolides	Bufonidae	Rhabdophis	Heterodon, Erythrolamprus, Lystophis, Waglerophis, Xenodon
Terpenes	Termites, slugs	None confirmed	Scolecophidia, Contia, Sibon, Dipsas, Duberria, Storeria, Pareatidae

TABLE 15.2 Some dietary toxins, their prey sources, and predators that sequester toxins

After Savitzky et al. 2012.

Animals that are bad-tasting, toxic, or venomous are often brightly colored (Toledo and Haddad 2009). This form of advertisement is called warning, or **aposematic**, coloration (see Chapter 13). The message conveyed is "Don't attack me! I will harm you!" Aposematic coloration is characteristic of amphibians that are defended with toxic chemicals (**Figure 15.25**) and of some venomous and toxic snakes. Toxic species that use crypsis as the first line of defense suddenly expose areas of aposematic coloration when discovered. Fire-bellied toads (genus *Bombina*) and the newt *Taricha granulosa*, for example, arch their backs and display bright ventral coloration. This posture is referred to as an **unken reflex**.

Defensive toxins are usually released onto the skin itself, but a few species have behaviors that increase the likelihood that a potential predator will contact the toxin. European fire salamanders (*Salamandra salamandra*) spray toxic skin secretions toward a perceived threat (Brodie and Smatresk 1990). The Japanese salamandrid *Echinotriton* and the Spanish salamandrid *Pleurodeles* both combine potent toxins with an injection system. When a salamander is bitten, its sharply pointed ribs are forced through poison glands, thus carrying toxins into the predator's mouth.

Not only are highly toxic amphibians chemically protected, but protection is extended to eggs and larvae. Rough skinned newts (*Taricha*) and harlequin frogs (*Atelopus*) provision eggs with TTX (Hanifin 2010). For *Taricha*, at least, larvae also have sufficient TTX to deter predation by dragonfly larvae (Gall et al. 2011). Eggs of the cane toad (*Rhinella marina*) contain concentrations of bufadienolides as high as those of adults; tadpoles of native frogs that eat cane toad eggs die (Hayes et al. 2009). Females of the dendrobatid frog *Oophaga pumilio* sequester alkaloids in ovarian eggs and in nutritive eggs that are fed to larvae during development. The alkaloids deter spiders but not snakes (Stynoski et al. 2014).

Dendrobatid frogs are only one of many taxa that use chemicals obtained from prey in their own defense (Savitzky et al. 2012). Several examples of defensive sequestration are now recognized, and others are suspected but not yet well documented (**Table 15.2**).

The Asian natricine snake Rhabdophis tigrinus is a welldocumented example of a species that exhibits defensive sequestration (Hutchinson et al. 2008; Mori et al. 2012). Individuals have a series of paired glands in the skin of the neck where bufadienolides from the toads they eat are stored (Figure 15.26A,B). The glands have clearly evolved as defensive structures. In R. tigrinus and some other Rhabdophis, individuals exhibit neck arching and neck butting behaviors that would expose predators to toxins that irritate mucous membranes and cause corneal injuries when spraved into the eve (Figure 15.26C,D). Female Rhabdophis transfer sequestered bufadienolides to their embryos through the egg volk or while the eggs reside in the oviduct. The amount of toxin provided to the offspring depends on the female's level of chemical defense, and offspring of well-defended mothers hatch with sufficient toxins for their own protection until they consume their first toads in the spring following hatching. In locations where Rhabdophis do not eat toads, adults and hatchlings are not chemically protected and individuals are more likely to attempt to escape than to display their neck area to predators.

MIMICRY Given that inedible animals that are aposematic gain protection from predators, animals that resemble protected species should gain protection as well. When different species, all with toxic properties, exhibit the same warning coloration, predators will generalize a bad experience with one species to all similar species. This is called Müllerian mimicry, named after Fritz Müller, the naturalist who first described such mimicry from his observations of butterflies in South America. In the Brazilian Amazon, the sympatric dendrobatid *Ameerega picta* and leptodactylid *Lithodytes* (formerly *Leptodactylus*) *lineatus* frogs are aposematic (black with yellow lateral stripes). While leptodactylids are typically cryptic and non-toxic, *L. lineatus* has evolved coloration that mimics that of the dentrobatid and is toxic as well (Prates et al. 2012). In eastern North







Figure 15.26 Nuchal gland toxins of *Rhabdophis tigrinus*. (A) Paired nuchal glands in the Asian natricine snake *Rhabdophis tigrinus* are seen under the skin (arrows). The head is to the left of the image. (B) Cross section of one pair of glands. (C) In response to being tapped by a human finger, the snake displays a neck-butting behavior and the nuchal glands rupture through the skin, releasing and spraying their toxic contents. (D) The droplets on the eyeglasses are spray from nuchal glands. (Photographs: A, B Alan H. Savitzky; C,D by Akira Mori.)

America, the eft stage of the salamandrid *Notophthalmus viridescens* and the plethodontid salamander *Pseudotriton ruber* exhibit similar aposematic coloration and produce, respectively, the extremely toxic chemicals tetrodotoxin and pseudotritontoxin (Figure 15.27A,B).

By contrast, predators may be duped by an edible species that looks like its noxious model. This phenomenon is called Batesian mimicry, named after Henry Walter Bates, another naturalist who studied butterflies in South America. In eastern North America, the resemblance of the erythristic





Figure 15.27 North American salamanders exhibit Müllerian and Batesian mimicry. (A) *Pseudotriton ruber* and (B) the eft stage of *Notophthalmus viridescens* are Müllerian mimics: they have toxic skin secretions and exhibit tail undulating displays that enhance their red aposematic coloration. (C) The erythristic (red) morph of *Plethodon cinereus* is edible to birds and is a Batesian mimic of the *Pseudotriton* and *Notophthalmus*. (Photographs: A, Edmund Brodie, Jr.; B, Troy Hibbitts; C, Harvey Pough.)



Figure 15.28 Coral snakes and their mimics. One (or perhaps more) species of the rear-fanged colubrid snake Pliocercus mimics venomous coral snakes (Micrurus, Elapidae) in southern Mexico and Central America. The colors and patterns of the coral snakes vary geographically, and that variation is paralleled by the colors and patterns of Pliocercus. In each illustration except (E), the coral snake is on the left and the mimic is on the right. (A) Micrurus fulvius. (B) M. limbatus. (C) M. diastema. (D) M. mipartitus. (F) M. diastema. (E) The snake on the left is *M. diastema* and the one on the right is M. elegans. Pliocercus, in the middle, combines elements of the patterns of both

bines elements of the patterns of both venomous species. (Courtesy of the artist, Frances J. Irish.)

morph (i.e., uniformly red rather than brown with a red stripe) of the edible eastern red-backed salamander *Plethodon cinereus* to the toxic eft stage of *Notophthalmus viridescens* has been interpreted as Batesian mimicry (**Figure 15.27C**). To test this hypothesis, Brodie and Brodie (1980) offered wild birds the choice of the erythristic *Plethodon* morph, the normal striped morph of this salamander, another edible species of salamander, and toxic red efts. Erythristic *Plethodon* were less likely to be eaten than were the normal morphs and the second edible salamander species, and efts had almost 100% survival—that is, birds avoided eating the model and the mimic salamanders, but ate the nonmimics.

A recent study confirmed the role of birds as the selective agents in this system. The visual systems of mammals and snakes are insensitive to the difference in color between *Notophthalmus* (the model) and the striped nonmimetic *Plethodon* morph. These predators do not perceive the erythristic morph as mimics; both morphs look alike to them (Kraemer and Adams 2013). In contrast, birds are sensitive to the color differences between the model and the nonmimetic morph, but cannot distinguish between the model and mimetic morph; they are duped by the mimic.

Venomous snakes are the most common models for mimetic systems involving reptiles (Pough 1988). Neotropical coral snakes (*Micrurus*) and the similarly patterned false coral snakes in several colubrid genera represent both Batesian and Müllerian mimicry (Figure 15.28). Snakes in this mimicry complex resemble each other in having red, black, and white or yellow rings around the body. Two families are represented: Elapidae and Colubridae. The colubrids include rear-fanged species that are Müllerian mimics of coral snakes, and nonvenomous species that are Batesian mimics of coral snakes and of the rear-fanged colubrids.

Observations by Edmund Brodie (1993) in Costa Rica provide direct evidence that coral snake patterns are actually aposematic and that predators avoid coral snakes in nature (Figure 15.29). He placed modeling clay replicas of coral snakes and of unicolored brown snakes on the forest floor, where the coral snake replicas were conspicuous and the brown replicas were cryptic. He also placed replicas of these snakes on sheets of white paper, where both were conspicuous. Attacks by birds were recorded as impressions of beaks in the clay. Birds attacked the brown replicas far more often than the coral snake replicas, irrespective of the background. This result means that coral snakes are aposematic to birds and are avoided.

When venomous models are common and a mistake by a predator can be lethal, selection should favor individual predators that generalize the characteristics of the lethal model broadly, and the protection conveyed by mimicry should be substantial even if the mimic is not very similar to the model (Pough 1988). In contrast, when models become



rare, selection should favor very precise mimics. The reason is that selection to avoid the model is relaxed, and only those mimics that closely resemble the model will receive any protection at all. For example, since the venomous coral snake *Micrurus fulvius* was extirpated in the North Carolina sandhills in 1960, its mimic, the nonvenomous kingsnake *Lampropeltis elapsoides*, may have become more similar in color pattern to coral snakes (Akcali and Pfenning 2014).

Avoiding capture

Running away is often the option of choice by edible animals after detection. This is the most frequently observed defensive mechanism of anurans (Toledo et al. 2011). Speedsters among reptiles include the zebra-tailed lizards (Callisaurus) of the southwestern North American deserts. Maximum sprint speed of a 10-g zebra-tailed lizard running bipedally is about 4 m/s (Irschick and Jayne 1999), whereas maximum sprint speeds of most lizards of that size range from 2 to 3 m/s (Van Damme and Vanhooydonck 2001). Running is often toward a refuge, and escape to treetops, crevices, holes, or dense vegetation may baffle a predator. Some arboreal species in Southeast Asia take flight-literally. They glide long distances using body parts modified into airfoils (see Figure 10.26). These include Rhacophorus frogs, which have enlarged webbed feet; agamid (Draco) and gekkonid (Ptychozoon) lizards, which have extensions of skin along the sides of the body; and snakes in the genus Chrysopelea, which flatten the trunk dorsoventrally (Socha 2011).

Other species escape predators simply by entering water. Aquatic turtles bask on logs and rocks from which they can quickly slip back into the water. Similarly, aquatic snakes and some large tropical lizards—such as *Iguana*, *Basiliscus*, *Hydrosaurus*, and *Physignathus*—rest in branches that over-



Figure 15.29 An experimental test of coral snake mimicry. Tricolor coral snake mimics and neutral brown snake replicas were made of modeling clay and placed on (A) white paper and (B) a natural background. Replicas were widely spaced under experimental conditions. (C) Bird attacks left impressions in the clay (U-shaped bill marks are seen here). The brown models recorded far more attacks than the tricolor replicas, irrespective of which background they were placed on. (From Brodie 1993.)

hang water. At the approach of a predator, the lizard drops into the water, and remains submerged for an hour or more.

Behavior and color patterns of snakes are coordinated in ways that facilitate escape from predators. Snakes that are longitudinally striped are usually diurnal and use rapid locomotion as a primary mode of escape from predators. Striping makes motion difficult to detect and speed difficult to judge. On the other hand, snakes that are blotched or banded usually have secretive habits and rely on crypsis. Blotches or bands make fixed reference points for the eye and enhance detection when the snake moves. However, rapid movement of a small-blotched snake blurs the bands so that the snake appears to be unicolored (Pough 1976). When movement is abruptly followed by stillness, the snake again becomes cryptic (**Figure 15.30**).

Studies of the North American garter snake *Thamnophis* ordinoides support the hypothesis that particular combinations of dorsal pattern and escape behavior are associated with higher fitness than are other combinations. By releasing and recapturing hundreds of juvenile snakes that had been previously scored for pattern and behavior, Brodie (1992) found that individuals with the highest survival exhibited one of two combinations: either striping and rapid locomotion or spotting and frequent reversals. He concluded that natural selection favoring these particular combinations was probably the result of the optical properties of color patterns during movement.

Birds and mammals tend to attack the heads of their prey, and the displays and distinctive coloration of the tails of some salamanders and squamates divert the attention of a





predator toward this less vulnerable part of the body. Many species that exhibit tail displays also exhibit **caudal autoto-my**: they shed their tails readily when attacked (see Figure 4.9), sometimes even before they are touched (Higham et al. 2013). This behavior facilitates escape because the predator may have grasped the tail itself or because the wiggling tail diverts the attention of the predator from the prey. The thwarted predator often eats the tail, thus obtaining a meal (albeit smaller than anticipated).

If running away is not an immediate option for an edible animal after it has been detected by a predator, individuals of many species stand their ground and exhibit threatening or startling behaviors (**Figure 15.31**). Threatening behaviors include lunging, gaping, hissing, tail lashing, and assuming postures that enhance size. The Australian agamid lizard *Chlamydosaurus kingii* suddenly spreads the large frill around its neck, gapes its mouth, and lunges at a predator (Shine 1990). Some harmless colubrid snakes spread their mandibular joints laterally, making their heads appear triangular, like those of the venomous vipers, and vibrate their tails, which produces a buzzing sound if they are in dry vegetation. These behaviors may make a potential predator hesitant to attack.

Some species suddenly reveal aposematic colors or patterns that startle or confuse a predator so that it ceases its attack. The otherwise drably colored snake *Erythrolamprus* (formerly *Liophis*) *epinephelus* suddenly flattens its neck and exposes yellow scales and interscale membranes; this display may also warn of toxicity (see Table 15.2). Some anurans, such as *Pleurodema* and *Eupemphix* (formerly *Physalaemus*) *nattereri*, puff themselves up with air and display large eyespots on their rumps. These eyespots give the impression of a large animal and may frighten away the potential predator. If this defense does not work and the predator continues to attack, the frogs produce a noxious secretion from glands located in the eyespots.

Preventing consumption

A few amphibians and reptiles have mechanisms that reduce the probability that they will be killed and eaten even after capture (**Figure 15.32**). Some small reptiles, and even some amphibians, inhibit ingestion by becoming hard to handle. Many species of frogs and toads inflate their lungs with air when provoked, thus swelling up and becoming difficult for a snake to grasp or manipulate. Rolling into a ball by the Australian typhlopid snake *Anilios* (formerly *Ramphotyphlops*) *nigrescens* may serve this purpose as well. Similarly, individuals of the cordylid lizard *Ouroborus* (formerly *Cordylus*) *cataphractus* enhance the defensive effects of spines and dermal armor by grasping their tails, thus forming a rigid sphere too large and awkward for most predators to handle, let alone swallow.

Adhesive skin secretions of some lizards and many amphibians prevent consumption. Australian geckos in the genus *Diplodactylus* have secretory glands in their tails. When the gecko is attacked, the predator is sprayed with a liquid Figure 15.31 Threat displays.

(A) The Panamanian colubrid snake Erythrolamprus epinephelus flattens its neck to expose yellow scales and interscale membranes. (B) The Australian agamid Chlamydosaurus kingii spreads its frill as a threat, and can follow up with ferocious bites. (C) A North American rattlesnake (Crotalus molossus) rattling; its rattle is seen at the left. (D) The Neotropical frog Eupemphix nattereri flashing evespots on its rump; the white flecks on the "eyes" are toxic secretions from granular glands. (Photographs: A, Robin Andrews; B, © David Watts/Alamy; C, John Cancalosi/Alamy; D, Edmund Brodie, Jr.)

(A)



expelled through hollow spines. The liquid turns into sticky threads that adhere to the predator, and distract it while the gecko escapes. Plethodontid salamanders are able to delay ingestion and even escape from garter snakes by immobilizing the snakes with their skin secretions (Arnold 1982). In one case, loops of a snake's body were glued for several days in the position that the snake initially used to grasp the salamander.

The adhesive strength of amphibian skin secretions can be formidable (Evans and Brodie 1994). Discs (1 cm²) stuck

Figure 15.32 Preventing consumption. (A) The spines of South Africa's giant girdled lizard (*Smaug giganteus*) are needle-sharp and deter predators. (B) The Australian blackish blind snake (*Anilios nigrescens*) rolls into a ball, presumably to avoid being eaten. (C) A South American Darwin's frog (*Rhinoderma darwinii*) feigns death to avoid becoming a meal. (Photographs: A, Robin Andrews; B, Sylvain Dubey; C, Martha L. Crump.)



together with the secretions of microhylid frogs (genus *Dyscophus*) took slightly more than 1.0 kg of mass (10 Newtons/ cm²) to separate. In contrast, discs stuck together with secretions of ambystomatid and plethodontid salamanders and the caecilian *Dermophis* took only 0.4 kg of mass (4 Newtons/cm²) to separate, an adhesive strength approximately that of rubber cement.

Death-feigning is a last-resort defensive mechanism. Its survival value depends on the predator breaking off an attack when the prev appears to be dead. This behavior may be especially effective against predators that rely on movement to elicit prey-killing behaviors. When the predator relaxes its grip or becomes inattentive, the prev is suddenly restored to life and escapes. Hognose snakes (Heterodon) of North America, for example, first hiss loudly, then strike if approached more closely. If harassment continues, they writhe violently and void feces and urine; the terminal behavior is to turn on their backs, gape their mouths, and feign death. The latency to death-feigning and its duration depend on the environment and the perceived threat. Individual Heterodon nasicus encountered in the field feign death sooner at high than at low environmental temperatures. Adults feign death longer than juveniles, and gravid females feign death longer than adult males and juveniles (Durso and Mullin 2013).

Frogs exhibit two forms of death-feigning (Toledo et al. 2010). Some species simply become inert—remaining motionless, keeping their eyes open with their limbs loose and extended (see Figure 15.32C). This behavior occurs among a wide range of taxa. A more elaborate form of death-feigning is associated with species with toxic skin secretions. Individuals exhibiting this behavior also remain motionless, but the limbs are held close to the body, the eyes are closed, and the body may be arched so that the head is flexed ventrally. Both forms of death-feigning accomplish the same purpose—the predator's attack may be halted. Death-feigning may have a second benefit for a toxic species: even if an individual is swallowed, it may be disgorged when the snake responds to toxic chemicals. In this event, its failure to struggle may have prevented traumatic injury.

15.6 ■ Coevolution of Predators and Prey

The metaphor for most interactions between predators and prey is the life–dinner principle; in any one interaction the prey can lose its life while the predator loses only a meal. As a result, selection favoring prey defenses is stronger than selection favoring specific counter-offenses of predators. For example, the sudden display of eyespots by a *Eupemphix nattereri* frog (see Figure 15.31D) may frighten away an avian predator. Selection may thus improve the mimicry of vertebrate eyes in frog populations. However, because the bird has multiple alternative prey items, selection is much less likely to affect the ability of birds to distinguish between the fake eyespots of frogs and the real eyes of dangerous predators.

In some situations, the strength of selection on predators can become as intense as it is on prey. When predators interact with really dangerous prey, the intensity of selection on both predator and prey is comparable and the two species become involved in an arms race in which defenses of the prey continue to improve in response to the evolution of specific counter-offenses by the predator (Brodie and Brodie 1999). Several decades of research by the father-son team of Edmund Brodie, Jr. and Edmund Brodie III, in collaboration with many colleagues, has provided the most thoroughly understood example of antagonistic coevolution (summarized in Brodie 2011). The coevolving partners are the garter snake Thamnophis sirtalis and its prey, the newt Taricha granulosa (Figure 15.33). These newts are truly deadly prey; an individual newt contains sufficient amounts of tetrodotoxin (TTX) in its skin to kill any predator-except Thamnophis. While all species of garter snakes have low levels of resistance to TTX, high levels of resistance are found only in populations of T. sirtalis that co-occur with the most highly toxic Taricha. In these populations, snakes safely consume amounts of TTX that would kill hundreds of humans (Brodie 2011). This level of resistance by snakes indicates that newts have commensurately high TTX levels.



Figure 15.33 Partners in coevolution. The rough-skinned newt (*Taricha granulosa*) sequesters enough tetrodotoxin (TTX) in its skin to kill almost any predator. But in some places where the garter snake *Thamnophis sirtalis* co-occurs with the newt, many snakes have high levels of TTX resistance, and can consume the newts safely. (Photograph by Edmund Brodie, Jr.)

These two species illustrate the fundamental criteria for coevolution: the newts exhibit variation in toxicity and the snakes exhibit variation in resistance. Snakes can assess the toxicity of a newt that they capture relative to their own resistance and reject or regurgitate newts that are too toxic for them to eat (Williams et al. 2003). Selection can thus favor increased resistance because resistant snakes get a meal and less resistant snakes do not. Newts are eaten or released depending on their level of toxicity; selection can thus favor greater toxicity because the more toxic newts survive whereas the less toxic newts are eaten (Williams et al. 2010).

Coevolution of snakes and newts turned out to be far more complex than originally anticipated from studies at a few localities. *Thamnophis sirtalis* has a wide distribution in North America and is sympatric with *Taricha granulosa* only in the Pacific Northwest (California, Oregon, and British Columbia). Where *Thamnophis* occurs without *Taricha*, individual snakes have very low levels of resistance to TTX. In contrast, where *Thamnophis* and *Taricha* co-occur, populations exhibit a mosaic of resistance and toxicity (**Figure 5.34A,B**). Snakes and newts appear to be on the expected trajectory of matched resistance and toxicity at only a few localities (**Figure 15.34C**). At some localities, both resistance and toxicity are low and snakes and newts do not appear to have coevolved at all, whereas at other localities snakes exhibit such high levels of resistance that they can safely consume any newt.

Studies of the molecular and physiological basis of resistance and toxicity provide insights into these discordant patterns of evolution (Brodie 2011; Feldman et al. 2012). TTX binds to voltage-gated sodium channels and prevents the propagation of action potentials along skeletal muscle fibers and nerve cells. The result is paralysis and death. Resistant snakes exhibit mutations that prevent TTX from binding to sodium channels; the particular mutations involve one to four amino acid substitutions in the sodium channel. Resistance varies as a function of the particular combination of substitutions. Because it takes only one or a few amino acid substitutions to greatly affect TTX resistance, Thannophis populations in which these mutations arise can suddenly make an adaptive jump that (1) allows the snakes to escape the arms race and (2) ends selection for greater toxicity of newts, because all newts captured are eaten and hence there is no selection for increased toxicity. The particular patterns of coevolution exhibited by a population are thus contingent on chance mutational events.



Figure 15.34 Geographic variation in resistance of *Thamnophis sirtalis* to TTX toxicity of *Taricha granulosa* Snakes (A) and newts (B) exhibit a mosaic of high resistance and high toxicity (red and other hot colors). Snake resistance is measured as the amount of TTX required to reduce the speed of an average adult female snake to 50% of baseline performance.

Newt toxicity is measured as the average amount of TTX in an adult newt. (C) Levels of resistance and toxicity are mismatched in much of the range of the two species and coevolution does not occur. Hot spots of coevolution occur where resistance and toxicity are closely matched (brown areas). (After Brodie 2011.)

SUMMARY

Amphibians and reptiles range from carnivorous to exclusively herbivorous.

Carnivorous species tend to be generalists, but feed on particular categories of prey (e.g., insects or vertebrates) and use particular behavioral repertoires for search, capture, and ingestion.

Cannibalism is particularly common among amphibian larvae because many individuals are crowded together; in some species, crowding is associated with the development of specialized cannibalistic phenotypes.

Among amphibians, only anuran larvae feed on plants.

Among lizard species, 12% are omnivores or herbivores and only 1% are strictly herbivorous (e.g., iguanid lizards).

Diets vary as a function of head or body size, season, and geographic location.

Searching for, seizing, and ingesting food items form a sequence of events that individuals perform many times throughout their lives.

Both innate and learned behaviors contribute to foraging success. The thermal environment of eggs during development, observation of the foraging behavior of other individuals, and experience with noxious, but not lethal, prey can affect the ability of individuals to learn new behaviors.

Many amphibians and reptiles exhibit one of two dichotomous foraging modes: active versus sit-and-wait foraging. Each mode has a characteristic sensory modality, morphology, physiology, prey characteristics, and reproductive allocation. Active foragers, for example, use vomerolfaction to detect prey and have slim bodies and heads, whereas sit-and-wait foragers use vision to detect prey and have stout bodies and heads.

The foraging modes of gekkotans are unlike those of active or sit-and-wait foragers. Gekkotans use a wider range of foraging modalities than other lizards, including cruise foraging and ambushing, and a wider range of sensory modalities than other lizards.

Herbivorous lizards are active foragers and use vomerolfaction to detect food but have the stout bodies and relatively large heads characteristic of sit-and-wait foragers.

Amphibians and reptiles serve as hosts for a diverse array of parasites.

The interaction between parasite and host is prolonged; parasitism may reduce the fitness of the host.

The kinds of parasites that infest amphibians and reptiles are the same as those that infest other vertebrates.

Internal parasites include single-cell protozoans and multicellular metazoans, mostly various types of worms. Transmission of the parasite may be direct or involve one or more intermediate hosts.

External parasites include leeches, mites, ticks, and mosquitos and other blood-sucking flies. Transmission of the parasite is directly from one host to another.

Amphibians and reptiles serve as food for a diverse array of predators and display a range of • defenses against being eaten.

Eggs and larvae are particularly vulnerable to predators because they are highly nutritious and lack effective defenses against many or most predators.

Defensive mechanisms of postnatal individuals, such as the secretion of toxic chemicals by amphibians and fleeing, biting, and discharging cloacal products by reptiles, are used by many species and reflect their common evolutionary history.

Specific defensive mechanisms include the fangs and venoms of viperid snakes, alkaloids in the skin of dendrobatid frogs, and blood squirting by some horned lizards.

Defenses are used hierarchically: crypsis is often the first line of defense, and other mechanisms are emploved after detection.

Antagonistic coevolution occurs when a predator and a prey species exhibit a reciprocal escalation of defensive and offensive mechanisms.

The snake predator Thamnophis sirtalis sometimes coevolves with its prey, the newt Taricha granulosa; in some localities, selection favors more toxic newts and greater resistance to tetrodotoxin (TTX) by snakes. Not all populations of newts and snakes exhibit escalation of defenses; the rate of coevolution, if it occurs at all, is affected by intrinsic (mutation) and extrinsic (ecological and historical) factors.

Go to the Herpetology Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

16 Populations and Species Assemblages

o far we have focused largely on attributes that all individuals in a species or a broader group share, such as the dewlap display of male Anolis lizards. Even the discussion in Chapter 15 of defensive behaviors in response to particular types of predators focused on shared traits. In this chapter our focus shifts to the aggregate properties of populations and species assemblages. We will start by discussing the demographic attributes of populations. Demography is the study of statistical properties of populations, including population size (i.e., the number of individuals), birth and death rates, age structure, and population growth rate. Next we will focus on multispecies assemblages, which have their own aggregate properties, including species richness (the number of species in an assemblage, which is a common meaning of the term biodiversity) and the relative abundance of individuals of each species. Finally, we will enlarge the geographic and taxonomic scales and discuss elevational and latitudinal gradients in species richness.

16.1 Population Ecology

Invasive Burmese pythons (*Python molurus bioittatus*) in the Florida Everglades illustrate a population problem. While the introduction of this large non-native snake is causing an ecological disaster (Dorcas and Willson 2011), no one really knows how many of them there are in the Everglades or how fast the population is growing (**Figure 16.1**). The Everglades is a huge area, much of it is inaccessible by road or boat, and the pythons are secretive, so counting every individual is clearly impossible. How, then, can ecologists answer these important demographic questions? In this section we will discuss how population size and other demographic parameters are estimated. In doing so, we will also illustrate the issues faced by natural resource managers when they confront a spectrum of invasive and native species whose populations are expanding or declining.

What is a population?

A **population** is a group of conspecific individuals living in an arbitrarily defined area. This area may be small enough that all members of the population are potential mates. For example, the distribution of the West Virginia spring salamander (*Gyrinophilus subterraneus*) is limited to General Davis Cave in West Virginia (Besharse and Holsinger 1977). In this case, the entire species constitutes a population. More typically, however, the full geographic range of a species includes many populations. The range of the timber rattlesnake (*Crotalus horridus*) spans much of the eastern and central United States. The population chosen for a study of gene flow among individuals might include just the timber rattlesnakes in a particular watershed, whereas a larger biogeographic unit, such as the southern Appalachians, could also be selected for such a study.

For most amphibians and reptiles, defining population in the context of the physical area occupied is straightforward-the population simply includes all the individuals of a species in a designated area, regardless of their age or stage of development. For some species, however, a geographically defined population is meaningless; many populations of sea turtles present this problem (Bowen and Karl 2007). Adult turtles return to the same nesting area year after year, so a breeding population can be associated with-a particular location. The difficulty is that both adults and hatchlings from one nesting area migrate to feeding areas that are hundreds or thousands of kilometers away from the nesting area. For example, hatchling loggerhead sea turtles (Caretta caretta) migrate from nesting beaches in Japan to feeding areas off Baja California, Mexico, a distance of about 10,000 km. Moreover, individuals from different nesting areas mingle in these feeding areas before they return to their natal beaches to breed. Populations of sea turtles thus have genetic continuity because they return to ancestral breeding areas, but individuals from different breeding populations intermingle during migration and (A)

(B)





in feeding areas. Sea turtles thus consist of metapopulations: large groups of individuals that can be separated into smaller subpopulations.

Population parameters and population dynamics

The two most fundamental questions asked about a population are, how large is it and how does its size change over time? Determining the size of a population is rarely straightforward because some, or even most, of the individuals in a population will not be detected during a census. To add to this problem, populations consist of subgroups that vary in detectability; sex or life stage may affect detectability, polymorphism may render some individuals more cryptic than others, and so on. As a result, simple counts of individuals are often inaccurate.

The study of **population dynamics**—the determination of changes in population size and the processes that influence those changes-is fraught with challenges. Conservation biologists, for example, cannot say that a population has been affected by global climate change if they cannot distinguish long-term trends from normal short-term fluctuations in population size (Pechmann et al. 1991), or if they cannot identify the causal mechanism linked to population change (see Chapter 17).

Ecologists have devised statistical methods to estimate parameters such as population size and survival rates, and to evaluate the strength of trends in long-term data sets. (Some of the pertinent literature is cited in Mazerolle et Figure 16.1 Reproductive potential of invasive Burmese pythons (Python molurus bivittatus) in Florida. (A) This reproductive female, the smallest captured to date, was just over 2 m long. (B) The reproductive tract of the same female contained 11 viable eggs. (C) The maximum total length of females in the invasive population is more than 5 m, and maximum clutch size is more than 80 eggs. (After Willson et al. 2014; photographs by Skip Snow and J. D. Willson.)

al. 2007; Bell and Pledger 2010; and Pérez-Mendoza et al. 2013.) We do not have the space to discuss estimation procedures per se, so we will focus instead on the insights that can be obtained from the analyses.

MARK-RECAPTURE STUDIES Data gathered by mark**recapture studies** can be used to estimate population size. These studies consist of a series of censuses during which individuals are captured, either given a unique mark if captured for the first time or recorded as marked if captured previously, and released back into the population.

A mark-recapture study of an endangered leiopelmatid frog provides a good example of the biological and statistical challenges of population estimates. Leiopelma pakeka became extinct on the New Zealand mainland, probably as a result of predation by introduced rats. By the early 1970s the species was confined to a small forest remnant on Maud Island. That population has been monitored for several decades, and Ben Bell and Shirley Pledger (2010) used 25 years of mark-recapture data at two $12 \text{ m} \times 12 \text{ m}$ sites to determine how the population fared over this period. Their results highlight the importance of detectability, because roughly half the frogs in the plots were underground during census visits (Figure 16.2A). Population sizes at each census were thus calculated as the number of frogs aboveground plus an estimate of the number of frogs underground. Bell and Pledger tested several statistical methods to select the one that provided the best estimate of population trends. Despite fluctuations in numbers from census to census and from year to year at both sites, analyses revealed that the population at site 1





Figure 16.2 Population sizes of Leiopelma pakeka at two sites on Maud Island, New Zealand. (A) Roughly half the frogs were underground at census visits between 1983 and 2008. Multiple censuses were taken in some years. (B) Sampling revealed substantial variation in estimates of population size from census to census and year to year. Despite this variation and the need to adjust each population estimate for the frogs that were underground, over the 25-year period statistical analysis revealed a small but significant increase in the size of the population at site 1 and no significant change at site 2. (After Bell and Pledger 2010; photograph © Tui De Roy/Minden Pictures/Corbis.)

increased in size over the 25 years of observation while the population at site 2 did not (**Figure 16.2B**).

Mark-recapture studies estimate how many individuals are present in a population, but they do not provide direct information about reproduction. Instead, changes in the estimated population size from one census to the next indicate the net effects of recruitment (addition of individuals to the population through reproduction and immigration) and of loss (mortality and emigration). Thus, markrecapture studies are often augmented by the collection of information on age-specific reproduction and survival (so-called **vital rates**) which can be summarized and analyzed.
LIFE TABLE ANALYSIS Vital rates are summarized in a life table. which can be used to estimate a population's growth rate, stable age distribution, and the sensitivity of each age to environmental change. Life tables are based on data for females and, ideally, they track the vital rates of a cohort (all of the female eggs or neonates produced in a breeding season) from age 0 until all the members of the cohort have died. This ideal is seldom met, especially for long-lived species, because the information would require decades to collect. Typically, vital rates are based on 1 to several years of data.

Table 16.1 shows a life table for the lizard Sceloporus graciosus; agespecific survival and fecundity from oviposition to age 10 are estimated from data collected in southern Utah over 3 years (see Tinkle 1973). The first column in the table is age in years (x) starting at oviposition.

Age in years (x)	Number of survivors (<i>I_x</i>)	Mortality (fraction that die, q _x)	Fecundity (average number of female eggs per female, <i>m</i> _x)	Annual egg production (l _x m _x)	
0 (oviposition)	1,000	0.77			
1	230	0.38		-	
2	143	0.47	2.9	415	
3	76	0.55	3.9	296	
4	34	0.62	4.4	150	
5	13	0.50	4.4	57	
6	7	0.50	4.4	31	
7	3	0.50	4.4	13	
8	2	0.50	4.4	9	
9	1	1.00	4.4	4	
10	0	-	0.0	0	

Data from Tinkle 1973.

^a Life tables are based on data for females and are usually normalized to an initial cohort of 1.

We have normalized this table to a cohort of 1,000 because whole numbers are easier to visualize.

The second column is the number of survivors (1.) based on an initial cohort size of 1,000. A plot of these data illustrates the survivorship curve for the population (Figure 16.3A). Oviposition of 1,000 eggs would result in 230 juveniles surviving to 1 year of age.

The third column in Table 16.1 is the age-specific mortality rate (q_x) , calculated as $(l_x - l_{x+1})/l_x$. (Age-specific survival, which is calculated as $l_{r+1}/l_{r'}$ is not shown in the table.) Eggs and hatchlings exhibit the highest mortality (77%), yearlings

the lowest (38%), and reproductive adults intermediate and relatively constant values. Overall, only 3% of individuals reach 4 years of age. The fourth column is fecundity (m_x) , the production of eggs. Starting in their second year of life, females deposit two clutches of eggs per year. Twoyear-old females produce an average of 2.9 eggs. The number of eggs rises to an average of 3.9 in the third year, to 4.4 in the fifth year, and stabilizes at that level.

The fifth column of the life table shows age-specific reproduction (l_m) —that is, the number of female eggs produced by all the females each age class. A plot of these data shows that 2-year-old females produce more eggs than any other age class, even though they have the smallest clutch size, because there are more reproductive individuals in this age class than in any other (Figure 16.3B). The contribution of older classes is smaller because there are fewer individuals in those classes. Indeed, female S. graciosus in their first 3 years of reproduction produce almost 90% of all the eggs produced during the lifetime of the cohort.

The sum of the number of eggs produced during the lifetime of the cohort (R_0) is called the net reproductive rate, and it provides a rough estimate of the viability of the popu-



Figure 16.3 Graphs of life table data for a population of the lizard Sceloporus graciosus. Survivorship and age-specific reproduction (l, and l, m,; columns 2 and 5, respectively, of Table 16.1) are graphed. (A) An initial cohort of 1,000 eggs results in only 230 individuals surviving to 1 year of age, after which annual survivorship declines at a fairly steady rate. (B) Females do not produce eggs in the first year. Two- and 3-year-old females are responsible for the largest reproductive contribution to the cohort.

TABLE 16.1 Life table for the lizard Sceloporus graciosus

lation. A cohort that starts with 1,000 female eggs must produce 1,000 female eggs to replace itself. In the study shown in Table 16.1, the cohort produced 975 female eggs; 975/1,000 equals a net reproductive rate of 0.975. This rate is slightly below 1.0, but the estimates used to construct life tables have some uncertainty, and 0.975 is probably not significantly different from 1.0, the replacement value. Thus, we can conclude that the size of this particular lizard population was probably stable during the lifetime of the cohort.

Population matrices are a statistical outgrowth of life tables that provide more precise predictions of the growth rates of populations than does the calculation of net reproductive rate we used for *Sceloporus graciosus* (see Caswell 2001). Comparative studies of eight populations of *S. grammicus* in central Mexico integrated mark–recapture and life table data with population matrices. Two populations had growth rates significantly higher than 1.0, one had a growth rate significantly lower than 1.0, and five had growth rates indistinguishable from 1.0 (Pérez-Mendoza et al. 2013). Given normal spatial and temporal variation in weather and other factors, these results suggest overall demographic stability of the populations.

Identification of the age classes that make the greatest contribution to population growth is an important application of life table analysis. For long-lived species such as the Mohave desert tortoise (*Gopherus agassizii*), large adult females (21 years and older) make the greatest contribution to reproduction (Doak et al. 1994). Consequently, for tortoises, sea turtles, and other long-lived species, conservation efforts that increase survival of adult females are likely to be more effective than efforts that protect eggs and hatchlings (see Figure 17.16) (Heppell 1998).

Population change and population regulation

A population is a dynamic entity. Its size may vary seasonally and from year to year, and a population may disappear temporarily or permanently. These population dynamics are the consequence of interactions between individuals and their physical and biological environments.

Interactions with the physical environment are usually density-independent. For example, a flood will drown some individuals independently of how many other individuals are in the population. By contrast, interactions with the biological environment are usually density-dependent. For example, the number of prey that an individual captures will be affected by how many other individuals are also searching for prey. Thus, the intensity of competition for food is a density-dependent factor.

Low levels of competition and predation allow population size to increase, whereas high levels lead to a decrease in population size. Density-dependent factors thus dampen the magnitude of changes due to density-independent factors and keep a population at the same average size over ecological time scales.

Long-term studies of the small lizard Anolis apletophallus (formerly A. limifrons) in Panama illustrate both densityindependent and density-dependent processes. Changes in population size from year to year are dramatic (**Figure 16.4**) because the young produced during one rainy (reproductive) season are the reproductive adults of the next season. Population density is highest following rainy seasons that are relatively long and dry. More eggs are produced during rainy months, and more eggs survive if rainfall during wet months is relatively low (Andrews 1988, 1991; Andrews and Nichols 1990).

What is the mechanism that connects rainfall to egg survival and hence to population density? To answer this guestion, David Chalcraft and Robin Andrews (1999) placed eggs in normal oviposition sites under leaf litter on the forest floor during the rainy season. They monitored egg survival on two control plots that received ambient rainfall and on ten experimental plots that were shielded from ambient rainfall with clear plastic sheets. Five of the experimental plots were watered to simulate relatively low rainfall, and five were watered to simulate relatively high rainfall. All egg mortality was the result of predation by Solenopsis ants, which discovered and killed eggs in an average of 13 days on the high rainfall plots compared with an average of 25 days on the low rainfall plots; fewer eggs survived on the high than low rainfall plots. Thus, rainfall directly affects the rate of predation by ants on eggs, and indirectly affects the amount of recruitment into the population.

Anolis apletophallus populations also experience densitydependent regulatory interactions through intraspecific



Figure 16.4 Population density of Anolis apletophallus on Barro Colorado Island, Panama. The number of lizards in the study area at the end of the wet season varied nearly 100-fold between 1971 and 1989, reaching a high of 152 lizards in 1978 and falling to 2 or 3 lizards in 1983, 1984, and 1985. (After Andrews 1991; photograph by Robin Andrews.)



Figure 16.5 Density-dependent body condition and recruitment of *Anolis apletophallus* **on Barro Colorado Island, Panama.** (A) Body condition of males and females (calculated as mass^{0.33}/snout-vent length) decreases as adult density (indexed by the density of adult males) increases. (B) The percentage of young individuals (juveniles and subadults) in the population decreases as the adult density increases. (After Andrews 1991.)

competition for insect prey and/or for territories (Andrews 1991). Body condition is negatively related to population density. That is, when density is high, the lizards have poorer body condition than they do when density is low (**Figure 16.5A**). The rate of egg production declines when females are in poor condition, so when densities are high, population growth is slowed. Conversely, at low densities, population growth is enhanced by greater egg production. Moreover, when adult density is high, the proportion of juveniles and subadults in the population is relatively low, suggesting that recruitment into the adult class is density-dependent (**Figure 16.5B**).

Population stability of amphibians and reptiles varies considerably among taxa, largely as a function of life-history attributes. Population sizes of short-lived species such as *Anolis apletophallus* vary considerably from year to year because size is a function of each year's reproductive success. In contrast, population sizes of long-lived species such as the Maud Island frog (*Leiopelma pakeka*) and the chuckwalla lizard (*Sauromalus obesus*) vary little from year to year. The reason is that when adult survival rates are high, the longlived adult population buffers annual variation in reproductive success. During 5 years of observation, population density of chuckwallas at a Colorado Desert site varied less than twofold (Abts 1987). Similarly, population densities of *Leiopelma pakeka* varied only fourfold over a 25-year period, whereas the density of the short-lived *Anolis apletophallus* changed by nearly 100-fold within 6 years.

16.2 Community Ecology

In Section 16.1 we discussed population parameters that are integral to determining population size and changes in population size over time. A population, however, is embedded in a biotic and physical environment that includes other species, habitat structure, and weather. Interactions with these and other factors affect how a population changes in size and how it is regulated. In a broad sense, an ecological **community** consists of all the species existing at a particular point in the landscape. Usually, though, ecologists study only a subset of the community. A herpetologist, for example, might choose the subset consisting of all the arboreal frogs and lizards in a rainforest. This subset is referred to as an **assemblage**, and we will use this term when we discuss specific studies of amphibians and reptiles.

The noise coming from a frog pond on a rainy evening can be deafening. Males of many different species may all be calling at once. Identifying the right species, let alone the right mate, would appear to be challenging for females (Figure 16.6). A community ecologist, however, has broader issues to resolve. Why do some species occur in this particular assemblage while others are absent? Do interactions among species favor some species over others? Is the physical environment (temperature and humidity) more or less significant than the biological environment (competition and predation)? How important are stochastic events, such as arrival order of frogs and weather conditions such as extreme drought, unusual cold or hot spells, tornadoes, hurricanes, and floods? Is the composition of the assemblage determined by present-day events, or is it influenced by events that occurred tens of thousands of years ago? Questions such as these have constituted the core of research in animal community ecology for decades.

Determinants of community structure

An early conclusion of ecologists was that **community structure** (i.e., the number of species, relative abundance of species, and their spatial and temporal arrangement within the community) is not random. Instead, communities are made up of species that fit together particularly well. In the 1960s and 1970s, ecologists concluded that interspecific competition was the main force organizing community structure. Over the past several decades, however, many ecologists have questioned the importance of competition



A	Lysapsus limellum	1	Hypsiboas puntatus		
В	Sphaenorhynchus carneus	J	Hypsiboas lanciformis		
С	Sphaenorhynchus dorisae	К	Leptodactylus wagneri		
D	Dendropsophus rossalleni		(Leptodactylidae)		
F	Snhaenorhunchus lacteus	L	Dendropsophus haraldschultzi		
	Sprittenormynemus increas	М	Scinax boesemani		
F	Dendropsophus triangulum	NI	Colores and allowed		
G	Dendropsophus "nanus-like"		Scinax nebulosus		
Н	Hypsiboas raniceps	0	Hypsiboas boans		

in structuring communities, and some have questioned whether communities have structure at all.

This shift in perspective is associated with the recognition that community structure is the result of processes that operate on many temporal and spatial scales as well as the day-to-day interactions among individuals. For example, the present-day composition of amphibian and reptile assemblages in Europe reflects the location of past glacial refugia more than it does current climatic conditions (Araújo and Pearson 2005). Community structure is also influenced by the regional dynamics of local immigration and extinction and by climate change.

To understand community structure, researchers must distinguish patterns from the mechanisms that cause them. A common pattern of community structure is that similar species differ in how they use the resources of the habitatfor example, by being active at different times of the day, using different microhabitats (small areas within a larger habitat, such as a fallen log versus leaf litter in a forest), or eating different food. The problem that community ecologists face in explaining how these patterns come about is that well-defined patterns can be produced by two or more mechanisms or by interactions among mechanisms. For example, differences in diet among coexisting species (pattern), while often interpreted as the result of avoiding competition through niche partitioning (mechanism), could simply be the result of preexisting differences in behavior or morphology (mechanisms).

Figure 16.6 Fifteen species of frogs call from the same floating meadow in Manaus, Brazil. The frog species are represented by circled letters and identified in the key. All except *Leptodactylus wagneri* are hylids. Each species has its own distinctive call, and the frogs partition calling sites by type of vegetation (identified below the drawings). *Salvinia* is a floating plant with tiny leaves that rest on the water's surface, *Reussia* is a water hyacinth that floats on the surface and extends its leaves upward, and *Paspalum* is a tall grass. Bushes in the transitional zone and trees in the flooded forest provide a variety of elevated calling sites. (After Hödl 1977.)

Patterns and mechanisms of amphibian and reptile assemblages

Studies of amphibians and reptiles have made critical contributions to community ecology. One reason for this is that many species have small body sizes, high population densities, small home ranges, and occur in assemblages of interacting species. These life-history features make amphibians and reptiles particularly suitable for manipulative field studies and controlled laboratory experiments.

COMPETITION One pattern often attributed to competition is **resource partitioning**—the differential use of resources by sympatric species in an assemblage. Differences among species extend from slight to substantial, and may involve one or several resources. Reviews of resource partitioning by amphibians and reptiles reveal considerable variation among assemblages in the resource that is partitioned (Toft 1985). In North American deserts, for example, food is the major resource partitioned by lizards, but in the Kalahari Desert of southern Africa, all lizards eat termites and partitioning of food resources is slight. However, lizards in the Kalahari exhibit considerable differences in microhabitat use and in time of activity. Australian desert lizards exhibit strong separation with regard to all three resources: food, microhabitat, and time of activity (Pianka 1986).

Several decades ago, most ecologists attributed resource partitioning to the influence of past or ongoing interspecific competition. Differences among sympatric species in morphology (especially body size and traits related to feeding), timing of activity, preferred habitat, and prey selection were thought to permit species to coexist by minimizing competition for limited resources. Subsequently, however, ecologists have questioned the relationship between resource partitioning and competition for several reasons. Species differ in morphology, physiology, and phylogenetic history, and it makes sense that they would use resources somewhat differently whether competition is an issue or not. Predation can lead to resource partitioning via differences in the times or places that a species forages. Furthermore, many species never reach population densities high enough that individuals need to compete for resources.

Demonstrating the importance of competition usually requires experimental manipulations in the field. For example, by removing individuals of one species, a researcher can measure the effect of that species on another. Arthur Dunham (1980) assessed competitive interactions between two small insectivorous lizards—the tree lizard (*Urosaurus* ornatus) and the canyon lizard (Sceloporus merriami)—in an area of the Chihuahuan Desert in Texas (Figure 16.7). He found that population density, foraging success, growth rate, body mass before hibernation, and lipid levels of *U. ornatus* were significantly greater in plots from which *S. merriami* had been removed than in plots where both species occurred. Differences occurred only during the two driest years of the 4-year study, however. The abundance of food was positively correlated with rainfall, and this observation suggests that these lizards compete only during periods of drought-induced food scarcity. The observation that the intensity of interspecific competition varied with environmental conditions indicates the importance of long-term studies in determining the impact of competition.

PREDATORS, PARASITES, AND PATHOGENS Predation occurs when one individual captures and eats another. The effects of predation may be direct or indirect. Most predators feed on more than one prey species in a community, and the choice of prey at any given moment often depends on the



Urosaurus ornatus



Sceloporus merriami





in June, is shown here for one dry year of the 4-year study. This pattern was not seen during the two wettest years of the study, suggesting that competition between these species is heavily influenced by environmental conditions. (After Dunham 1980; photographs by Robert Shantz/Alamy and R. D. Bartlett.)





(B) A. wattsi





relative abundance of different prey species. As a given prey species increases in abundance, it may become a primary diet item for increasing numbers of predator species. Eventually, increased predation pressure will reduce the density of that prey species, making it a less preferred prey item. Thus, predation can shape community structure by modifying the abundance of prey populations. For amphibians, the size of the pond and the **hydroperiod** (the length of time a site contains water) may have an indirect influence on predation by modifying the abundance and composition of the predator assemblage (Hero et al. 1998; Azevedo-Ramos et al. 1999).

Like competition and predation, parasites operate in a density-dependent manner and may regulate the density of species and alter a community's composition (Dobson and Hudson 1986). Given that roughly half of all animal species are parasites, their importance in shaping host communities is probably underappreciated. A parasite invading a community could affect some species and not others. Shifts in competitive and predator–prey interactions could restructure the community by reducing the number of species **Figure 16.8 Malaria affects competition between two species of Anolis.** The two species of *Anolis* that occur on the island of St. Maarten in the Lesser Antilles are similar in size and strongly competitive. *A. gingivinus* (A) occurs throughout the island, whereas *A. wattsi* (B) is found only in the central hills (dashed outline). (C) The distribution of the two species is mediated by malaria. At every site where *A. gingivinus* occurs alone, malaria is either absent or very rare (open circles). Where the two species of *Anolis* coexist, malaria is present in *A. gingivinus* (filled circles). (After Schall 1992; photographs by Joseph Schall.)

present and by affecting densities of the constituent species. Ecologists tacitly acknowledge that parasitism may be extremely important in structuring communities, but only a few empirical studies have documented this phenomenon.

An important exception is Joseph Schall's 1992 study of malaria parasitism and the distribution of *Anolis gingivinus* and *A. wattsi* on the

Caribbean island of St. Maarten (**Figure 16.8**). *A. gingivinus* occurs throughout the island, but *A. wattsi* occurs only in the central hills. The malarial parasite *Plasmodium azurophilum* is common in *A. gingivinus* in some areas, but it rarely infects *A. wattsi*. The distribution of the parasite relative to the lizards is intriguing. *A. gingivinus* occurs alone in areas where the parasite is absent, but *A. wattsi* is present wherever the parasite infects *A. gingivinus*. *A. wattsi* apparently can compete successfully with *A. gingivinus* only in the central hills, where *A. gingivinus* is weakened by malaria. Malaria thus mediates competition between *A. gingivinus* and *A. wattsi* and determines the present distribution of the two species on the island.

Pathogens (bacteria, viruses, and fungi) also affect assemblage structure. When pathogens affect species differently, they can change the outcome of interactions. Joseph Kiesecker and Andrew Blaustein (1999) studied the effects of a pathogenic water mold, *Saprolegnia ferax*, on competitive interactions between the tadpoles of the Cascades frog



Figure 16.9 Interactive effects of *Saprolegnia* fungus and *Rana* tadpoles on *Pseudacris* tadpoles. *Pseudacris* regilla tadpoles appeared to be unaffected by the *Saprolegnia* pathogen (data shown in green), but they had higher survival, faster development, and were larger at metamorphosis when they were exposed to both the pathogen and *Rana* cascadae tadpoles than when they were exposed to the *Rana* tadpoles alone (data shown in blue). (After Kiesecker and Blaustein 1999.)

(*Rana cascadae*) and the Pacific treefrog (*Pseudacris regilla*, formerly *Hyla regilla*). Larval recruitment of *Rana* was reduced by 46% in the presence of the pathogen, but survival of *Pseudacris* was not affected. In the absence of the pathogen, *Rana* tadpoles had strong negative effects on the growth, development, and survival of *Pseudacris* tadpoles. The competitive interaction was reversed in the presence of the pathogen, however, because *Pseudacris* was not affected and *Pseudacris* tadpoles had higher survival, faster development, and were larger at metamorphosis (**Figure 16.9**). These results show how a factor that changes the outcome of interactions can influence the structure of assemblages.

INTERACTIONS BETWEEN COMPETITION AND PREDATION

Competition and predation can interact to affect community structure. Assemblages of larval amphibians have been used to illustrate this phenomenon because they are often found in a well-defined space, such as a small pond, where controlled experimental manipulations are feasible. Larval assemblages include competitors (filter-feeding tadpoles) and predators (salamander larvae) that prey on each other as well as on tadpoles. Researchers have used enclosures in natural ponds or artificial ponds (often cattle watering tanks) to simulate natural habitats (Wilbur 1997).

Enclosures in natural or artificial ponds can be stocked with predetermined quantities of food, tadpoles of competing species, predatory salamander larvae, and predatory insects, and physical conditions (e.g., shading, hydroperiod) can be modified. Because all variables in these experiments can be controlled, powerful parametric statistics can be used to detect direct effects of predation and competition as well as interactions among these and other variables. Results of these experimental studies suggest that both intraand interspecific competition and predation are important in structuring assemblages and that these factors interact in complex ways (Alford 1999).

Competition may be particularly intense among tadpoles that develop in temporary ponds, because each individual must garner enough food to metamorphose before the pond dries. In contrast, because predators are likely to reduce the densities of tadpoles in permanent ponds, individuals might experience reduced interspecific competition. David Skelly (1995) tested this idea by studying two species of treefrogs in southeastern Michigan: the striped chorus frog (Pseudacris triseriata) and the spring peeper (P. crucifer) (Figure 16.10). The species show marked differences in the types of sites where tadpoles develop; striped chorus frogs usually occur in more temporary ponds, spring peepers in more permanent ponds. In order to understand the basis for this pattern, Skelly examined the effects of pond drying, competition, and predation on the survivorship, size, and developmental time of tadpoles of the two species in temporary, intermediate, and permanent ponds.

Field experiments revealed that striped chorus frogs grew larger and survived better than spring peepers in temporary ponds. In contrast, spring peepers grew larger and survived better than striped chorus frogs in permanent ponds. Although the chorus frogs developed faster than the peepers—and therefore had a better chance of escaping a drying pond—they also seemed to be more vulnerable to predators. A surprising result was that interspecific competition exerted little or no effect on the outcome of the experiment.

In the laboratory, Skelly (1995) observed behavioral differences between the tadpoles that explained his experimental results. The more active a tadpole is in gathering food, the more it can grow and develop. But activity makes a tadpole conspicuous to predators. Skelly found that chorus frog tadpoles are more active than spring peeper tadpoles. This activity allows them to grow and develop faster, but it makes them more vulnerable to predation.

The structure of larval amphibian assemblages is also influenced by the order in which species deposit their eggs in a pond (referred to as priority effects) and by the order



Figure 16.10 Two species of treefrogs breed in markedly different types of aquatic sites. In an experiment carried out by David Skelly (1995), striped chorus frogs (*Pseudacris triseriata;* A) grew larger and survived better than spring peepers

of hatching. All else being equal, species that deposit their eggs early are likely to become dominant as predators or as competitors because they are the largest larvae in the pond. Cope's gray treefrogs (Hyla chrysoscelis) avoid artificial oviposition sites with certain predators (fish and Ambystoma salamanders) and with conspecific larvae (Resetarits and Wilbur 1989). Female meadow treefrogs (Isthmohyla pseudopuma) also avoid artificial oviposition sites with conspecific tadpoles that cannibalize both eggs and tadpoles (Crump 1991). The timing of oviposition may also affect interactions between species, determining levels of competition and predation. For example, aquatic adults of the red-spotted newt (Notophthalmus viridescens) eat eggs of the tiger salamander (Ambystoma tigrinum), but when the surviving tiger salamander larvae are large enough, they eat newt larvae (Morin 1983). Similarly, marbled salamander (Ambystoma opacum) larvae may either compete with or prey on larval spotted salamanders (A. maculatum), depending on the body sizes of the two species (e.g., Stenhouse et al. 1983).

HABITAT COMPLEXITY Assemblage structure can be influenced strongly by habitat complexity. For example, species richness of desert lizards increases in parallel with increas-

(*Pseudacris crucifer*; B) in temporary ponds (C), whereas peepers grew larger and survived better than chorus frogs in permanent ponds (D). (Photographs by R. D. Bartlett.)

ing plant structural diversity and overall microhabitat diversity (Pianka 1967, 1986). Studies of *Anolis* lizards emphasize the importance of the relationship between morphological and behavioral traits and habitat structure in explaining how these lizard assemblages are organized (e.g., Moermond 1979, 1986; Pounds 1988; Losos 1990). The availability of a complex matrix of tree-limb diameters, angles, and heights provides the structural resource for an assemblage of lizards with different jumping modes.

Presence or absence of many species of amphibians at breeding ponds depends on the proximity of suitable habitat for adults. Wood frogs (*Rana sylvatica*), red-spotted newts (*Notophthalmus viridescens*), and spotted salamanders (*Ambystoma maculatum*) occur in ponds surrounded by forest, whereas tadpoles of leopard frogs (*Rana pipiens*) and American toads (*Anaxyrus americanus*) are found in ponds in meadows (Guerry and Hunter 2002).

PHYSIOLOGICAL TOLERANCES Because each species has a unique set of physiological attributes, each species exhibits unique preferences and tolerances to its physical environment. These preferences and tolerances explain, in part, why species are found where they are, their observed abundances, and why they use the resources they do.

Caribbean Anolis lizards provide a good example of the effect of physiological tolerances on assemblage structure and composition. In Puerto Rico, A. gundlachi is found in the rainforest, whereas A. cristatellus is found at the edge of the rainforest or in open areas (Figure 16.11). These two trunkground species are closely related, are similar in body size, and are generalized insectivores. One might assume that the habitat partitioning they exhibit is the result of presentday competition. A more likely explanation, however, is that the difference in habitat use reflects different physiological tolerances. A. gundlachi is less heat-tolerant than A. cristatellus, a physiological difference corresponding to the microhabitats they occupy—shade for *A. gundlachi* and sun for *A*. cristatellus. In September 1989, Hurricane Hugo provided a test of the hypothesis that habitat differences are the result of physiological tolerances (Reagan 1991). Strong winds removed the canopy of forest trees in many places. When this happened, individuals of A. gundlachi left their former perches on tree trunks and retreated to lower perches that were shaded by fallen debris. Thus, it is physiological tolerances and preferences, not the presence of A. cristatellus, that prevents A. gundlachi from using sunny perch sites in open areas.

WEATHER The structure of an assemblage can vary considerably through time as a function of unpredictable or random events such as weather conditions. For example, the effect of weather on the relative abundance and composition of an assemblage of lizards from the Chihuahuan Desert in New Mexico was documented over 5 consecutive years (Whitford and Creusere 1977). The amount and seasonality of rainfall in the region are unpredictable, and spring annual plants grow only in years when rainfall in late fall or winter exceeds 75 mm. Heavy rains in midsummer produce a larger than normal biomass of grasses and forbs. Primary productivity (amount of carbon fixed by

photosynthesis) strongly affects the abundance and activity of the arthropod prey that the lizards eat. During years of above-average rainfall, insect abundance increased, resident species of lizards increased either their clutch size or their frequency of egg laying, and immigrant species from wetter habitats became established in the study sites. In contrast, during years of belowaverage rainfall, insect abundance was reduced, resident species reduced either their clutch size or their frequency of egg laying, and immigrant species exhibited reduced population sizes or disappeared entirely. Thus, weather is a strong force

Figure 16.11 Habitat differences between *Anolis. Anolis gundlachi* (A) lives in shade beneath the forest canopy, whereas *A. cristatellus* (B) lives at the edge of forest and in sunny areas created by treefalls in the forest. (Photographs: A, courtesy of Manuel Leal.; B, © John Sullivan/Alamy.) in structuring the lizard assemblages in the Chihuahuan Desert, and these assemblages can change on a yearly basis.

Weather patterns also affect the larval assemblages of amphibians that breed in temporary ponds (Pechmann et al. 1989). In a study of three wetland sites in South Carolina that were monitored over 3 to 8 years, the sites filled with water each winter and dried during the spring or summer, but the actual dates of filling and drying varied considerably among sites and years. Five species of salamanders and 11 species of anurans deposited eggs at these three sites. The number of species that successfully produced juveniles was positively correlated with the number of days the site contained water (**Figure 16.12**). Likewise, the total number of metamorphosed juveniles (all species combined) was positively correlated with pond duration.

Prolonged drought can strongly modify the composition of assemblages and the interactions among species of terrestrial amphibians. Drought affects short- and longlived species differently. Short-lived species may be locally eliminated, at least temporarily, until colonization from adjacent areas occurs. In contrast, long-lived species may experience only reduced reproduction and thus decreased population density. An extremely dry El Niño year may have contributed to the extinction of golden toads (*Incilius periglenes*) from the Monteverde Cloud Forest Reserve in Costa Rica during the late 1980s (Crump et al. 1992; Pounds and Crump 1994). During the same time period, 40% of the anuran fauna (20 species) disappeared from the area (Pounds et al. 1997, 1999).

EFFECT OF HUMANS ON ASSEMBLAGE STRUCTURE

Many of the assemblages we see today reflect activities of humans in the comparatively recent past. When Europeans began exploring the New World, they thought they had found vast, undisturbed areas of wilderness. We know now that Native Americans managed many of these landscapes

(A) A. gundlachi



(B) A. cristatellus





and in the process vastly altered them, even causing animal extinctions (Nabhan 1995). On a smaller scale, even the harvesting of a single hardwood tree from a tropical forest affects the composition and structure of the lizard assemblage (Vitt et al. 1998). The habitat disturbance re**Figure 16.12 Effect of hydroperiod on anuran reproduction at three sites in South Carolina.** (A) The number of species that successfully produced juveniles increased with the number of days the site contained water. (B) The total number of metamorphosed juveniles (all species combined) also increased with hydroperiod. Each data point represents one site for 1 year. Notice the extreme range of breeding success at Rainbow Bay: from 0 to 75,644 metamorphosed juveniles, representing 0 to 15 species. (After Pechmann et al. 1989.)

sulting from cutting a tree is much greater than that associated with a natural treefall because of trampling by people and the wood shavings left behind. The newly opened gap allows more sunlight to penetrate to the forest floor than if the tree had fallen naturally. Human-made treefall gaps have higher temperatures than natural treefall gaps. Forest lizards such as *Anolis gundlachi* cannot tolerate these high temperatures, and they move elsewhere. In contrast, heliothermic lizards (e.g., *A. cristatellus*) move into humancreated gaps where they benefit from enhanced basking opportunities. On this local scale, the lizard assemblage is greatly altered.

The reptile fauna on tropical Pacific islands consists of a mixture of native and introduced species. Polynesians and Melanesians inadvertently introduced geckos and skinks throughout much of the Pacific during their extensive travels about 4,000 years ago. More recent settlement by Europeans has further modified assemblage composition. For example, the Asian house gecko (*Hemidactylus frenatus*) has been introduced to many tropical Pacific islands since the 1930s. The density of the native mourning gecko (*Lepidodactylus lugubris*) is often reduced where the house gecko is present (**Figure 16.13**). Kenneth Petren and Ted Case (1996) interpreted this decline as a result of exploitative competition. House geckos are larger, can run faster, and are more efficient at harvesting insects that are clumped around light



Figure 16.13 Competitive interactions between two species of geckos. Introduced Asian house geckos (*Hemidactylus frenatus*) compete with native mourning geckos (*Lepidodactylus lugubris*) on the island of Oahu, Hawaii. In the absence of house geckos, approximately 80% of native mourning geckos survived

to the end of the 5-month study, but when house geckos were present, survival of mourning geckos decreased to about 60%. In contrast, survival of house geckos increased as the density of mourning geckos increased. (After Petren and Case 1996; photographs by Picade LLC/Alamy and R. D. Bartlett.) sources. The authors suggested that construction of European-style buildings with flat, open walls and lights that attract high densities of insects was probably responsible for shifts in interactions, abundances, and composition of species within these lizard assemblages.

16.3 ■ The Dynamic Nature of Assemblages

(A)

140

120

100

80

60

40

20

140

120

100

80

60

40

Days after August 1)

Median arrival date

Days after August 1)

Median arrival date

(C)

We have emphasized the dynamic nature of assemblages in the previous sections and discussed some of the factors that cause species richness, assemblage composition, and interspecific interactions to change through time. In this section we will focus on two areas of study: the impact of changes in global climate on herpetological assemblages, and the changes associated with ecological succession as previously cleared rainforest progresses toward second-growth forest.

Impact of climate change

Climate change affects amphibian and reptile assemblages directly and indirectly (Donnelly and Crump 1998). Temperature change can alter population sex ratio for reptiles with temperature-dependent sex determination. Increases in temperature can trigger earlier emergence from hibernation and earlier breeding. Stress that results from changes in temperature and moisture lowers immune function in some species and leads to outbreaks of pathogens, causing

2008

2003

1998

1998

2003

2008



Figure 16.14 Change in breeding phenology of four species of amphibians at Rainbow Bay, South Carolina, over 30 years. Four species of amphibians shifted their timing of reproduction by 15 to 76 days over 30 years of warming temperatures. (A) Marbled salamander (Ambystoma opacum) (autumn-breeding). (B) Ornate chorus frog (Pseudacris ornata) (winter-breeding).

(C) Dwarf salamander (Eurycea quadridigitata) (autumn-breeding). (D) Tiger salamander (Ambystoma tigrinum) (winter-breeding). The two autumn-breeders (A and C) began breeding later because it stayed warm longer, and the two winter-breeders (B and D) began breeding earlier because it got warm earlier. (After Todd et al. 2011; photographs by R. D. Bartlett.)

differential mortality of species in an assemblage. Changes in the activity and abundance of individuals of some species will affect the assemblage as a whole, creating opportunities for radically different species interactions. On a larger geographic scale, the composition of assemblages is changed because the geographic ranges of some species expand and those of others contract.

To assess the effect of climate change on the breeding phenology of amphibian assemblages, Brian Todd and colleagues (2011) analyzed a 30-year (1979–2008) record of the dates of migration by 10 species of anurans and salamanders to a breeding site in South Carolina. The breeding site, Rainbow Bay, is approximately 1 ha (10,000 m²) in size. The site typically fills with rainwater in late autumn and dries up in late spring or summer. Terrestrial adults of various species of salamanders and anurans migrate to the bay each year and lay their eggs. During the 30-year period, mean minimum air temperatures during the September–February prebreeding and breeding periods increased by an estimated 1.2°C.

Four species that breed in Rainbow Bay have shifted their timing of reproduction by 15 to 76 days in the past 30 years. Two species that breed in autumn (the dwarf salamander, *Eurycea quadridigitata*, and marbled salamander, *Ambystoma opacum*) arrived at the breeding site progressively later over the study period, and two winter-breeding species (tiger salamander, *Ambystoma tigrinum*, and ornate chorus frog, *Pseudacris ornata*) arrived significantly earlier (**Figure 16.14**). Warming temperatures have altered competitive and predator-prey interactions for all the species in the assemblage, and the rates of change, ranging from 6 to 37 days per decade, are among the most rapid of any so far reported.

Recovery of assemblages following habitat destruction

Tropical forests are being cleared for lumber, crops, and pasture at an alarming rate worldwide. Some cleared land is later abandoned because of reduced soil fertility. As a consequence, secondary forests have replaced much of the original primary forests. Do secondary forests serve as refugia for species normally found in primary tropical forests? This question has been addressed at the assemblage level in various parts of the world. We will highlight the results of three studies of Neotropical amphibians and reptiles that provide quite different answers to this question.

In the first study, the number of species was higher in primary forest than in successional forest and plantation forest, but the total number of individuals did not differ among forest types. Observations were made in the Jari River area of northwestern Brazilian Amazonia. In the late 1960s and 1970s, about 10% of the area was cleared and native forest was largely replaced by non-native *Eucalyptus*, which are fast-growing and provide a relatively quick source of lumber and firewood. The area is now a complex mosaic of *Eucalyptus* plantations interspersed with areas of secondary forest and surrounded by more than 1 million ha of primary forest.

Toby Gardner and colleagues (2007) compared the leaflitter frogs and lizards of three forest types (five replicate sites of each type): mature primary forest, Eucalyptus plantations (4-5 years old), and secondary forest (14-19 years since abandonment). During their 2-year study, the authors collected 1,739 frogs (23 species) and 1,937 lizards (30 species) (Figure 16.15). Ninety-six percent of all frog species were found in primary forest, and about one-third of these were found only in primary forest; one species was found only in secondary forest. Eighty-one percent of all lizard species were found in primary forest, and about one-third of these were found only in primary forest; four species were found only in Eucalyptus plantations. More species of frogs were found in secondary forest than in Eucalyptus plantations, whereas numbers of lizard species in these two forest types were similar. The Eucalyptus sites were dominated largely by generalist species with widespread distributions. The authors concluded that "secondary forest does not provide a substitute for primary forest, and in the absence of further evidence from older successional stands, we caution against the optimistic claim that natural forest regeneration



Figure 16.15 Secondary forests have lower species richness than primary forests, but a similar abundance of frogs and lizards. This conclusion comes from a 2-year study carried out in northwestern Brazilian Amazonia (Gardner et al. 2007), in an area made up of *Eucalyptus* plantations interspersed with secondary forest and surrounded by primary forest. More species of frogs were found in secondary forest than in *Eucalyptus* plantations, whereas numbers of lizard species in these two forest types were similar.

in abandoned lands will provide refuge for the many species that are currently threatened by deforestation."

In the second study, species richness did not differ across successional stages, but individual abundance was substantially lower in the two earliest successional stages than in the two oldest. Adriana Herrera-Montes and Nicholas Brokaw (2010) compared the occurrence of frogs, lizards, and snakes from four successional habitats during a 1-year study at a lower montane area of northeastern Puerto Rico (three replicates per habitat type): pasture (still with cattle), voung forest (1-5 years since pasture abandonment), intermediate forest (10-20 years since pasture abandonment), and advanced forest (40 years since pasture abandonment). Habitat and microclimate changes associated with forest age included increased plant species richness, larger average stem density, greater herb cover, greater canopy cover, and less variable relative humidity and temperature. All these changes alter resources for feeding, basking, egg laying, and other activities.

The authors recorded a total of 6 frog and 13 lizard and snake species and 7,993 individuals at the 12 sites (**Figure 16.16**). While the number of species observed was not related to successional stage, successional stage affected assemblage composition. Diversity and similarity measures indicated that **assemblage equitability** (distribution of abundance of species) of frogs tended to decrease through succession, whereas squamates showed the opposite pattern. The results of this study support the idea that second-



Figure 16.16 Successional stage has a greater effect on the numbers of individuals than on the number of species. This conclusion comes from a 1-year study carried out in Puerto Rico (Herrera-Montes and Brokaw 2010).

ary forests are important for the conservation of amphibian and reptile species richness in highly human-modified landscapes.

In the third study, young second-growth forests had species richness and assemblage composition of frogs similar to those of old-growth forests. Branko Hilje and T. Mitchell Aide (2012) studied forests of different ages in northeastern Costa Rica following abandonment as cattle pastures and compared these with old-growth forests (three replicates of each forest type): second-growth forests 10–16 years old, second-growth forests 17–23 years old, second-growth forests 24–28 years old, second-growth forests 36–48 years old, and old-growth forests. The authors found that even the youngest forests had similar species richness and assemblage composition as old-growth forests. They concluded that secondary forests can potentially mitigate the negative effects of deforestation and other loss of habitat.

The primary lesson that can be drawn from the contrasting results of these three studies is that the proximity of secondary forest to primary forest and the presence of appropriate habitat for dispersal play important roles in determining the extent to which secondary forests serve as refugia for species normally found in primary forests:

- In Puerto Rico, the secondary-forest sites were within 100 m of primary forest, and recolonization allowed rapid recovery of species richness (Herrera-Montes and Brokaw 2010).
- At the other extreme, in Brazil, secondary-forest sites that were more than 1 km from primary forest recovered only 60% of the primary forest species after 14–19 years of recovery, and the species composition of the secondary-forest sites differed greatly from that of primaryforest sites (Gardner et al. 2007).
- In Costa Rica, species recovery was slower than in Puerto Rico, although secondary forests (10–16 years of recovery) had similar numbers of species and assemblage composition as old-growth forests (Hilje and Aide 2012). Relatively rapid recolonization occurred in young forests even though the average distance to source areas (primary forests) was about 500 m—a distance intermediate between those in the Puerto Rican and Brazilian studies. In Costa Rica, however, young forests were connected to source areas by corridors of riparian vegetation, living fences, and other land uses that facilitated dispersal.

16.4 Gradients in Species Richness

When Victorian-era naturalists explored the equatorial regions of South America, Africa, and Asia, the sheer numbers of species astonished them. A deciduous forest in England, for example, has about 20 species of amphibians and reptiles. In contrast, the same area of Amazonian rainforest might have 200 species. This observation illustrates a general biological phenomenon: the numbers of species of most

Latitudinal gradients

Most major animal and plant taxa exhibit latitudinal gradients in species richness on both global and continental scales (Hillebrand 2004). While latitudinal gradients are well documented for modern and ancient biotas, the mechanisms responsible are only beginning to be understood. The problem with many of the numerous explanations proposed in the past is that they do not address ultimate causality (Lomolino et al. 2006). Recent studies of amphibians and reptiles identify factors that are fundamental contributors to species richness gradients.

PATTERNS The number of amphibian and reptile species reported for 22 continental sites declines more or less linearly from equatorial to temperate latitudes (Figure 16.17). In this example the highest-latitude site (i.e., farthest from the Equator) is in Austria (48°N) and has 28 species, and the lowest-latitude site, in Ecuador (0°), has 173 species. The variance in species richness at any latitude reflects both habitat diversity and habitat type. For example, at roughly the same latitude the mesic (i.e., moderately wet) and seasonally flooded Pantanal savannah of Brazil has substantially more species than the xeric (arid) and seasonally burned savannah at Lamto, Ivory Coast. Not surprisingly, frogs, lizards, and snakes-groups with worldwide geographic distributions that extend far north and south of the Equator-display latitudinal gradients in species richness, whereas caecilians and crocodylians, which have smaller geographic distributions, do not.

Caecilians and crocodylians are largely limited to tropical latitudes, and within the tropics caecilians are largely associated with rainforests. The circumtropical distributions of these taxa presumably reflect long-term physiological adaptation to the warm and moist conditions of equatorial regions. In contrast, salamanders and turtles have their highest species richness in temperate regions: salamanders in eastern North America and Eurasia (the radiation of salamanders in Central and South America is comparatively recent) and turtles in southeastern North America and southeastern Asia. Biogeographic factors related to the distributions of caecilians, salamanders, turtles, and crocodylians are discussed in Chapter 5.

EXPLAINING LATITUDINAL GRADIENTS As a first principle for explaining latitudinal gradients in species richness, Mark Lomolino and colleagues (2006) proposed that latitudinal gradients must reflect the way in which fundamental



Figure 16.17 Latitudinal gradient in species richness of amphibians and reptiles. Sites are distributed globally, and each point represents the total number of species present (or likely to be present) in areas of 25 km². Sites mentioned in the text are identified. (After Vitt and Caldwell 2014.)

geographic features of Earth affect speciation and the dispersal and extinction of species. Fundamental geographic features include (1) climate and (2) the distribution of land area. Latitudinal gradients in temperature, moisture, and energy are established by the uneven distribution of solar energy on Earth: equatorial regions receive far more solar energy per unit of area than do polar regions. The wobble in Earth's rotation establishes gradients in the magnitude of seasonal variation in solar energy and in day length. Over millions of years, plate tectonics have contributed to spatial variation in these fundamental geographic features, and hence to patterns in species richness.

Climate and productivity are highly correlated with species richness, both in general and for amphibians and reptiles (Qian et al. 2007; Buckley et al. 2008; Field et al. 2008). In a now-classic study, Joseph Schall and Eric Pianka (1978) reasoned that if the species richness of herpetofaunas is causally related to climate, then the relationship between species richness and local climatic features should display the same pattern on different continents. Comparing herpetofaunas in the United States and Australia, Schall and Pianka found that despite differences in latitude (the United States is farther from the Equator) and climate (Australia is drier), group-specific associations between climate and species richness were similar:

- Species richness of frogs and turtles is most strongly and positively correlated with mean annual rainfall and negatively correlated with mean annual hours of sunshine.
- Species richness of lizards is most negatively correlated with mean annual rainfall and most strongly and positively correlated with mean annual hours of sunshine.

Species richness of snakes is strongly and positively correlated with both mean annual rainfall and mean annual temperature.

These patterns make intuitive sense: aquatic frogs and turtles are most species-rich in wet areas, heliothermic lizards in sunny areas, and the relatively mesic-adapted snakes in warm and wet areas.

The observation that climatic factors are correlated with species richness does not mean that climate by itself is the ultimate causal mechanism that explains greater species richness at the Equator than at more northerly latitudes. A causal mechanism has to explain, for example, why high productivity of tropical rainforests is associated with high species richness rather than with an increase in the abundance of individuals of a small number of species (Buckley and Jetz 2010). Ultimately, species richness is the net outcome of the addition of species through speciation, loss through extinction, and shifts in distribution through dispersal. Recent analytical advances in phylogenetic comparative methods now provide the tools to analyze the history of organismal diversification in its biogeographical context.

R. Alexander Pyron and John Wiens (2013) evaluated the global species richness of amphibians (**Figure 16.18**). They generated a phylogeny for 2,871 amphibians (more than 40% of extant species) and assembled information on range, local climates, and habitat productivity. They then used this information to address two primary questions about species richness gradients with analyses based on the species-based phylogeny, family-level clades, and the faunas of 12 global ecoregions.

Figure 16.18 Global richness of 6,117 species of amphibians. The data are the number of species in 5-degree grid cells plotted on a logarithmic scale. (From Pyron and Wiens 2013.)

Pyron and Wiens first addressed the question of whether the fundamental processes of speciation, extinction, and dispersal vary between temperate and tropical regions. Their analyses document high speciation rates and low extinction rates in the tropics, and low speciation rates and high extinction rates in temperate regions. The species richness gradient established by latitudinal differentials between speciation and extinction is reinforced by low dispersal out of the tropics into temperate regions, and by much higher dispersal into the tropics from temperate regions.

Overall, species richness is highest at the Equator. South America, for example, was first colonized by extant amphibian lineages about 96 million years ago (mya). The current species richness of more than 2,300 species is the result of rapid diversification of relatively young families. In contrast, the temperate Nearctic was colonized by extant amphibian lineages much earlier, about 200 mya. As a result of this early colonization and subsequent high extinction rates, the current Nearctic fauna consists of only about 300 species, including many ancient, species-poor clades.

The second question addressed by Pyron and Wiens is whether variation in rates of speciation, extinction, and dispersal are related to ecological factors such as the species' **climatic niche** (an aggregate index based on 21 climatic variables), proxies of energy availability (actual evapotranspiration, net primary productivity, and mean annual temperature), the area occupied by clades, and other factors. They found that equatorial climatic niches are associated with high rates of speciation and low rates of extinction and that temperate-zone climatic niches are associated with low rates of speciation and high rates of extinction. Diversification at the family level was positively linked to area occupied by the families and to net primary productivity. Finally, ecoregion-based analyses identified area and energy (actual evapotranspiration) as



important determinants of species richness and rejected the hypothesis that richness was related to the amount of time for diversification.

Elevational gradients

Species richness also varies as a function of elevation; the numbers of species at the base of mountains is greater than at their tops. In some ways, traveling up in elevation parallels traveling toward the poles: mean temperature and height of vegetation both decrease. While climate and productivity variables are correlated with species richness on both latitudinal and elevational gradients, these correlations are weaker on elevational gradients (Field et al. 2009). The reason, in part, is that the two types of gradients differ in fundamental ways. Elevational gradients are much shorter—a few kilometers as opposed to the thousands of kilometers from equatorial to polar latitudes. Moreover, elevational gradients have latitude as a second geographic dimension, and latitude affects climatic seasonality, which in turn affects species richness.

PATTERNS OF SPECIES RICHNESS Animals and plants frequently exhibit hump-shaped patterns in which species richness increases with elevation until it reaches a peak at low to mid-elevations and then decreases (Rahbek 1995). In Asia, for example, species richness of spiny frogs (Dicroglossidae) is hump-shaped over an elevational gradient from 0 to 5,000 m (Hu et al. 2011). Sister groups exhibit hump-shaped curves, but the elevation of highest species richness differs by about 1,000 m (Figure 16.19). Humpshaped distributions of amphibian and reptile species richness are presumably associated with the hump-shaped distributions of climatic factors such as moisture or net primary productivity. Mountains often have a mid-elevation zone with enhanced moisture because of condensation (the cloud zone of tropical mountains) or because rainfall is relatively high and evaporation relatively low (arid mountains) (Rahbek 1995; McCain 2010).

MECHANISMS Annual variation in temperature is profoundly affected by latitude. Mean monthly temperature at the Equator scarcely changes through the year; in temperate regions a range of 20–30°C or more is typical. Similarly, uniform temperatures characterize elevational gradients on tropical mountains, and thermal overlap between elevations is low. In contrast, highly variable temperatures characterize elevational gradients in the temperate zone, and thermal overlap between elevations is substantial (Janzen 1967). As a result of adaptation to a narrow seasonal range in ambient temperature, tropical organisms have narrower thermal tolerances and hence narrower elevational ranges than do organisms in the temperate zone (Huey 1978; van Berkum 1988).

Do such latitudinal differences in physiological adaptation reflect mechanisms of speciation? Observations of plethodontid salamanders indicate that they do: sister spe-



Figure 16.19 Elevational patterns in species richness of spiny frogs. Patterns shown are for the sister clades Paini (N = 33 species) and Quasipaini (N = 8 species) on elevational gradients in Asia. Species were counted in sequential 200-m increments in elevation. (After Hu et al. 2011.)

cies in tropical Mesoamerica (central Mexico into northern Costa Rica) have substantially less overlap in elevational ranges and ambient temperature regimes than do temperate-zone sister species (Kozak and Wiens 2007). Elevational gradients in themselves thus appear to promote speciation in the tropics, while geographic isolation is required for speciation in the temperate zone.

Patterns of species richness on elevational gradients are associated with gradients in climate and productivity (Field et al. 2009). Nonetheless, because elevational gradients are short and geographically diverse, patterns may also reflect the evolutionary history of particular groups. Bolitoglossine salamanders in Mesoamerica provide a good example of this phenomenon. To explain the hump-shaped distributions of bolitoglossines (Figure 16.20A), Wiens and his colleagues (2007) used a time-calibrated phylogeny to test two hypotheses. One is that the mid-elevation peak in species richness reflects ecological factors that promote a high rate of species diversification (speciation rate minus extinction rate). The second hypothesis is that diversification rates do not differ among elevations, but that species richness is higher at mid-elevations because these areas have been colonized the longest, thus allowing more time for species to evolve and accumulate.

The time since colonization hypothesis is supported by a strong positive relationship between species richness in elevational zones and the estimated time of first colonization of that zone (Figure 16.20B). Historically, bolitoglossine salamanders colonized Mesoamerica from North America. The invasion front followed the mid-elevation montane habitats that are most similar climatically to the temperate



Figure 16.20 Elevational patterns of species richness of bolitoglossine salamanders in Mesoamerica. (A) A hump-shaped pattern of species richness is a function of elevation. (B) Species richness was measured in 500-m elevational increments as a function of the estimated oldest date when each elevational band was first colonized. (After Wiens et al. 2007.)



habitats occupied by salamanders in North America. Such a route would have been the easiest path into the tropics for species already adapted to cool mesic habitats (Wiens et al. 2007).

SUMMARY

Population ecology is concerned with the aggregate properties of the members of populations.

The statistical properties of populations (their demographics) include numbers of individuals, birth and death rates, age structure, and population growth rate.

A population is a group of conspecific individuals that live in some arbitrarily defined area.

A population may occupy a restricted geographic area such as a pond, or occupy an extensive area such as the eastern United States.

Not all populations are restricted to exclusive geographic areas. Sea turtles, for example, consist of metapopulations—populations that are defined on the basis of their different breeding areas but that intermingle during migration and in feeding areas.

The two most fundamental questions asked about a population are what is its size and how does its size change over time?

Determining population size is usually difficult because some, or even most, individuals present will not be detected during a census.

Ecologists have devised statistical methods to estimate population parameters such as population size and survival rates from matrices of capture or absence of individuals in a series of censuses.

Another approach to demographic analysis is to summarize information on reproduction and survival in a life table. Life table analyses provide estimates of population growth rate, stable age distribution, and the sensitivity of each class to environmental change.

Population dynamics are the consequence of interactions between individuals and their physical and biological environments.

Population size or composition or both may vary seasonally, from year to year, and over decades.

- Interactions with the physical environment are typically density-independent and involve factors such as weather and geophysical disturbances.
- Interactions with the biological environment are typically density-dependent and involve such factors as inter- and intraspecific competition, predation, and parasitism.
- In general, density-dependent factors dampen the magnitude of change due to density-independent factors and keep a population at the same average size over ecological time scales.

Community ecology focuses on the multispecies patterns that occur within a site or across the landscape.

In a broad sense, a community consists of all the species existing at a particular point in the landscape.

An assemblage is a subset of species of a community; for example, a herpetologist might study the assemblage of arboreal frogs and lizards at a rainforest site.

Community-level patterns include the number of species, absolute and relative densities of those species, and patterns of resource use.

Community ecology also focuses on the mechanisms that generate those patterns.

A central question in community ecology is whether assemblages are random groupings of species, or structured groups of interacting species.

Community structure results from processes that operate on many temporal and spatial scales.

Studies of amphibians and reptiles have made valuable contributions to answering some of the questions central to community ecology.

Mechanisms such as competition and predation are occurring all the time, and they can have subtle influences on patterns even though they may not by themselves be responsible for overall patterns.

One pattern often attributed to competition is resource partitioning.

Predators, and the cryptic and little-studied effects of parasites and pathogens, can profoundly influence interspecific interactions and assemblage composition.

Competition and predation often interact to structure assemblages; the relative importance of competition and predation (and interactions between these factors) depends on the kinds of organisms that make up the assemblage and the nature of the environment.

Assemblage structure can be strongly influenced by the heterogeneity of the environment.

Physiological tolerances explain, in part, why species are found where they are, their observed abundances, and why they use the resources they do.

The outcome of interactions in any assemblage can be changed or modified by unpredictable events such as extreme weather conditions.

Many of the geographic distributions and assemblage compositions we see today may reflect past activities of humans.

Herpetofaunal assemblages are dynamic.

Species richness, composition, abundance, and interactions of herpetofaunal assemblages will be increasingly affected by climate change. Amphibian and reptile assemblages that are disrupted by habitat fragmentation, modification, and destruction have the potential to recover, at least in part, if there are refugia into which individuals from the assemblage can disperse.

■ The most important factors affecting the number of species in a given area (species richness) include the geophysical properties of Earth (distribution of solar energy, distribution of land area) and the fundamental biological processes of speciation, extinction, and dispersal.

Species richness of amphibians and reptiles varies with latitude, with the highest number of species found at the Equator and the fewest toward the poles.

Latitudinal gradients in species diversity are characteristic of anurans and squamates. Caecilians and crocodylians have circumtropical distributions, whereas species richness of salamanders and turtles is highest in warm temperature regions.

Species richness also varies with elevation. Many species exhibit hump-shaped distributions, where the number of species increases with elevation to a peak at mid-elevations and then decreases at the highest elevations.

Species richness of both latitudinal and elevational gradients is correlated with factors related to climate and primary productivity.

Species richness on latitudinal gradients is the result of high rates of speciation and low rates of extinction in the tropics relative to the temperate zone. Net dispersal is from the temperate zone into the tropics.

Species richness on elevational gradients can be affected by historical factors such as the relative lengths of time that particular elevational zones have been occupied by particular groups.

Go to the *Herpetology* Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

PART IV What Are Their Prospects for Survival?

CHAPTER 17

Conservation and the Future of Amphibians and Reptiles



17 Conservation and the Future of Amphibians and Reptiles

rchie Carr (1909–1987), one of the great champions of amphibians and reptiles, was a professor, naturalist, conservationist, author of popular books and articles, and a world authority on sea turtles. Six decades ago, in *The Windward Road* (1955), Carr warned of the impending decline of one of his favorite animals, the green sea turtle (*Chelonia mydas*):

Where twenty years ago most Caribbean shore was wilderness or lonesome cocal [coconut grove], aluminum roofing now shines in new clearings in the seaside scrub. The people are breeding too fast for the turtles. The drain on nesting grounds is increasing by jumps. It is this drain that is hard to control, and it is this that will finish Chelonia.

It is not only sea turtles that are disappearing. Amphibian and reptile populations are declining worldwide.

17.1 ■ Declining Populations of Amphibians and Reptiles

The International Union for the Conservation of Nature (IUCN) assesses the conservation status of animal and plant species worldwide and maintains the Red List of Threatened Species, a catalog of the conservation status of animal and plant species. Threatened species are classified as Critically Endangered, Endangered, or Vulnerable. We lack information for many species; those that cannot be evaluated are designated Data Deficient. Because many species have not been evaluated and many others have been evaluated over only part of their range, the Red List is a conservative estimate of the species threatened with extinction. Version 2014.2 of the list classifies nearly onethird of amphibian species (31.2%) and one-fifth of reptile species (21.7%) as Critically Endangered, Endangered, or Vulnerable; 25% of amphibians and 18% of reptiles are classified as Data Deficient (Table 17.1, p. 560). An analysis

published in the journal *Nature* was even more pessimistic, listing 41% of the known species of amphibians as threatened (Monastersky 2014).

Amphibians

In the past three decades herpetologists have reported worldwide declines in populations of frogs, salamanders, and caecilians (see Collins and Crump 2009). Amphibian declines are occurring at a rate estimated to be 200 times that of historical extinction levels (McCallum 2007). The extent of decline varies from region to region and within and among species. Population declines have been reported from every continent where amphibians occur and from both montane and lowland areas. Here are a few examples:

- Western United States: From the mid-1970s to the early 1980s, 11 populations of western toads (*Anaxyrus boreas boreas*) disappeared from the West Elk Mountains of Colorado (Carey 1993), and Yosemite toads (*A. canorus*) declined drastically in the high elevations of California's Sierra Nevada (Sherman and Morton 1993). California red-legged frogs (*Rana aurora draytonii*) have disappeared from more than 70% of their historic range in California (Davidson et al. 2001), and other ranids are declining in California and Oregon. Tiger salamanders (*Ambystoma tigrinum*) have disappeared from many high mountain lakes in Colorado where they were once abundant (Harte and Hoffman 1989).
- Eastern and Central United States: Green salamanders (Aneides aeneus) at seven sites in the southern Appalachian Mountains of North Carolina have declined by 98% since 1970 (Corser 2001). Since the early 1900s, populations of amphibians in northwestern Iowa have declined by about three orders of magnitude. To envision the extent of this loss, Michael Lannoo (1998) suggested "imagine a large football stadium at capacity, say 75,000 people. Now imagine it with 75 people. This is the estimated magnitude of our loss."

- Latin America: Early, dramatic declines and disappearances in Central America include the golden toad (*Incilius periglenes*; Figure 17.1A) and harlequin frogs (*Atelopus*; Figure 17.1B) (Crump et al. 1992; Pounds and Crump 1994). Most species of *Atelopus* are declining throughout Central and South America (e.g., La Marca and Reinthaler 1991). At least eight species of endemic frogs in Puerto Rico have declined drastically (Joglar and Burrowes 1996). Since the late 1980s, populations of at least 24 species from the Andes of Ecuador have declined or become extinct.
- Europe and the Middle East: All seven native species of amphibians have declined in Britain (Beebee 2014). Fire salamanders (*Salamandra salamandra*; Figure 17.1C) have declined in The Netherlands (Martel et al. 2013), and the midwife toad (*Alytes obstetricans*; Figure 17.1D) has disappeared from some ponds in a national park near Madrid, Spain (Bosch et al. 2001). Populations of three species of Kurdistan newts (*Neurergus*) have disappeared from the Zagros Mountains of western Iran (Rastegar-Pouyani 2003).
- Asia and the Pacific: Declines in China include the Gansu toad (*Bufo minshanicus*), Inkiapo frog (*Rana chensinensis*), and Songpan slow frog (*Nanorana pleskei*) (Fellers et al. 2003). Gunther's whipping frog (*Taruga eques*) has almost disappeared from mountainous tea-growing areas

of Sri Lanka (Melvani 1997). The Coromandel New Zealand frog (*Leiopelma archeyi*), endemic to New Zealand, has declined drastically in part of its range (Bell 1999).

We know less about the population status of caecilians than we do about anurans and salamanders, in large part because of the secretive nature of caecilians. Two-thirds of the 178 recognized species of caecilians are classified as Data Deficient—a much higher proportion than for anurans and salamanders (see Table 17.1). We need to focus more research effort on the population biology of caecilians to better understand what is needed for their conservation (Gower and Wilkinson 2005).

Some reported declines have involved substantial portions of species assemblages. A survey along a transect in the Sierra Nevada in the Yosemite area of California revealed that at least five of the seven species of frogs and toads have suffered serious declines (Drost and Fellers 1996). Likewise, multiple declines have been reported from California's Central Valley (Fisher and Shaffer 1996). At least 14 species of endemic stream-dwelling frogs have disappeared or declined sharply in montane rain forests of eastern Australia (Richards et al. 1993; Laurance et al. 1996). Twenty species (40%) of the anuran fauna from the high-elevation vicinity of Monteverde, Costa Rica disappeared during the late 1980s, and many other species there declined in numbers (Pounds et al. 1997, 1999). During the 1990s many species



Figure 17.1 Amphibians have declined worldwide. (A) The golden toad (*Incilius periglenes*) once endemic to a small mountain range in Costa Rica, is now apparently extinct. (B) Harlequin frogs (*Atelopus*) are declining throughout Central and South America. (C) The fire salamander (*Salamandra sala*-

mandra) has declined drastically in The Netherlands. (D) The midwife toad *Alytes obstetricans* has disappeared from some ponds in a national park near Madrid, Spain. (Photo-graphs: A, Martha L. Crump; B, © Paul A. Zahl/Science Source: C, © Paul Freed; D, R. D. Bartlett.)

of frogs declined in a remote high-elevation cloud forest site at Las Tablas, Costa Rica (Lips 1998), and in an upland site in western Panama (Lips 1999).

Reptiles

Reptiles may be in even greater danger than amphibians of worldwide extinction. We began this chapter by quoting Archie Carr's 1955 lament for the decline of the green sea turtle (*Chelonia mydas*; **Figure 17.2A**). In 2000, Whitfield Gibbons and his colleagues warned of extensive reptile declines. Thirteen years later, Monika Böhm and her colleagues (2013) published the first global analysis of extinction risk in reptiles. Their study focused on a random



Figure 17.2 Reptiles in decline. (A) The green sea turtle (*Chelonia mydas*), found in tropical and subtropical seas around the world, is listed as Endangered and is an iconic representative of threatened sea life. (B,C) In Central America, green iguanas (*Iguana iguana;* B) and spiny-tailed iguanas (*Ctenosaura similis;* C) are a prized food source and have been overharvested, leading to population declines. (Photographs: A, © Dave Fleetham/Design Pics/Corbis; B, C, R. D. Bartlett.)

sample of 1,500 species of reptiles and revealed that nearly one in five of these species is threatened with extinction. The proportion of threatened species of reptiles is highest in freshwater environments, in tropical regions, and on oceanic islands. To cite just a few examples:

- In the United States, bog turtles (*Glyptemys muhlenbergii*) and map turtles (*Graptemys*) are declining in the East (Buhlmann and Gibbons 1997). Wood turtles (*Glyptemys insculpta*) have declined in parts of Connecticut (Garber and Burger 1995). Desert tortoises (*Gopherus agassizii*) have declined in the Southwest (Jacobson 1994), as have gopher tortoises (*Gopherus polyphemus*) in the Southeast (Smith et al. 1998). Bunchgrass lizards (*Sceloporus scalaris*) have declined in the Chiricahua Mountains of southeastern Arizona (Ballinger and Congdon 1996). Texas horned lizards (*Phrynosoma cornutum*) have disappeared from parts of their range (Goin 1992).
- On other continents, short-headed legless skinks (*Acontias breviceps*) have declined in southeastern South Africa (Branch 1998), and Nile crocodiles (*Crocodylus niloticus*) are declining at Loskop Dam in northern South Africa (Botha et al. 2011). Green iguanas (*Iguana iguana*) and spiny-tailed iguanas (*Ctenosaura similis*) have declined in parts of Central America (Figure 17.2B,C) (Fitch et al. 1982). Many species of freshwater turtles are declining in Asia (Cheung and Dudgeon 2006).
- Among island species at risk, the gecko Nactus pelagicus has disappeared from the islands of Guam and Tinian (Rodda 1992). Tuatara (Sphenodon punctatus) have disappeared from the main islands of New Zealand and from many offshore islands (Daugherty et al. 1990; Cree 2014). Although Galápagos tortoises (Chelonoidis) were once common on at least nine islands in the Galápagos archipelago, populations of the tortoises on most of the islands are now severely depleted, and three islands no longer have any endemic Chelonoidis species (Cayot 2008; Edwards et al. 2014).

We have few long-term population studies of snakes, but observations suggest that snakes also are declining in diverse habitats worldwide. Investigators surveyed populations in several climates—temperate, Mediterranean, and tropical—and reported "an alarming trend." (Reading et al. 2010). Of 17 populations of 8 species of snakes in the United Kingdom, France, Italy, Nigeria, and Australia, they found that, over a relatively short period of time, 11 populations had declined sharply, 5 populations remained stable, and 1 showed a marginal increase.

17.2 ■ Major Themes in Biodiversity Conservation

We will emphasize three major themes in this chapter. First, if a conservation program is to be effective, it must involve the local people. As an initial step, the cultural

TABLE 17.1 INUMber of threatened amphibian and reptile species							
Taxon	Extinct/ Extinct in the Wild	Critically Endangered/ Endangered	Vulnerable	Data Deficient	Total number of species evaluated by IUCN		
Amphibians							
Anurans	34	1128	552	1437	5674		
Salamanders	2	180	93	60	558		
Caecilians	0	5	3	118	178		
Total amphibians	36 (0.6%)	1313 (20.5%)	648 (10.1%)	1615 (25.2%)	6410		
Reptiles							
Turtles	7	75	59	11	228		
Rhynchocephalia (tuatara)	0	0	1	0	1		
Squamates (lizards, snakes)	15	425	331	765	4003		
Crocodylians	0	7	4	0	23		
Total reptiles	22 (0.5%)	507 (11.9%)	395 (9.3%)	776 (18.2%)	4255		
Birds (total) ^a	145 (1.4%)	632 (6.1%)	741 (7.1%)	62 (0.6%)	10,425		
Mammals (total) ^a	79 (1.4%)	690 (12.5%)	509 (9.2%)	799 (14.5%)	5513		

TABLE 17.1 - Number of threatened amphibian and reptile species

Data from IUCN Red List, v. 2014.2, www.iucnredlist.org.

^aBirds and mammals are included for comparison. These numbers represent the best estimates available, but their precision varies. For example, the small numbers listed for caecilians probably reflect the difficulty in gathering information about fossorial species rather than indicating we should not be concerned about this group. The proportion of species for which we lack enough information to classify their status is large, especially for amphibians.

perceptions, values, and opinions of local people must be considered. How do they view the species in question? If a threatened species is feared or hated, it might be possible to change that perception, or at least to understand, overcome, or work around that bias. Local people must be given tangible reasons to preserve a habitat and its flora and fauna. Long-term conservation will not be accomplished simply because it is judged to be morally right by conservationists; it must be perceived as beneficial to local people-if not economically, at least as life-sustaining and enriching.

Second, humans are responsible for many amphibian and reptile declines. The most important negative effect of humans on amphibians and reptiles is destruction of their habitats. Thus, the most important action we can take to protect amphibians and reptiles (outside of human population control) is protection of their habitats. Other ways in which we negatively affect amphibians and reptiles are through introduced species, environmental pollution, commercial exploitation for food, skins, pets, and other uses, and our part in effecting climate change.

Finally, more research is essential for successful conservation. We don't know enough about most species to be certain that we are protecting the right habitats, the right resources, or the right life-history stages. Without knowledge of habitat requirements, reproductive biology, lifehistory characteristics, dietary needs, and movement patterns, conservation efforts may be ineffective.

17.3 Human Perceptions of Amphibians and Reptiles

Humans interact with other animals in many ways, and our perceptions of them range from admiration to fear (Crump 2015). Our behavior toward other animals is influenced by cultural perceptions-we protect the animals we admire, and we kill those we associate with evil. For example, on the island of New Caledonia, children are warned not to kill lizards because they might be the child's ancestors. Yet in Iran, lizards are often killed because they are believed to carry the devil's soul.

Perhaps because turtles seem well designed to carry burdens on their backs, they feature prominently in myths of creation and are often revered. In various cultures in India, China, Japan, and North and South America, huge turtles are believed to support mountains and even entire continents. In some parts of the Amazon Basin, however, turtles are despised because they are believed to be associated with human sin.

Crocodylians are worshipped in parts of Madagascar, where the spirits of chiefs are believed to pass into crocodiles after death. But elsewhere in Africa, people fear and kill crocodylians because they attack livestock, pets, and people. Even in ancient Egypt, where the city of Crocodilopolis was built on the banks of the Nile, people had conflicting views of crocodiles. In some areas people con-



sidered the animals to be sacred, even mummifying them, while other ancient Egyptians considered crocodiles to be noxious beasts.

In some parts of the world, people revere frogs because they are thought to possess supernatural powers. Both Old and New World legends hold that lunar eclipses occur when a great frog swallows the moon. Myths from India, China, and Siberia tell that the world rests on the back of a frog; whenever the frog moves, earthquakes shake the world. The alternating appearance and disappearance of frogs and their seemingly magical metamorphosis have led to the worship of frogs as symbols of fertility, resurrection, and creation. People worldwide use amulets, charms, and talismans of frogs to bring luck, ward off the evil eye, or bring rain (Figure 17.3). In contrast, some folklore suggests that toads are evil and should be avoided-for example "a toad's breath will cause convulsions in children." Toads frequently symbolize ugliness; in Shakespeare's Richard III, the king is called "a poisonous hunch-back'd toad."

This dichotomy of perception is even stronger in regard to snakes. Snakes have been a source of fascination and fear for humans throughout recorded history; snakes are both worshipped and despised. Snakes symbolize love or hate, procreation or death, health or disease. They hold a focal position in mythology, and in many cultures they are the most honored of all mythical supernatural beings. Snakes are associated with rejuvenation and immortality because of their ability to shed their old skin and acquire a fresh one. This ability, no doubt coupled with the power of venom that some snakes possess, has led to the prominence of snake cults and ophiolatry (snake worship) throughout the world.

Snakes were important symbols for early cultures throughout the Americas. The Mayas, Aztecs, and Incas all had abundant mythologies about snakes. Rattlesnakes were respected, honored, and protected by most Native American tribes in North America. Snakes still play a promi**Figure 17.3 A pre-Columbian frog talisman.** This frog pendant was cast in gold by a Costa Rican artist between 500 and 800 years ago. Frog motifs appear in native art from across the globe and thoughout history, due in part to their association with life-sustaining water and rainfall. (Photograph © World History Archive/Alamy.)

nent role among the Hopis of northern Arizona, who look upon snakes as messengers to their gods. Each August the Hopis gather up bull snakes (*Pituophis*), striped whipsnakes (*Coluber*), and rattlesnakes (*Crotalus*) for an elaborate 9-day ceremony that climaxes with a ritual Snake Dance, during which priests dance while holding live snakes in their mouths. The snakes are entrusted with prayers and, when released, relay the prayers for rain and adequate crops to the gods.

During the Revolutionary War (1775-1783), Christopher Gadsden, an American general, designed a flag with a coiled rattlesnake above the motto "Don't Tread on Me." The snake on the Gadsden flag, as it came to be known, provided the perfect symbol for vigilance, deadly power, and ethics: rattlesnakes warn before striking; they don't start fights, but once engaged they don't back down. Rattlesnakes are not universally respected in North America, however. They are persecuted through roundups, events during which rattlesnakes are collected and killed (Weir 1992). Dozens of rattlesnake roundups, superficially legitimized by civic or charitable organizations as fundraisers, are held in the United States every year. Ostensibly the excuse is to rid the vicinity of dangerous snakes, but some of these events have turned into community extravaganzas that capitalize on the public's fear of rattlesnakes.

Depending on the perspective of the local culture, people have positive or negative attitudes that influence their likelihood of believing that amphibians and reptiles are worth conserving (Crump 2015). Conservation efforts must work within the regional culture to be successful.

17.4 ■ Impact of Humans on Amphibians and Reptiles

Conservation biologists warn that we are experiencing the early phase of the sixth major extinction episode in Earth's history (e.g., Wilson 1992; Wake and Vredenburg 2008). The current rate of extinctions has been estimated to be 1,000 times higher than the normal background extinction rate (the number that would happen without human effects), and future rates may rise to 10,000 times the background rate (De Vos et al. 2015). The present extinction episode differs from those of the past in that humans are responsible, either directly or indirectly, for most current extinctions (Pimm et al. 1995). Following are some of the major ways humans negatively affect amphibians and reptiles.

Habitat modification and destruction

The single most important negative impact that humans have on amphibians and reptiles is habitat modification and destruction. Many habitats are shrinking or disappearing as a result of human population growth and economic development. On October 31, 2011, the world's human population reached 7 billion. The good news is that the current rate of human population growth is about 1.14% per year—a decrease from its peak of 2.19% in 1963. The bad news is that even though the *rate* of increase is down, the human population is so large (more than 7.3 billion as of 2015) that in absolute numbers it is still growing rapidly. Log on to the World Population Clock (www.worldometers.info/worldpopulation) to get the latest figure—and watch as the numbers increase every fraction of a second.

Increasing numbers of people require more land and increase the global demand for natural products. The areas of the world with the highest levels of biodiversity are also those with the highest rates of human population growth (Cincotta et al. 2000). Habitat destruction often goes hand in hand with the social problems of poverty, lack of education, and economic disruption. For this reason, consideration of the needs and rights of local people must be an integral part of any conservation effort.

DEFORESTATION Although forests currently cover only about 30% of Earth's area, about 80% of the world's terrestrial biodiversity is found in forests (Conservation International 2011). Forests worldwide are being destroyed and converted to pastures, cattle ranches, agricultural areas, mines, and human residential areas (**Figure 17.4**). An estimated 80% of the planet's original forest has already been cut down. Not only does the loss of forests directly affect wild animals living in those areas, it also affects the local

human populations and has domino effects on a much wider spatial scale. Deforestation can lead to loss of biodiversity, soil degradation and erosion, and changes in climatic variables, including humidity, atmospheric temperature, rainfall, aridity, and levels of atmospheric carbon dioxide.

To mark 2011 as the International Year of Forests, Conservation International (2011) highlighted the ten most atrisk forested areas worldwide. Five of them are in the Asia-Pacific region (Indo-Burma; New Caledonia; Sundaland; the Philippines; and the mountains of southwest China). Three are in Africa (the coastal forests of eastern Africa; Madagascar and the Indian Ocean islands; and eastern Afromontane forests). One is the Atlantic forest of South America, and the tenth is forest in the California Floristic Province of North America. Each of these ten forests has lost at least 89% of its original habitat. Furthermore, each is a hotspot of diversity, housing at least 1,500 endemic species of plants.

Tropical forests are some of the most species-rich habitats in the world; more than 80% of all species of amphibians and reptiles occur in tropical areas. Many of the ten countries in the world with the highest rates of deforestation from 2000 to 2005 are in the tropics. Brazil, with the highest rate of deforestation, is responsible for the loss of 15% of the Amazon rainforest just since 1970. Experts predict that at the current rate of worldwide deforestation, within 30 years there will remain neither extensive tropical forests nor their endemic amphibian and reptile faunas.



Figure 17.4 Tropical forests worldwide are being destroyed rapidly. (A) Aerial view of clearcut tropical rain forest in Brazil. The forests of the Amazon River basin are rapidly being cleared for timber, roads, farm and ranchland, and other human purposes. (B) A logging road in Sarawak, Indonesia, another location where once-extensive tropical forest is rapidly disappearing. (Photographs: A, © Chad Ehlers/Alamy; B, © David Hiser/ National Geographic/Corbis.)







Figure 17.5 Flatwoods salamander (Ambystoma cingulatum). These amphibians, restricted to the coastal plain of the southeastern United States, have declined markedly due to timber harvesting that modifies the landscape in ways that interfere with the species' life history, including their migration to breeding sites. (Photograph by R. D. Bartlett.)

CRITICAL HABITAT Humans change the landscape in ways that destroy breeding habitat for amphibians. For example, we drain and fill wetlands for human habitation. Small isolated wetlands are particularly vulnerable to human modification because they are viewed as less valuable than larger habitats (Moler and Franz 1987). Rather than simply being dwarf versions of large wetlands, however, small wetlands (especially those that are free of fish) often provide a unique habitat for wildlife that prefer smaller bodies of water. Protection of small wetland sites is a constant battle as developers fight for the right to dredge and fill habitat for building opportunities.

Lakeshore development also reduces breeding opportunities for amphibians when shoreline vegetation is converted to lawns. Shallow-water habitats, where many amphibians lay their eggs, are stripped of vegetation and converted to sandy swimming areas. Loss of both artificial and natural ponds often goes hand in hand with agricultural reform. A marked reduction in the number of ponds in an agricultural area of northern France resulted in a loss of amphibian breeding sites: of 199 ponds recorded in 1994–1995, only 86 (43%) remained in 2006–2008 (Curado et al. 2011).

Bruce Means and his colleagues monitored the largest known breeding migration of the flatwoods salamander (*Ambystoma cingulatum*; **Figure 17.5**) for 22 years in Florida. They watched the population dwindle from 200 to 300 adult salamanders per night crossing the highway in 1970–1972 to less than 1 per night on average in 1990–1992 (Means et al. 1996). The practice of converting native longleaf pine savanna to bedded slash pine plantation may have been responsible for the species' decline. Bedding is a silvicultural practice whereby the topsoil is plowed into long parallel ridges to elevate the newly planted trees so that their roots are raised above the water level. This conversion may have interfered with many aspects of the salamanders' biology, including migration to breeding sites, successful hatching, feeding, and finding suitable retreat sites after metamorphosis.

ROADS Humans convert and develop the land in different ways, depending on the needs of the community, accessibility of the land, and potential productivity of different sites. Roads are a major source of mortality for many amphibians and reptiles. Amphibians are especially vulnerable to death on roads because pond-breeding species make round-trips from their terrestrial home ranges to breeding sites in the spring, and because juveniles move from the ponds to terrestrial habitats after they metamorphose. Amphibians are not the only victims on roads, however. Female aquatic turtles are killed when they leave their home ponds and move overland to find nest sites. Snakes often forage at night, and on cool nights the only method these ectotherms have to raise their body temperatures is to rest on roads that retain heat from the sun. Road mortality resulting from these behaviors can be substantial (e.g., Beaudry et al. 2010; Gerow et al. 2010).

The effect of road mortality can extend well beyond the road itself. Population sizes of leopard frogs (Rana pipiens) are affected up to 1.5 km from roads (Carr and Fahrig 2001). In addition, many species of amphibians and reptiles exist as **metapopulations**, that is, as groups (subpopulations) of individuals, often associated with a particular pool or pond (see Chapter 16). The subpopulations increase and decrease in size-sometimes disappearing entirely-as a result of immigration and emigration of individuals and as environmental conditions change. Continuous migration among the subpopulations maintains genetic diversity within the metapopulation and repopulates empty ponds. Roads, however, cause genetic isolation among subpopulations when they act as barriers to movement within metapopulations (Fahrig et al. 1995; Beebee 2013; Laurisjssens and Stark 2013). Rulon Clark and his colleagues (2010) found that timber rattlesnakes (Crotalus horridus; Figure 17.6A) in hibernacula isolated by roads had significantly lower genetic diversity than snakes in hibernacula in contiguous habitat. They attributed the difference to the inability of snakes from the isolated hibernacula to migrate because of roads.

ANTHROPOGENIC HABITAT IMPROVEMENT Habitat modification by humans doesn't always affect animals adversely. For some species, certain habitat modifications actually improve conditions for their existence. Populations of the Florida king snake (*Lampropeltis getula floridana*; Figure **17.6B**) have increased in some areas where native habitat has been converted to sugarcane fields. The high density of rodents associated with the cane fields provides additional food, and the banks of limestone dredge material along the irrigation canals provide shelter for the snakes. In arid regions, agricultural practices that make more standing water available (e.g., irrigation ditches, stock ponds, and flooded fields) have benefited resident amphibians and allowed other species to expand their ranges. Construction of



Figure 17.6 Opposite effects from anthropogenic habitat change. (A) Timber rattlesnakes (*Crotalus horridus*) have declined in many areas of the eastern U.S. where they once were common. The decline is due to habitat destruction and persecution by humans. (B) Some populations of the Florida king snake (*Lampropeltis getula floridana*) have benefitted from anthropogenic habitat change where native habitat has been converted to sugarcane fields, which have a high density of rodents. (Photographs: A, © Robert E. Barber/Alamy; B, Barry Mansell/SuperStock/Corbis.)

outhouses and shower facilities in arid areas of Australia's Northern Territory creates environments where frogs can survive during dry periods. Some lizards (especially geckos) and snakes are more common around human dwellings than in more natural habitat because of the abundance of insect and rodent prey.

Introduction of exotic species

As humans have migrated around the world, we have brought goats, pigs, sheep, and cattle for food, and cats and dogs for companionship, and we have accidentally brought rats as stowaways on ships. We have introduced non-native animals for biological control, for example cane toads (*Rhinella marina*) into Hawaii and Australia to eat cropdamaging insects in the sugarcane fields. Non-native animals sometimes become established after they are released by owners who tire of their pets, such as Burmese pythons (*Python molurus*) released in the Florida Everglades. Invasive animals can wreak havoc on native herpetofauna in several ways: they might eat amphibians and reptiles, trample the habitat, compete with them for food, or introduce disease.

PREDATORS AND COMPETITORS INTRODUCED ONTO

ISLANDS Because deleterious effects are often especially strong on islands, human-induced introductions of exotic animals to islands provide insights concerning the impact of predation on species that have not evolved with these predators. Introduced domestic dogs and cats have had devastating impacts on populations of rock iguanas (Cyclura carinata) and on smaller lizards on Pine Cay in the Caicos Islands (Iverson 1978). Mongooses from India were introduced to Jamaica in 1872 to kill rats in the sugarcane fields. Diurnal mongooses are not effective predators on nocturnal rats, however, and the mongooses did not remain in cane fields; instead they moved into forests where they prev heavily on birds and reptiles. The introduced mongooses are thought to be responsible for the elimination or drastic reduction of several lizard species, including the Jamaican ground iguana (Cyclura collie).

South Pacific iguanas of the genus *Brachylophus* have likewise been particularly affected by human introduction of domestic mammals. These lizards evolved in an environment free of ground-dwelling predators. Iguanas are now scarce or absent on islands where feral cats are abundant (Gibbons and Watkins 1982). To make matters worse, introduced goats and pigs have destroyed the understory vegetation, and with this loss of cover the lizards are more vulnerable both to their natural predators and to cats.

FISH AND AMPHIBIANS DON'T MIX Introduced fish have caused the local extinction of amphibian populations, presumably by eating the tadpoles. For example, introduced trout are thought to be responsible for extirpations of populations of harlequin frogs (Atelopus) in Costa Rica. Populations of mountain yellow-legged frogs (Rana muscosa) disappeared from many lakes and streams in the Sierra Nevada of California earlier in the last century due to the introduction of trout. Introduced fish also may have indirectly caused population declines and disappearances of R. muscosa in more recent years by isolating the remaining populations (Bradford et al. 1993). Because the frogs can survive only in waters lacking fish, their habitat has become fragmented, making reestablishment of populations more difficult. Roland Knapp and Kathleen Matthews (2000) found that the percentage of total water-body surface area occupied by trout was a highly significant predictor of the percentage of water-body surface area occupied by both tadpoles and adults of mountain yellow-legged frogs in 14 watersheds of the Sierra Nevada (Figure 17.7).

Introduced mosquitofish and crayfish may have caused localized declines of California newts (*Taricha torosa*) from streams in the Santa Monica Mountains (Gamradt and



Figure 17.7 More fish = fewer frogs. A study of mountain yellow-legged frogs (*Rana muscosa*) in 14 watersheds of the Sierra Nevada in southern California revealed that the more trout present, the fewer the number of tadpoles and adult frogs. Each dot represents a watershed in one of the two study areas listed. (After Knapp and Matthews 2000.)

Kats 1996). Mosquitofish eat larval newts, and the crayfish eat newt eggs and larvae. Crayfish also aggressively attack newts and drive them onto land, away from the aquatic breeding sites (Gamradt et al. 1997).

INTRODUCED AMPHIBIANS AND REPTILES Amphibians and reptiles themselves are being moved around the world at an increasingly rapid rate (Kraus 2009). In part this is because the animals are popular as pets. Some of these animals escape or are released when the owner tires of them. Amphibians and reptiles are also transported accidentally with cargo on ships and planes and with nursery plants. These alien species may survive in their new habitat and establish breeding populations. In some cases they have been implicated in the declines of native amphibians and reptiles.



Figure 17.8 Change in the relative abundance of lizards on Guam, 1945–1990. After the accidental introduction of the brown tree snake (*Boiga irregularis*) to Guam, probably in the early 1950s, many populations of forest birds disappeared. Without birds to eat, the snakes turned to feeding on lizards, especially geckos and varanids. (After Rodda and Fritts 1992.)

The brown tree snake (*Boiga irregularis*) was unintentionally introduced onto the island of Guam sometime after World War II, probably in the early 1950s. Most likely it arrived as a stowaway on a military cargo ship from somewhere in its native range in the South Pacific. The snakes have reproduced so successfully that in some places there are 50 snakes in an area the size of a football field. The snakes have drastically reduced or extirpated not only populations of endemic birds but also several species of lizards, especially the native geckos (**Figure 17.8**) (Rodda and Fritts 1992; Fritts and Rodda 1998; Wiles et al. 2003). The snakes also cause frequent power outages by climbing on power lines, electrical boxes, and transformers.

The Cuban treefrog (*Osteopilus septentrionalis*), a newcomer to south Florida in the 1940s, was probably introduced by humans. The species has since expanded its range into north-central Florida. This exotic species has high fecundity, a large body size, a broad diet, and an extended breeding season. Furthermore, it is extremely adaptable and can tolerate environmental perturbations. These characteristics have allowed the frogs to outcompete and displace some of the native treefrogs (Meshaka 2001).

Although bullfrogs (*Rana catesbeiana*) are not native west of the Rocky Mountains, they have been introduced to many areas in the West and have expanded their ranges. Most were introduced for human consumption, some as far back as the late 1800s. During the Gold Rush in California, live frogs were shipped west and released into streams and ponds, where they successfully reproduced. Native ranid frogs have declined in many areas where bullfrogs are now found. Bullfrogs are voracious predators, and they eat other frogs. In addition, bullfrog tadpoles can outcompete tadpoles of other species (Kupferberg 1997), and native tadpoles may not recognize and respond to the chemical cues given off by predaceous bullfrogs (Kiesecker and Blaustein 1997).

Pollution

Environmental pollution has been implicated as a cause for some amphibian population declines. Amphibians have been touted (especially by the popular media) as being sensitive biological indicators of environmental deterioration because their highly permeable skin rapidly absorbs toxic substances. Although we lack data to support the idea that amphibians are more sensitive than other taxa (Collins and Crump 2009; Kerby et al. 2010), amphibians are affected by pollutants such as pesticides, high concentrations of heavy metals and road salt washed into aquatic breeding sites, and poisoning resulting from mining and logging operations. Even if they do not kill the animals outright, contaminants can have devastating sublethal effects on amphibians. Some chemicals may stunt growth and development, cause anatomical deformities or abnormal behavior, or affect reproduction by disrupting hormones. Numerous laboratory studies document the sensitivity of amphibian embryos and larvae to many different environmental contaminants (see Sparling et al. 2010).

There are too many forms of pollution that affect amphibians and reptiles to discuss them all. Instead, we will focus on three: endocrine disrupters, noise, and plastic trash.

ENDOCRINE DISRUPTORS Some forms of chemical contamination interfere with the endocrine system of animals. In humans, certain contaminants may cause an increased incidence of breast cancer and endometriosis in females and testicular cancer and lowered sperm count in males. In other animals, environmental contaminants cause reproductive disorders such as altered fertility, reduced viability of offspring, impaired hormone secretion or activity, and modified reproductive anatomy. Reptiles may be especially susceptible to the effects of such contaminants because of their lability in sex determination (Guillette and Crain 1996; see Chapter 9).

One example is the effect of polychlorinated biphenyls (PCBs), industrial chemicals such as those used in fire retardants and adhesives, which persist and **bioaccumulate** (that is, concentrations build up as the chemicals are consumed and passed upward through the food chain). PCBs vaporize readily and are transported long distances through the atmosphere. Some PCBs have a molecular structure so similar to that of estrogen that they act as estrogen when they enter an animal's body. These **endocrine-disrupting contaminants**, or **EDCs**, can alter sexual differentiation. For example, PCBs can reverse gonadal sex in the red-eared slider (*Trachemys scripta*), a species with temperaturedependent sex determination (Bergeron et al. 1994). PCBs counteract the effects of cool temperatures that produce males and instead induce ovarian development, creating females. Unnatural altering of sex determination can have disastrous effects on populations.

Louis Guillette and his colleagues (1994, 2000) studied possible causes of reproductive failure in American alligators (Alligator mississippiensis) in Lake Apopka, a contaminated lake in central Florida. The alligators in Lake Apopka are exposed to the pesticide dicofol and to DDT and its metabolites that originated from a major chemical spill at a nearby pesticide plant. Clutch viability (i.e., the percentage of eggs in a clutch that produce viable hatchlings) was significantly lower at Apopka than at the control site. Of the eggs that did hatch at Apopka, 41% died within 10 days compared with less than 1% at the control site. Six-monthold females from Apopka had significantly higher plasma estradiol concentrations than females at the control site, as well as abnormal ovarian morphology. Juvenile males had only about 25% the concentration of plasma testosterone as males from the control site, and their penises were abnormally small. These data suggest that this form of environmental contamination has detrimental effects on endocrine and reproductive functions and depresses reproductive success in alligators. It remains to be seen what effect embryonic exposure to these EDCs will have on reproductive fitness through time.

Atrazine, a widely used waterborne herbicide, affects the endocrine system of amphibians. Current evidence from both laboratory and field studies (Hayes et al. 2002a,b; 2006b) suggests that atrazine causes gonadal abnormalities in male frogs, including retarded testes development and feminization of the male reproductive organs. These effects



Figure 17.9 Exposure to atrazine lowers plasma testosterone levels in mature male frogs. Sexually mature male African clawed frogs (*Xenopus laevis*) were exposed to 25 ppb atrazine every 3 days for 46 days. Control males and females were treated identically except without exposure to atrazine. In this study, testosterone levels in males exposed to atrazine plummeted, reaching levels below those of control females. (After Hayes et al. 2002a,b; photograph by R. D. Bartlett.)

are induced in African clawed frogs (*Xenopus laevis*) at levels of atrazine well below the standards set for human drinking water by the U.S. Environmental Protection Agency. Furthermore, sexually mature male *Xenopus* exposed to atrazine under laboratory conditions suffer a tenfold decrease in testosterone levels (**Figure 17.9**).

The widespread effects of atrazine across taxa suggest that the herbicide may pose a threat to amphibians in general. Tyrone Hayes and his colleagues (2002a,b) studied populations of *Rana pipiens* from different regions in the United States and found that anywhere from 10% to 92% of the males in a given population showed gonadal abnormalities. The researchers hypothesized that atrazine induces genetic expression of aromatase, an enzyme that promotes the conversion of testosterone to estrogen. Atrazine is generally applied to crop fields during spring rains, a time when many frogs and salamanders lay their eggs. Thus this endocrine disruptor could have serious effects on the demography of wild populations of amphibians.

In another study, Hayes and his colleagues (2006a) quantified the effects on *Rana pipiens* of nine pesticides four herbicides (including atrazine), three insecticides, and two fungicides—used on cornfields in Nebraska. The authors recorded effects of each pesticide alone as well as mixtures of pesticides. Although some of the individual pesticides inhibited larval growth and development, the effects of pesticide mixtures were much more pronounced. Tadpoles exposed to mixtures took longer to metamorphose and were smaller at metamorphosis. Both of these characteristics could negatively affect larval survival. In addition, the nine-pesticide mixture damaged the thymus, resulting in immunosuppression, which led to meningitis and other diseases caused by waterborne bacteria.

NOISE POLLUTION Anthropogenic noise has become a prominent element of the environment and affects animals in at least two ways (Francis and Barber 2013). Sudden unexpected sounds (e.g., noise from vehicular traffic, planes, and boats) that are perceived as threats elicit defensive reactions such as freezing in place or moving away from the source of the noise. When these responses interfere with normal activities, such as foraging, they can reduce the fitness of the affected individuals. Sustained noise, such as the sound of traffic, can interfere with an animal's ability to detect important stimuli, such as the approach of a predator, or to communicate with conspecifics.

The reliance of anurans on vocalizations during mating makes them especially susceptible to the impacts of chronic noise. Frogs (and birds) that live in cities or near highways must cope with traffic noise, which is loudest at frequencies below 1,000 Hz (Herrera-Montes and Aide 2011; Kaiser 2011). Some species of anurans minimize acoustic interference by increasing the dominant frequencies of their calls, whereas other species increase the intensity (loudness) or the repetition rate of their calls (Parris et al. 2009; Cunnington and Fahrig 2010; Hoskin and Goosem 2010). Each of these responses has potential costs. In general, large male anurans have calls with lower frequencies than do smaller males of the same species, and females of some species prefer to mate with males that have low-frequency calls (see Chapter 14). Thus, a male that shifts his call to a higher dominant frequency risks diminishing his appeal to females. Increasing the intensity or repetition rates of calls increases the energy cost (see Chapter 7). The higher cost of calling more loudly or more often may shorten the time a male can call during a night or limit the time he can spend in a chorus during a breeding season (Kaiser et al. 2011). Because the time a male spends in a breeding chorus is the best predictor of his reproductive success, a male that reduces his chorus tenure is likely to reduce his fitness.

PLASTIC TRASH Plastic objects dumped into the world's oceans may be out of sight for us, but sea turtles encounter and inadvertently eat this trash (Figure 17.10) (National Research Council 1990). Green turtles (Chelonia mydas) ingest plastic bags as they feed on plant material, and leatherbacks (Dermochelys coriacea), whose primary diet is jellyfish, may mistake plastic bags for prey. These foreign materials may interfere with the turtles' digestive processes, respiration, and buoyancy, and some plastics are toxic. To determine whether ingestion prevalence by sea turtles has increased over time, Qamar Schuyler and his colleagues (2014) analyzed 37 studies published between 1985 and 2012 that reported on data gathered from before 1900 through 2011. They found that the prevalence of ingestion is increasing for some species. For example, the prevalence of debris ingestion by green turtles increased from 30% in 1985 to 50% in 2012. Debris ingested by sea turtles ranged from cigarette butts, balloons, and fishhooks to styrofoam and rope, with plastic being the most widely reported item.



Figure 17.10 Plastic pollution endangers wildlife. A green sea turtle (*Chelonia mydas*) suffocates after ingesting a mass of plastic waste. (Photograph © FLPA/Alamy.)

Commercial exploitation for food

Many people eat amphibians and reptiles because they are readily available and a good source of protein. As a traditional food, such exploitation generally has had little impact on local populations of these animals (e.g., Cooke 1989). Unfortunately, modern commercialization of amphibians and reptiles for the world's luxury food market is generally done without regard to population dynamics and has often led to depletion of wild populations. Most of the frogs that are killed for human consumption end up not as a critical component of local peoples' diet, but in distant lands as gourmet dishes (e.g., stir-fried frog legs smothered with oyster sauce, frog legs au gratin, frog legs teriyaki, and giant bullfrog chop suey). The same is true for reptiles, whose meat is served either as an oddity or as a delicacy in such forms as steaks, soups, stews, pies, creoles, burgers, and even spaghetti.

Commerce in frog legs is substantial. The most commonly eaten frogs are American bullfrogs (*Rana catesbeiana*) in North America, edible frogs (*Pelophylax esculentus*) in Europe, Asian bullfrogs (*Hoplobatrachus tigerinus*) in southern Asia, and African bullfrogs (*Pyxicephalus adspersus*) in Africa. Exploitation of frogs for human food can have drastic effects not only on the frog populations themselves, but their decline can affect multiple aspects of the ecosystem (Warkentin et al. 2009; Altherr et al. 2011). Thus, since 1987 India has banned the export of frog legs because densities of insect pests increased dramatically in agricultural areas where frog densities had declined. Bangladesh followed suit with a ban in 1989. Currently, Indonesia is the largest exporter country of frog legs, followed by China (Kusrini and Alford 2006).

- Commerce in reptile meat is also substantial (Schlaepfer et al. 2005). Between 1979 and 1987, approximately 45,000 kg of alligator meat was sold annually from regulated harvests in Louisiana. Central Americans have eaten green iguanas (*Iguana iguana*) and spiny-tailed iguanas (*Ctenosaura similis*) for centuries (see Figure 17.2B,C). The combination of extensive habitat destruction and overhunting has caused drastic declines of both species (Fitch et al. 1982). Females are exposed to especially heavy hunting pressures because their unlaid eggs are delicious and are believed by many to increase sexual potency.
- The sustainability of populations of freshwater turtles and tortoises in Southeast Asia is in doubt because millions of animals are collected each year and shipped to China for its food markets (Behler 2000; Cheung and Dudgeon 2006; Sung et al. 2013). China imports turtles and tortoises from Bangladesh, Pakistan, India, Nepal, and other countries because its own turtle populations have been dramatically depleted. Now experts warn that within a few years many species of turtles and tortoises from Southeast Asia will become extinct. Because turtle populations are declining throughout Southeast Asia, Asian markets are now importing turtles from North America. Because turtles have a low reproductive rate, this level of exploitation is not sustainable.

Commercial exploitation for skins, art, souvenirs, and other uses

Many amphibians and reptiles are killed each year and made into cheap souvenirs. Teeth and claws from crocodylians are sold as curios, and their feet are made into key rings. Rattlesnake rattles, fangs, and freeze-dried heads are popular

		Number of skins exported		
Species	Country/region	2000	2004	2008
Crocodylians			1 11 11 12 12 12	
Alligator mississippiensis	U.S.A.	249,155	368,409	230,464
Crocodylus niloticus	Africa	147,311	140,497	169,295
Caiman crocodilus fuscus	Central/South America	840,993	621,691	533,549
Lizards				
Tupinambis merianae	South America	122,292	225,722	163,760
Tupinambis rufescens	South America	242,924	124,370	67,138
Varanus salvator	Indonesia	538,005	427,737	325,666
Varanus salvator	Malaysia	254,801	213,442	113,477
Varanus niloticus	Africa	265,389	180,222	100,746
Snakes				
Malayopython reticulatus	Southeast Asia, Indo-Pacific	400,000	280,000	330,000

TABLE 17.2 Magnitude of international trade in some reptile skins

Data from Webb et al. 2012.

(B)



Figure 17.11 Products made from amphibians and reptiles. Items for sale in 2013 in Okinawa, Japan, included (A) purses made from whole toads and (B) shamisens (three-stringed musical instruments) with snakeskin fronts. (Photographs by Martha L. Crump.)



souvenirs. Toads (particularly *Rhinella marina*), iguanas, and turtles are stuffed, fitted with glass eyes, and varnished.

Frog and toad skins are used in the manufacture of shoes, purses, belts, key cases, and other novelties (Figure 17.11A). Frog leather is used for binding small books, and frog skins are also used in making glue and for coverings of artificial fishing lures. Toad skin is used to make change purses, slippers, and shoes. Reptile skins have long been used for making shoes, boots, purses, belts, buttons, wallets, lamp shades, and even musical instruments (Figure 17.11B). Populations of many species of boas, pythons, crocodylians, and monitor lizards are declining because of heavy hunting pressure for their skins. Between 1999 and 2008, an average of 1,318,244 crocodylian skins (13 species and subspecies total) were exported annually (Caldwell 2010). Table 17.2 provides a comparison of various reptiles traded for their skins.

An unusual example of commercial exploitation of snakes is for crocodile food. Tonle Sap Lake in Cambodia is the largest wetland in Southeast Asia. An estimated 6.9 million snakes are harvested from the area each year, most destined to become food for crocodiles living at Cambodian farms (Brooks et al. 2007, 2010). Cambodian farmed crocodiles consume between 2.7 and 12.2 million snakes per year. This take represents the largest exploitation of any snake assemblage in the world and has caused local population declines. The market price for crocodiles has been declining since 2003, and with it has come a concomitant decline in the demand for snakes as crocodile food. This would be good news, except that the snake collectors are developing alternative markets for the snakes—including human snack food.

Hallucinogens, hunting magic, and medicine

People have long valued amphibians and reptiles for their secretions, toxins, fat, and other body parts to improve our health and well-being.

HALLUCINOGENS AND HUNTING MAGIC Anthropologists have speculated that ancient cultures of Mesoamerica may have used toad secretions as hallucinogens during religious ceremonies. Numerous small toad-shaped bowls have been found in archaeological sites in Veracruz and adjacent areas of southeastern Mexico; a prominent feature of toad images on the bowls is the parotoid glands. Wade Davis and Andrew Weil (1992) speculated that the toad used by pre-Columbian people was the Colorado River toad (Incilius alvarius) (Figure 17.12A). This species is unique within the genus (and within the animal kingdom, so far as is known) in possessing a specific enzyme that converts the alkaloid bufotenine to one of the most powerful hallucinogens known in nature, 5-methoxy-N,N-dimethyltryptamine. Huge amounts of this hallucinogen (up to 15% of the dry weight of the gland) accumulate in the parotoid glands. The authors corroborated (through personal experience) informants' reports that smoking the dried parotoid secretion of I. alvarius results in hallucinations.

The Mayoruna men of Brazil use skin secretions from the giant monkey frog (*Phyllomedusa bicolor*) as a drug for **Figure 17.12 Anuran chemicals.** (A) The Colorado River toad (*Incilius alvarius*) is unique in producing an enzyme that converts the alkaloid bufotenine to one of the most powerful hallucinogens known in nature. (B) The Australian green treefrog (*Litoria caerulea*) produces the valuable polypeptide caerulein in the granular glands of its skin. Synthetic forms of caerulein are marketed as pharmaceutical drugs for humans. (Photographs: A, © R. C. Clark, Dancing Snake Nature Photography; B, © ImageBroker/Alamy.)

(A)



hunting magic (Daly et al. 1992). Frogs are harassed until they release defensive secretions, which are dried and later applied to fresh burns on the skin of a hunter's arm or chest. The substance enters the bloodstream rapidly through the open burn wounds, causing repeated vomiting, and the person eventually falls into a condition described as a feeling of being very drunk. This secretion supposedly improves the hunter's aim, makes him more powerful, and sharpens his senses. Women occasionally take the drug in the belief that it allows them to work harder.

TRADITIONAL AND MODERN MEDICINE Isolation, identification, and characterization of chemical compounds found in the granular glands of anuran skin have led to the development of drugs both for human and for veterinary use (Tyler et al. 2007). The polypeptide caerulein found in the Australian green treefrog (*Litoria caerulea*) (**Figure 17.12B**) has been used as a stimulant to restore gut motility following surgically induced muscle relaxation and to dilate the gall bladder prior to radiography. Synthetic forms of caerulein are now available under the trade names of Ceruletid, Takus, Ceosunin, Cerulex, and Tymtran. Traditional Chinese medicine has long used preparations of anuran skin for antibiotic purposes, and some current scientific research is focusing on magainins, antimicrobial peptides synthesized in the skin of African clawed frogs (*Xenopus laevis*).

More than 200 pharmacologically active alkaloids have been extracted and identified from the skin of anurans. Frogs use these alkaloids as chemical defense against predators. Since investigators have learned how these alkaloids affect nerve and muscle tissue of a target victim, considerable effort has been made to synthesize and use these alkaloids as research tools in neurobiology (Grenard 1994). For example, batrachotoxin (found in the dendrobatid genus *Phyllobates*) prevents the closing of sodium ion channels in the surface membranes of nerve and muscle cells. The result to a victim that has been exposed to batrachotoxin is that an influx of sodium ions electrically depolarizes the cell membranes; thus, the nerve cells cannot transmit impulses and the muscle cells remain in a contracted state and cannot function. The end result is heart failure. Neurobiologists currently use batrachotoxin as a research probe for voltagesensitive sodium channels. In a radiolabeled form it is being used to study the interaction of local anesthetics and anticonvulsants. Epibatidine, a unique class of alkaloids, has so far been isolated only from the dendrobatid genus *Epipedobates*. Epibatidine is a powerful painkiller; experiments with rats suggest that it is many times more potent than morphine (a plant alkaloid), nonsedating, and probably nonaddictive.

Pets

Millions of amphibians and reptiles are collected from the wild and imported to the United States every year for sale in the legal pet trade. A 2013 survey reported that 5.6 million households in the United States keep a total of 11.5 million pet reptiles (American Pet Products Association 2013). We also keep millions of amphibians as pets (Figure 17.13A). In addition, millions of amphibians and reptiles are collected each year in the United States and exported for the foreign legal pet trade. Add to those numbers the animals collected illegally around the world, and the totals are truly astounding. Many collected animals die before they are shipped, and many more die en route. Others die in pet stores, and most of the relatively few that are eventually sold die because well-meaning owners cannot or do not provide the food and environmental conditions their exotic pets require.

Collection for the pet trade can seriously harm amphibian and reptile populations. Consider North American box turtles (*Terrapene*; Figure 17.13B), which are popular pets not just in the United States but in Europe and other countries as well. According to U.S. Fish and Wildlife Service, approximately 74,000 Gulf Coast box turtles (*Terrapene carolina major*) were exported from the United States between 1992 and 1994 (Buhlmann 1996). Collection continues, and as a result populations of box turtles are declining in many areas (Dodd 2001).

North American box turtles are a good example of the importance of public opinion for conservation. The USFWS

(B)

Figure 17.13 Amphibians and reptiles are popular pets worldwide. (A) A boy holds his pet horned frog (*Ceratophrys*). (B) Collection for the pet trade is a drain on populations of Gulf Coast box turtles (*Terrapene carolina major*). (Photographs: A, © Science Photo Library/Alamy; B, © R. C. Clark, Dancing Snake Nature Photography.)



solicited information from scientists and the public on population sizes, levels of trade, and the effect of harvesting on box turtle populations. Based on the input received, box turtles were afforded some protection in 1994. Subsequently, the USFWS Office of Scientific Authority issued a statement that the 1996 export quota for box turtles from anywhere in the United States would be zero. This decision was based largely on the input from numerous scientists and from the public, who argued that the risk of continued population decline was great and that we don't know enough about the population biology of the turtles to determine a sustainable level of harvest.

Research and teaching

Amphibians and reptiles play a prominent role in scientific research. The study of frog eyes provided our first information about processing of visual information by the vertebrate retina, and frogs have been important model organisms for developmental biology and experimental embryology research. Approximately 12% of the 105 Nobel Prizes awarded in physiology or medicine from 1901 to 2014 have depended on frogs for the research (AnimalResearch. Info 2014). Reptiles feature prominently in studies of functional anatomy, immunology, molecular biology, neurobiology, physiology, ecology, behavior, and many other areas (Lutterschmidt 2013).

Research collections range from very small (one or two individuals per species, to confirm the identity of the species studied) to very large (e.g., many individuals per species for community-wide inventories or large series of animals for studies of morphological variability). Although data are lacking concerning what effect, if any, such collection might have on small and declining populations, scientists have become more sensitive to the issue. Collection practices are being reconsidered, and alternative types of documentation are being collected.

Ben Minteer and his colleagues (2014) have proposed alternatives to collecting specimens from small, isolated populations. In the journal *Science*, they suggested that "the multivariate description of a species that results from combining high-resolution photographs, sonograms (as appropriate), molecular samples, and other characteristics that do not require taking a specimen from the wild can be just as accurate as the collection of a voucher specimen without increasing the extinction risk." In response, more than 100 scientists signed a letter published in the same issue of *Science* stating that, given increasing rates of habitat loss and global climate change, scientific collections of voucher specimens are more critical than ever for studies of ecology, morphological diversity, and evolution, and for conservation and management efforts (Sills 2014). Scientific debate is healthy, and this one no doubt will rage for a long time.

Frogs are widely used in medical and biological teaching for dissection and demonstration. Collectors for biological supply houses in North America have long been aware that many local populations of ranid frogs are declining. In the early 1970s almost all leopard frogs (*Rana pipiens*) used in teaching (13 million) and research (2 million) were captured from wild populations (Nace and Rosen 1979). The impact of this collecting was enormous. One commercial supplier's volume declined from an average of 30 tons of frogs per year (about 1 million individuals) in the late 1960s to 5 tons in 1973, not because of decreased demand but because of the difficulty in finding frogs.

Wild populations can no longer meet the demand for ranid frogs needed in teaching and research, and many frogs currently used for these purposes are laboratory-bred. In addition, instructors increasingly use demonstrations or have groups of students work with one specimen, and fetal pigs are used more often as an alternative to frogs for classroom dissections. Alternatives to dissecting real animals include watching a video presentation, dissecting a threedimensional model, or virtually dissecting a frog using a computer program (see www.froguts.com).

Global climate change

It is becoming increasingly clear that human activities have a hand in bringing about global climate change. The changes in temperature and rainfall predicted by computer models are far more diverse than the shorthand term "global warming" implies. Some regions will become warmer, but others will get colder, and precipitation will increase in some regions while it decreases in others. Spring rains are predicted to decrease in some areas while autumn rains increase. Overall, extreme conditions of both temperature and precipitation will become more frequent. These changes are coming rapidly. The speed at which temperature and precipitation are expected to change in the 21st century is at least 10,000 times the rates of change historically experienced by extant lineages of amphibians and reptiles (Quintero and Wiens 2013).

Temperature changes could affect amphibians and reptiles in many ways. As ectotherms, they depend on the environment to maintain body temperatures. Beyond this, range distributions could change, sex ratios could be altered for species with temperature-dependent sex determination, and timing of breeding could change.

Changes in **phenology** (the seasonal cycles of animals and plants) already show the effects of temperature change (Ivits et al. 2012). While most studies of animals have focused on birds (Hurlbert and Liang 2012), changes in the annual cycles of amphibians and reptiles have been reported. Spring peepers (*Pseudacris crucifer*; **Figure 17.14A**), wood frogs (*Rana sylvatica*), bullfrogs (*Rana catesbeiana*), and gray treefrogs (*Hyla versicolor*) in upstate New York now start calling 11 to 14 days earlier in the spring than they did between 1900 and 1912 (Gibbs and Briesch 2001). In Italy, European asps (*Vipera aspis*; **Figure 17.14B**) emerged from hibernation and began feeding 15 to 20 days earlier and entered hibernation about 30 days later in 2011 than in 1987 (Rugiero et al. 2013).

The consequences of changes in phenology are difficult to predict because an ecological web of species is involved. Extending the activity season sounds as if it would be beneficial to a species of snake, but that is true only if the snake's prey species show corresponding changes in their activity seasons. In turn, those species rely on yet more species, and so on. It is unlikely that all of the trophic levels that a particular snake species depends on will show parallel changes in phenology. Thus, the sensitivity of any species to climate change will be determined indirectly, via the ecological web of which it is a part.

Increasing temperatures in Mexico appear to have caused the extinction of 24 of 200 populations of lizards studied by Barry Sinervo and his colleagues (2010). To predict future extinctions, Sinervo and his colleagues verified physiological models of extinction risk with observed local population extinctions and extended projections worldwide. Their conclusions and projections are dire. They estimated that since 1974, 4% of all lizard populations have become extinct. By 2080, local lizard population extinctions are projected to reach 39% worldwide. Furthermore, they warned that lizard species extinction probabilities would reach 6% by 2050 and 20% by 2080. The authors suggested that global effort (A)

(B)



Figure 17.14 Climate change is affecting seasonal cycles. (A) Male spring peepers (*Pseudacris crucifer*) in upstate New York start their mating calls as much as two weeks earlier in the spring compared with the norm of 100 years ago. (B) European asps (*Vipera aspis*) in Italy emerge from hibernation earlier and enter hibernation as much as a month later than they did 20 years ago. (Photographs: A, David McIntyre; B, © Prisma Bildagentur AG/Alamy.)

to reduce CO_2 might avert the 2080 scenario, but that it is unlikely that the 2050 scenario of a 6% loss in lizard species can be averted.

Interaction among factors

Many of the factors discussed above probably interact with other factors to cause population declines (e.g., Hayes et al. 2010). For example, the effects of climate change interact with other stressors, such as pollution, invasive species, ultraviolet B radiation (UVB), and pathogens (e.g., Bancroft et al. 2008; Rohr and Palmer 2013). The eggs of pond-breeding amphibians are often attacked by a fungus, *Saprolegnia ferax*, and mortality from fungus infection is increased by UVB (Kiesecker and Blaustein 1995). Because water blocks the passage of UVB, eggs near the surface receive more UVB than eggs deeper in the water. In years of low rainfall, the breeding pools of western toads (*Anaxyrus boreas*) are shallow, eggs are close to the water surface, and the intensity of UVB radiation reaching the eggs is high (Kiesecker



Figure 17.15 UVB radiation increases the mortality of toad eggs exposed to a fungus. In this experiment, western toad (*Anaxyrus boreas*) eggs were covered with filters that either transmitted or blocked UVB radiation. The eggs were then exposed to *Saprolegnia* fungus and egg mortality was measured at depths of 10, 50, and 100 cm. Nearly 60% of the eggs at the 10 cm depth were killed by the fungus when they received UVB radiation, but mortality was only 22% when UVB was blocked. At depths of 50 and 100 cm, the UVB-filtering effect of the water protected the eggs, and mortality was the same with or without the UVB-blocking filter. (After Kiesecker et al. 2001; Andy Blaustein, pers. comm.)

et al. 2001). Thus, mortality caused by *Saprolegnia* infections is higher in dry years than it is in wet years (**Figure 17.15**).

Interaction among climate change, disease, and loss of genetic diversity appears to threaten the last known population of timber rattlesnakes (*Crotalus horridus*) in New Hampshire (Clark et al. 2011). Genetic analyses revealed that, compared with six populations of timber rattlesnakes from New York's Adirondack region, the New Hampshire population lacks genetic diversity. Furthermore, many of the New Hampshire snakes exhibited morphological abnormalities, indicative of inbreeding depression. After a year of exceptionally high summer rainfall in 2006, many snakes died from a skin infection that caused lesions around the head, chin, and body. The source of the infection is unknown, but it appears to be fungal. Clark and his colleagues noted that snakes that emerge from hibernation in New York sometimes have what seem to be identical lesions, but that these are nonlethal and typically disappear after the animals shed. Inbreeding depression and increased susceptibility to disease often go hand in hand, and this appears to be another example of that interaction.

17.5 ■ Patterns of Species Extinction and Extirpation

Humans are responsible for most current extinctions, extirpations, and population declines of amphibians and reptiles. Species harvested for human use are in danger of overexploitation by humans. Beyond exploited species, we can identify several broadly overlapping categories of species that are most likely to become extinct. These same characteristics apply to other vertebrate groups as well.

Long-lived species

Species that live a long time (e.g., many turtles) exhibit a suite of life-history characteristics—delayed sexual maturity, low fecundity, and high adult survival rates—that constrain the ability of populations to respond to increased mortality (Congdon et al. 1993). Adult survival is the vulnerable component for long-lived species. If adult longevity is reduced by commercial harvesting, populations can no longer sustain themselves. For example, adult snapping turtles (*Chelydra serpentina*) are often heavily exploited for food. Harvesting 20% of turtles older than 15 years could result in a 50% reduction in the population size within 25 years. Limiting the harvest to older turtles would extend the amount of time the population is sustainable (**Figure 17.16**) (Congdon et al. 1994).



Figure 17.16 Effect of increased harvesting mortality on the decline of the common snapping turtle (*Chelydra serpentina*). The scenario shown here is the result of a computer simulation. Postponing the onset of the same level of harvesting mortality results in a much longer time until the population is reduced by 50%. This relationship argues for protection of adult and older juvenile snapping turtles, not just eggs and hatchlings. (After Congdon et al. 1994.)
Species with low reproductive rates

Some amphibians and reptiles reproduce only every other year, or even less frequently. Species with low reproductive rates are less likely to recover quickly from population declines. For example, two species of file snakes (Acrochordidae) from the Indo-Australian region are highly prized for their skins because their scales, unlike those of most snakes, are non-overlapping. In some years as many as 300,000 individuals are killed and their skins tanned for shoes and handbags. At least one of these species, Acrochordus arafurae, has such a low reproductive rate that populations cannot withstand much commercial harvesting (Shine et al. 1995). Litter size is small (an average of 17 young), gestation time is long (about 6 months), and only 7% of the females sampled were reproductive, the lowest proportion recorded for any species of snake (Shine 1986). Individual female A. arafurae almost certainly do not breed even every other year.

Species that have poor dispersal and colonization abilities

Many amphibians, especially salamanders, move only small distances in their lifetime. If a population's habitat is destroyed or modified, the population may be doomed to extinction. In some populations of box turtles (see Figure 17.13B), individuals have very small home ranges—12,000 m² (1.2 ha) or even less over the course of many years (Stickel 1989). Consequently populations are extremely vulnerable to impacts caused by humans, such as overcollecting for the pet trade and death on roads. Once a box turtle population reaches a low density and therefore has low genetic variability, it is unlikely to recover given the poor dispersal and colonization abilities of box turtles.

Continental endemics

This category includes species that have unusually restricted distributions and require specialized habitats. Endemics may be abundant in the restricted areas where they occur, but they often have rigid habitat requirements. Often it takes only a small alteration of the environment to endanger a species that is restricted geographically. The vulnerability of such species stems from the fact that if local populations are extirpated, there is no chance for recolonization. Three examples of such species are apparently now extinct: the golden toad (*Incilius periglenes*; see Figure 17.1A), restricted to one small mountain range in Costa Rica, and two species of gastric-brooding frogs (*Rheobatrachus*; see Section 17.8) endemic to restricted stream habitats in rain forest of southeastern Queensland, Australia (Tyler 1991; Crump et al. 1992).

Oceanic island endemics

Communities on islands seem to be extraordinarily fragile, and most extinctions of amphibians, reptiles, birds, and mammals within the past several hundred years have occurred on islands. Island species are often extremely vulnerable to predators such as cats, dogs, mongoose, and rats introduced by humans. Associated with a long history of living in a predator-free habitat, these species do not have efficient antipredator defenses. Other adverse factors include severe habitat destruction and excessive hunting pressure from humans.

Tuatara (*Sphenodon punctatus*) became extinct on the main islands and some of the smaller islands of New Zealand, in some cases due to competition and predation associated with sheep, goats, and rats introduced by the early settlers. Rats probably eat eggs and juveniles and compete with tuatara for food. Introduced rats apparently also have caused the extinction of several species of *Leiopelma* frogs in New Zealand. Only three species of the genus exist today; the largest of these, *L. hamiltoni*, is found only on two rat-free islands. Feral pigs and other introduced species have nearly caused the extinction of tortoises on the Galápagos Islands.

Species with colonial nesting habits

When large numbers of animals gather for breeding activities, they are extremely vulnerable to exploitation by humans and to predation by mammals associated with humans. The classic example is sea turtles, particularly species such as Kemp's ridley (Lepidochelys kempi), which engages in mass nesting, a phenomenon called an arribada (arrival). In the 1940s, on one day alone, an arribada estimated at more than 40,000 Kemp's ridleys nested on a remote area of beach called Rancho Nuevo, between Tampico, Mexico, and Brownsville, Texas. By the 1960s the huge arribadas had vanished, and only small nesting groups of females were observed. The main reason for this decline is thought to be commercial exploitation of the eggs and nesting females. For decades people gathered the eggs and transported them to markets in Mexico City and elsewhere, where they were sold for food and as aphrodisiacs. By the mid-1970s the estimated number of nesting females had dropped to under 1,000, making Kemp's ridley critically endangered. Fewer than 500 females nested on Rancho Nuevo in 1992.

The future may be brighter for the turtles as a result of international protection, however. In 2011, 20,570 Kemp's ridley nests were documented in Mexico; 81% of these were located along the coastline patrolled at Rancho Nuevo (U.S. Fish & Wildlife Service 2012). These nests were produced by at least 7,000 females, representing an impressive comeback in two decades.

Migratory species

Migratory amphibians and reptiles are vulnerable because some of them migrate across national boundaries, and even if a species is protected by one country, it may be exploited in the country to which it migrates. This is the case for green sea turtles (*Chelonia mydas*), protected in Australia but exploited when they migrate to Indonesia. Furthermore, the migration routes of sea turtles may take them through polluted waters or human-modified landscapes and otherwise subject them to a greater range of environmental problems than are experienced by more sedentary species.

17.6 Conservation Options

Conservation programs must be multifaceted, involving research, education, legislation, habitat protection, and if appropriate, captive breeding and management programs. Ultimately the most successful conservation programs are those that identify and address the reason a species is endangered and at the same time provide economic or other benefits to local people. Conservation biology is a synthetic field that applies the principles of ecology, biogeography, population genetics, economics, sociology, anthropology, philosophy, and other theoretically based disciplines to the maintenance of biological diversity throughout the world (Meffe and Carroll 1997).

Habitat protection

The most important action we can take for amphibians and reptiles is to protect habitat. Because of the intense pressures on the environment caused by the ever-growing human population, preservation of land that benefits all plants and animals is a critical priority. The good news is that worldwide the land area under some form of conservation protection has more than doubled since 1985—from a little more than 6.5 million km² to more than 16 million km² in 2012 (Kareiva and Marvier 2012).

Habitats for multispecies assemblages can be protected by establishing parks, reserves, and conservation easements with private landowners. If a reserve is to be established, how should it be designed? This question has generated considerable debate and discussion. Basically, we need to consider three aspects: biological considerations, the culture of indigenous peoples, and political and economic constraints and realities (Meffe and Carroll 1997).

The biological considerations include location, size, and shape of the area to be protected. Reserve size depends on the biology of the particular species of concern and on the number of individuals needed to ensure a viable population-that is, one that will maintain at least its current size. In a now-classic paper, Mark Shaffer (1981) defined the minimum viable population (MVP) as the smallest number of individuals required to have a 99% chance of the population surviving for the next 1,000 years in spite of "demographic, environmental, and genetic stochasticity, and natural catastrophes." The concept is extremely useful in theory, but in practice it is difficult to apply. Some biologists recommend that vertebrate populations need at least 500 to 5,000 individuals to preserve genetic variability, but most work with MVPs has been with mammals. We have no quantitative estimates of MVPs for amphibians or reptiles. Furthermore, recent work has suggested that neither data nor theory support a general applicability of the concept, raising doubt about the usefulness of MVPs for conservation planning (Flather et al. 2011).

Other questions that must be considered include whether the reserve can be connected to other natural areas, how the surrounding land is used, and whether this land use presents a threat to the reserve. In planning nature reserves, we need to minimize the degree of habitat fragmentation in order to minimize extinction rates. Where the habitat is fragmented, corridors connecting the fragments can help increase available habitat.

Because wetland areas are disappearing throughout the world, there is a need to reestablish areas where amphibians can breed. Creating a pond is a complex undertaking, however. Characteristics such as size, water depth, and hydroperiod (length of time the site holds water) must be considered for the species in need of protection. For seasonally flooded ponds, the timing of inundation may be critical (Paton and Crouch 2002). In addition, the proximity of the pond to forest may be crucial (Guerry and Hunter 2002).

One innovative idea concerning habitat preservation has been the **debt-for-nature swap** whereby millions of hectares of land have been set aside as reserves in exchange for release of national governments from international loan debts (Ayres 1989). Developing countries collectively owe more than \$4 trillion to international financial institutions, and many of these countries are unable to repay their loans (World Bank 2012). As a result, financial institutions are often willing to sell the debts at huge discounts. Debt-fornature swaps work as follows. First, an international conservation organization (e.g., Conservation International or The Nature Conservancy) works with the debtor country in developing a conservation project. The project often involves land protection, but it can be some other worthwhile conservation endeavor, such as environmental education. The conservation organization then purchases part of the loan at a discounted price, which frees the debtor country from future payments on that part of the loan. In return, the debtor country agrees to fund the chosen conservation project.

Coexistence with humans

Not all species need to have reserves set aside for their protection. Although some species do require complete habitat protection, altering our use of unprotected environment may allow other species to coexist with humans.

SHARE THE ROADS Vehicles traveling on roads are the dominant mode of transportation for people throughout most of the world. New roads are continually being built for the convenience of the ever growing and increasingly mobile human population. Roads fragment habitat; with the growing network of roads, animals are increasingly forced to cross roads during their daily or seasonal activities and are often killed doing so (see Beebee 2013 for a review of the effect of roads on amphibians).

In the 1960s Europeans began experimenting with corridors that could link crucial habitats for amphibians, such as a wooded area on one side of a road and a breeding pond on the other. The primary design involves drift fences (upright, fencelike structures usually made of metal or plastic). An animal cannot cross the drift fence, so it moves along



the fence to a tunnel that provides an underpass beneath the road (**Figure 17.17**). Considerable engineering research has focused on designing tunnel systems that allow safe crossing for amphibians. The design must incorporate ideal temperature, air circulation, humidity, and light level conditions, or amphibians will not use the structures. Furthermore, tunnels work only if the associated drift fences are maintained. These tunnels now are used elsewhere in the world for reptiles and amphibians, including spotted salamanders (*Ambystoma maculatum*), pine snakes (*Pituophis melanoleucus*), and turtles and tortoises.

TURN OUT THE LIGHTS Another example of how humans can modify their behavior to share critical habitat concerns nesting beaches of sea turtles. As hatchling turtles emerge at night, they instinctively head toward the brightest horizon, which would normally be the sky over the ocean's surface. On beaches with artificial lighting, however, hatchlings confuse residential lights for moonlight or starlight. Instead of heading for the ocean, they become disoriented and head toward the residential area. Many hatchlings ultimately desiccate or are run over by cars.

Many U.S. coastal communities now have beachfront light ordinances that prohibit lights during designated time periods. In Florida, for example, ordinances for some nesting beaches generally permit lights only until 11:00 PM. The absence of artificial light for the rest of the night allows emerging turtles to orient correctly toward the ocean. Un-

fortunately, not all turtles wait until 11:00 PM. Approximately 31% of loggerheads (*Caretta caretta*) emerging from their nests at Melbourne Beach, Florida, do so before 11:00 PM on any given night (Witherington et al. 1990). Low-pressure sodium vapor streetlights have proved to be less of a problem for both adult female turtles and hatchlings than incandescent lighting. Thus, in areas along nesting beaches where artificial lighting cannot be completely eliminated,

Figure 17.18 Turtle excluder device (TED).

The device attaches to trawling gear and allows shrimp to remain trapped while most sea turtles can escape. The use of TEDs has drastically reduced the number of sea turtles drowning in shrimp nets. low-pressure sodium vapor lights may be a partial solution to the problem.

CATCH SHRIMP, NOT TURTLES Research conducted in the 1970s and 1980s suggested that in the United States more sea turtles die as a result of drowning in shrimp trawls than from all other human-induced sources of mortality combined. The National Research Council reported in 1990 that up to 50,000 loggerheads and 5,000 Kemp's ridleys (*Lepidochelys kempi*) drowned annually in shrimp trawls in U.S. waters; several other species were severely affected as well.

Significant progress has been made in reducing this source of mortality by attaching turtle excluder devices (TEDs) to shrimp-trawling gear (Figure 17.18). A TED is a small net or metal grid inside the shrimp net that keeps the shrimp in but allows most species of turtles to escape. The most effective TED designs exclude 97% of sea turtles.

In 1981, the U.S. shrimping industry was encouraged to use TEDs on a voluntary basis, but because the devices are large and cumbersome they were not widely accepted. By 1987, laws required the use of TEDs. Improvements in the design of TEDs continue to be made. In an analysis of sea turtle bycatch data in U.S. fisheries from 1990 to 2007, Elena Finkbeiner and her colleagues (2011) found that mitigation measures have greatly improved the situation. Before fisheries-specific bycatch mitigation measures (including TEDs) were established, the average annual sea turtle bycatch was 346,500, with an average of 71,000 turtles dy-



ing each year. After implementation of the measures, the average number of sea turtles caught annually decreased to 137,800 sea turtles (a 60% reduction), and the number of deaths fell to 4,600 (a 94% decrease).

Other benefits of using TEDs are that the shrimp fishermen don't have to deal with handling the heavy turtles, damage to the shrimp catch is eliminated, and unwanted bycatch such as jellyfish and horseshoe crabs is reduced.

Research

One constraint on effective conservation is a lack of information about the basic biology of the species in question. Ideally, basic research should include examination of population size and structure, age-specific survivorship and sources of mortality, habitat preference, spatial requirements and activity patterns (including migrations to feeding and breeding sites), reproductive patterns and frequency of breeding activity, lifehistory traits (including age at maturity and longevity), social behavior, feeding ecology, and genetic variability.

We must be careful not to employ conservation solutions that are **halfway technology**—that is, "fixes" instituted after the problem has already occurred that do not address the underlying causes of the problem (Frazer 1992). An example

of halfway technology would be releasing 1,000 toads into an area where the native toad population recently became extinct, without investigating the causes of extinction or whether the environment is still appropriate for that species. We must understand the causes behind the problem, and to do this, we need more basic research. Following are three critical areas in need of research.

Figure 17.19 Discrepancy between size of habitats used by turtles and extent of the wetland area protected. Ellenton Bay is a 10-ha isolated wetland area in the Atlantic coastal plain in South Carolina. The area enclosed by ring a is protected by U.S. wetland statutes. Habitats within ring b would be protected by the strictest state statutes. Ring c encloses 90% of the turtle nesting sites (red dots) and hibernation sites (green dots), but protection of 100% of these sites is not attained until ring d (which has a maximum diameter of approximately 1 km). Wetland statutes do not adequately protect the habitats of these semiaquatic turtles throughout their life cycles; terrestrial buffer zones are needed. (After Burke and Gibbons 1995.)

CRITICAL HABITATS Before convincing arguments can be made for habitat protection for a given species, we must have identified the spatial requirements of that species during all of its life-history stages and during both the breeding and nonbreeding seasons. If a frog species migrates from wooded areas to aquatic sites to breed, not only must both areas be protected, but corridors between the sites also must be protected, especially if roads fragment the habitat. It is useless to protect the breeding sites and woods if most individuals get killed on roads during breeding migration.

Vincent Burke and Whitfield Gibbons (1995) studied three species of semiaquatic turtles that live in a wetland area in South Carolina to determine the effectiveness of current wetland policies. Federal statutes protect wetlands larger than 0.4 ha by requiring delineation of the wetland– upland border and then preventing development from occurring within the wetland area. Burke and Gibbons found that all of the turtles' nesting sites and terrestrial hibernation burrows occurred outside the federally delineated boundary and that critical habitats extended 275 m beyond the wetland boundary (**Figure 17.19**). In this case, current wetland statutes do not adequately protect the habitats that



these turtles require throughout their life cycle. Terrestrial buffer zones are essential.

LIFE-HISTORY CHARACTERISTICS Data concerning lifehistory traits, age-specific mortality, and the causes of mortality are crucial for identifying which life-history stages most in need of protection. For example, sea turtles are long-lived, highly fecund animals that have extremely high natural mortality at the egg and hatchling stages. In some species survivorship to reproductive maturity has been estimated to be less than 1%. This combination of traits suggests that conservation measures must be directed primarily at the subadult and adult stages rather than at the egg or hatchling stages.

More than \$4 million was spent protecting the eggs of Kemp's ridley (*Lepidochelys kempi*), the most endangered species of sea turtle, on the nesting beach in Mexico. Thousands of eggs were airlifted from Mexico to the United States, where they were laboratory-raised and then released into the ocean at 9 to 12 months of age. This effort turned out to be halfway technology. Although nesting females were protected, these efforts were wasted because so many adults drown in shrimp nets. With the use of TEDs, the adult nesting population is now recovering. The most effective way to protect these turtles is to reduce the mortality of adults and subadults by protecting them from shrimp trawlers.

GENETIC DIVERSITY Measuring genetic diversity is critical for effective conservation efforts (Hunter 2002). It is important to know whether a species has high or low genetic diversity because the lower the diversity, the less equipped the species is to deal with changing environments and the more likely it is to suffer a loss of fitness due to expression of deleterious recessive alleles in the homozygous condition. Once the levels of genetic polymorphism (the percentage of genetic loci for which the frequency of the most common allele is less than some arbitrary threshold, often 95%) and heterozygosity (proportion of genetic loci for which the average individual is heterozygous) are known, a population can be managed more effectively. The heterozygosity index estimates how much of a species' total genetic diversity is due to within-population variability and how much to among-population variability.

Why is the heterozygosity index relevant? If a species has high within-population diversity, each population could represent a substantial part of the genetic diversity of the entire species. But if within-population diversity is low and among-population diversity is high, numerous populations are required to retain the genetic diversity of the species. The more we know about genetic variability and population demography, the better we can understand the extinction process.

Although few studies have determined within- and among-population genetic diversity of amphibians and reptiles, this information is critical for understanding the consequences of genetic bottlenecks, random genetic drift, and inbreeding. Low genetic diversity can interact with other factors in causing populations to decline, as has been hypothesized for the last remaining population of timber rattlesnakes (*Crotalus horridus*) in New Hampshire (see Section 17.4). There are many opportunities—and challenges—involved in applying genetic approaches to biological conservation (Frankham 2010).

Education

The success of conservation and management programs ultimately depends on how well the programs are tailored to the interests and needs of the people on whose land the threatened or endangered animals live. Citizens must understand not only the need to conserve wildlife but also the rationale for doing so. Effective education methods that involve local people include construction of museum and zoo displays, distribution of pamphlets and newsletters, radio and television programs, participation as nature guides and park guards, and production of materials for use in schools. Children are usually receptive to new ideas, and they are naturally curious and enthusiastic. They are the ones who will be making policy decisions in the future.

ECOTOURISM Each year millions of people spend their vacations viewing wildlife in the animals' native habitats. Education can and should be a vital component of ecotourism (tourism based on natural history). Ecotourism provides an opportunity to educate the public about the value of both wildlife conservation and habitat protection (**Figure 17.20**). Ideally, a long-term benefit is a change in attitudes toward nature. Ecotourism also represents a valuable source of income. In Costa Rica, ecotourism is the leading source of foreign exchange and nongovernmental employment (bananas rank second, coffee third).

Loggerhead turtles (Caretta caretta) are an excellent species for ecotourism because they are fascinating, impressive, and easily watched when they come ashore to lay eggs. Many organizations conduct guided turtle watches in Florida, providing an ideal opportunity to educate the public about the biology of sea turtles and the need to conserve them. The concern has been raised, however, that these watches might be detrimental to the turtles despite rigid guidelines that participants must follow. The effects of organized watches were evaluated by comparing the nesting behavior and hatchling success of two groups of loggerheads: females that were observed by an organized turtle watch group, and control females that were not observed (Johnson et al. 1996). The results were good news. Although the observed turtles spent significantly less time camouflaging their nests than did the control turtles, hatching success and hatchling emergence success of the observed and control groups did not differ. These results should encourage other countries to capitalize on sea turtles for ecotourism, provided that guidelines are enforced so that disturbance to nesting females is minimized.



Figure 17.20 Female green sea turtles (*Chelonia mydas***) and eco-tourists.** The Costa Rican beach at Totuguero is the largest green sea turtle rookery in the Caribbean and has been protected as a national park since 1970. The park (its name means "land of the turtles") brings thousands of tourists each year, many of whom come to see the nesting sea turtles and hatchlings. (Photograph © Jarno Gonzalez Zarraonandia/Shutterstock.)

PARTICIPATION IN RESEARCH The next step beyond ecotourism is providing opportunities for people to participate in conservation-based research projects. Earthwatch is one of several nonprofit organizations that bring together laypersons interested in wildlife with scientists who both need help in their field studies and wish to educate the interested public. The program is immensely successful. By the end of 2013, more than 1,400 research projects had been supported in over 120 countries, and more than 100,000 people had participated in these projects. Herpetological projects involved studies of sea turtles on nesting beaches in the U.S. Virgin Islands and Mexico's Yucatán Peninsula, population studies of diamondback terrapins (*Malacle-mys terrapin*) in South Carolina, and surveys of amphibians and reptiles in Brazilian rain forest, Madagascar, and the South China Sea islands.

National legislation

Countries vary widely in their level of national protection of amphibians and reptiles. Some countries provide no protection at all. At the other extreme are countries such as Belgium, where all amphibians and reptiles, with the exception of two common species of ranid frogs, have been protected since 1973.

In the United States, the Endangered Species Act of 1973 provides protection for both domestic and foreign species classified as either endangered or threatened. Endangered species are those that are in danger of extinction throughout all or a significant portion of their range; threatened species are those that are likely to become endangered within the foreseeable future throughout all or a significant portion of their range. Once a species is listed as endangered or threatened, activities detrimental to that species (e.g., collection and habitat destruction) are restricted and a team of experts develops a recovery plan. The objective of the recovery plan is protection so that ultimately the species will recover from the threat of extinc-

tion; the goal is eventual removal of species from the list (**Figure 17.21**). The status of listed species is reviewed every 5 years, and recommendations for delisting or reclassification are made as warranted. As of February 2014, 29 species and subspecies of amphibians and 39 species and subspecies of reptiles were listed under the U.S. Endangered Species Act.

Control of international trade

The 1960s brought increased awareness worldwide of environmental issues ranging from pollution to extinction. With realization of the alarming rate of extinctions, governments around the world instituted national legislation to protect



Figure 17.21 An endangered species' success story. This hatchling American alligator *(Alligator mississippiensis)* belongs to a species that was listed as endangered but was removed from the Endangered Species Act list in 1987 because populations had recovered. They are still considered "threatened due to similarity of appearance," however, because of their resemblance to the American crocodile (Crocodylus acutus). Keeping the threatened status for *A. mississippiensis* helps protect the crocodile, which is considered endangered in parts of its range. (Photograph by R. D. Bartlett.) their wildlife. By the early 1970s, however, it became clear that international laws were needed to control trade in wildlife. In 1972 the United Nations Conference on the Human Environment adopted the idea of a convention on trade in endangered species. The following year a conference was held in Washington, D.C., with the goal of drafting an international endangered species treaty. The result was **CITES**, the **Convention on International Trade in Endangered Species of Wild Fauna and Flora**, drafted by 81 nations.

The aim of CITES is not to stop trade of wildlife and their products, but instead to regulate trade based on assessment of the status of each species of concern. The CITES treaty mandates that international trade in species (and products thereof) listed by the convention is unlawful unless authorized by permit. An important aspect of CITES is that consumer nations agree to share responsibility for international trade in plants and animals with producer nations by forbidding the importation of illegal wildlife and their products. As of February 2014, 178 countries had joined the convention and signed the CITES treaty. Only a minority of amphibians and reptiles traded are regulated by CITES, however. As of February 2014, 146 species of amphibians and 793 species of reptiles were covered.

Reestablishing populations

Increasing effort is being focused on reestablishing self-sustaining populations of threatened or endangered species in the wild by moving individuals from one site to another or by releasing captive-raised individuals into the wild. Although proactive approaches seem laudable and are extremely popular with the public, their track record is spotty (Dodd and Seigel 1991). Fortunately, however, reestablishment efforts seem to be improving (Germano and Bishop 2009). Reestablishment projects are attempted in several ways:

- Repatriations involve releasing animals into areas that were formerly or are currently occupied by that species. For example, a species of lizard might be released into habitat that experienced a human-caused forest fire that killed all the individuals formerly living there.
- Translocations involve moving animals into areas that were not historically occupied by that species. Translocations could be a tool to conserve species that are unable to adapt to climate change, as has been suggested for tuatara on New Zealand (Miller et al. 2012). Extreme care must be taken with translocation to avoid disrupting the biology of the native fauna. If the introduced species hybridizes with native species, as has been documented for some ranid frogs, the hybrid may be competitively superior to the native species; the result may be an eventual decline of the native species.
- Relocations involve moving animals from areas where they are threatened (e.g., by impending deforestation) to areas where they would be less vulnerable to loss of habitat. Ideally, animals should be relocated to areas historically occupied by that species.

- Captive propagation involves maintaining adults in captivity and raising their offspring. The ultimate goal of captive propagation is reintroduction into the wild.
- Head-starting involves collecting eggs from a nesting site, raising the eggs in captivity, rearing the hatchlings to a size that will reduce their vulnerability to predators, and releasing the young into the wild. An example of a success story is the work being done at the Charles Darwin Research Station in the Galápagos Islands, where Galápagos tortoises (Chelonoidis) and Galapágos land iguanas (Conolophus subcristatus) are captive-reared (Figure 17.22). Once the young animals are past the size of greatest vulnerability to predators, they are released onto islands where predators and competitors are controlled. In December 2014 ten newly hatched saddleback tortoises (Chelonoidis ephippium) were found on Pinzón Island (Aguilera et al. 2015); they may be the offspring of head-started individuals released there in the 1960s.





Figure 17.22 Head-starting Galápagos tortoises (*Chelonoidis*). (A) A captive adult tortoise on Santa Cruz Island in the Galápagos. (B) Juvenile tortoises are raised until they are less vulnerable to predators, at which time they are released. (Photographs by Martha L. Crump.)

Farming and ranching

One way to reduce the number of wild animals that are harvested for human use is to raise species of economic value in captivity for future harvest or trade. Two types of commercial operations exist: farms and ranches. Farming represents a closed system, where the operations breed their own stock; other than the initial breeding stock, no animals are taken from the wild. The negative aspect of farming is that because all the animals marketed are captive-bred, there often is no incentive to protect wild populations or their natural habitat. In contrast, ranching involves taking eggs or hatchlings from the wild and raising them for market. Because ranching depends on sustainable harvest, considerable emphasis is placed on protecting both the habitat and wild populations.

CROCODYLIANS Alligators and crocodiles have been bred in captivity since the early 20th century, although most of the early efforts were tourist attractions, such as the St. Augustine Alligator Farm Zoological Park, established in Florida in 1893. As populations of crocodylians declined in the wild and came under national and international protection, raising the animals in captivity became a viable option for leather production. In the 1960s, operations focusing on the American alligator (Alligator mississippiensis) were established in Louisiana, Georgia, and Florida. In South Africa, the business of raising crocodiles began in the late 1960s, and by 1992 there were 40 licensed farms. Today, crocodylians are raised for their skins in many countries. Although captive breeding of crocodylians is carried out because of the demand for their skins, an additional economic benefit is the meat. A successful crocodile farm in South Africa can harvest 20,000 individuals per year and export the meat to Europe and Asia (Tosun 2013). Crocodile meat is promoted as a healthy source of protein because of its unsaturated lipid profile and low sodium content. The main species harvested for meat are the American crocodile (Crocodylus acutus), Nile crocodile (C. niloticus), and Siamese crocodile (C. siamensis) (Tosun 2013).

FROGS Frog farming has been developed in the United States, Indonesia, Taiwan, and Brazil, among other places. Although farming frogs is not economically feasible on a small scale, larger operations have been successful. In Brazil, eight large companies with a total of 600 establishments farm American bullfrogs (*Rana catesbeiana*). Each year these operations produce about 400 tons of meat, mostly for the domestic market; 1,500 to 4,000 animals are slaughtered daily. The animals' legs are consumed, their livers are made into paté, and their fat is used by the perfume industry (Rocha-Miranda et al. 2006).

CAPTIVE BREEDING FOR THE PET TRADE Captive breeding of many exotic species of amphibians and reptiles for the pet trade is taking pressure off wild populations. Most leopard geckos (*Eublepharis macularius*), green iguanas (*Iguana iguana*), and horned frogs (*Ceratophrys*) sold in pet stores are captive-bred. Some non-native species are exported from the United States in greater numbers than they are imported, thanks to captive breeding. For example, 952 spurred tortoises (*Geochelone sulcata*) were imported from Africa in 1995; over twice as many (2,332) were exported that same year. Zoos are leaders in the field of captive breeding of the amphibians and reptiles they display.

Captive breeding can be beneficial, but there can also be problems. For example, mass-breeding operations may foster disease. Hatchling red-eared sliders (Trachemys scripta) (Figure 17.23) raised on turtle farms in Louisiana, Mississippi, and Arkansas used to be sold by the millions in pet stores across the United States. The hatchlings were fed raw chicken that was often infected with Salmonella bacteria. Children who handled baby turtles or touched contaminated water from the turtle bowl and then put their fingers into their mouths sometimes contracted salmonellosis, and sale of hatchling turtles was banned by federal law in 1975. Since the ban took effect, the turtle farms have continued to export millions of hatchling red-eared sliders to Europe, Asia, and Latin America, where they are popular as pets. In the 5-year period between 1989 and 1994, an estimated 26 million hatchlings were exported from U.S. turtle farms to other countries. Although personnel at the farms no longer feed contaminated chicken to the turtles, Salmonella bacteria are still present in the water and soil from so many decades of high levels of infestation, and turtles still become infected. Even treatment of the eggs and hatchlings with antibiotics hasn't eliminated the problem, as antibiotic-resistant strains of the bacteria have developed.



Figure 17.23 Hatchling red-eared slider (*Trachemys scripta***). This species was a popular pet in the United States from the 1950s through the early 1970s. When children handled their pet turtles, they sometimes were infected with salmonellosis. Although the sale of hatchling red-eared sliders has been banned in the United States since 1975, the turtles are still being farmed and exported as pets. (Photograph by R. D. Bartlett.)**



Figure 17.24 Stress of trade adversely affects health of green pythons (Morelia viridis). The graph plots body weight against snout-vent length of green pythons from the Aru Islands, Indonesia. Green circles represent snakes measured on the day they were collected in the wild. Red circles represent individuals recorded further along the trade chain. (After Lyons and Natusch 2011; photograph © Siegfried Kuttig/ ImageBroker/Corbis.)

Captive breeding has other problems as well. Turtles are rapidly declining in Asia, in large part because of China's insatiable demand for the animals as food and for use in traditional medicine. Turtle farming does not appear to be a sustainable practice, however, because successive generations of farm-raised turtles show a marked decrease in reproductive success. Therefore, breeders continually seek wild-captured animals to inject new life into their businesses. More than 1,000 turtle farms in China are the primary purchasers of wild-caught turtles, posing a major threat to the survival of China's native turtles (Shi et al. 2007).

Another potential problem with breeding farms is laundering of illegally caught animals. For example, green pythons (Morelia viridis) from Indonesia are highly sought as pets, in large part because of their ontogenetic color change. Juveniles are either red or yellow at birth and change to green by the time they reach about 65 cm in length. More allegedly captive-bred green pythons are currently exported from Indonesia than any other species of reptile, but are these animals truly captive-bred? Jessica Lyons and Daniel Natusch (2011) surveyed wildlife traders in several provinces of Indonesia to assess the trade in these snakes. Their data revealed 4,229 illegally collected wild green pythons from August 2009 to April 2011. The authors traced the snakes from their point of capture to breeding farms in Jakarta. From these farms, the snakes were exported for the pet trade. Lyons and Natusch estimated that at least 80%

of the green pythons exported from Indonesia each year are illegally harvested from the wild and traded under the guise of being captive-bred. Not only are the animals collected illegally, but also they are mistreated. The general health of the pythons being traded was poor; animals often were malnourished or showed symptoms of disease or infection (**Figure 17.24**).

Sustainable harvesting

To many people, the goals of conservation versus use of resources in need of protection seem mutually exclusive. Conservation, however, has long been closely tied to the value and use of re-

sources. Unfortunately, resources are often harvested at levels that are not sustainable. **Sustainable harvesting** means removing individuals from a population in such a way that the resource is renewable—that is, so that the population can continue indefinitely. Often adult stages are harvested because they provide the most meat or leather, but the lifehistory characteristics of many species of amphibians and reptiles (especially snakes, turtles, and crocodylians) make harvesting adults inadvisable. Many species have a relatively late age at first reproduction, high egg and neonate mortality coupled with high adult annual survival, and infrequent breeding. For these species, harvesting adult animals will have a much larger negative impact on population size than will harvest of juveniles or subadults.

Martin Schlaepfer and his colleagues (2005) addressed the issue of harvest sustainability of wild-caught amphibians and reptiles. Their study focused on the United States, which, unlike most countries, tracks the imports and exports of all amphibians and reptiles. Furthermore, the United States represents one of the largest markets in the world for wild-caught amphibians and reptiles. From 1998 to 2002, the United States imported about 14.7 million wild-caught amphibians and about 7.6 million wild-caught reptiles and exported about 1.3 million wild-caught amphibians and about 26 million wild-caught reptiles. Clearly, research needs to focus on estimating how many individuals can be removed from populations to ensure a sustainable harvest. We also need better monitoring efforts and legislation to ensure that the commercial trade in amphibians and reptiles does not jeopardize their long-term survival.

17.7 ■ Declining Amphibians: A Model Issue

Amphibian populations have been disappearing at an alarming rate, at least since the 1980s. The decline of amphibians is the first recognized modern extinction event to affect an entire vertebrate class. Perhaps we can use it as a lens through which to see and understand more clearly the larger picture of worldwide loss of biodiversity. Here we will take a closer look at some of the causes of amphibian declines and attempts to mitigate them.

Possible causes of declines

The sizes of amphibian populations naturally fluctuate greatly, passing through cycles of growth and decline. For this reason it can be difficult to know whether a declining population is experiencing a low point in its cycle—a decline in response to natural variation in environmental conditions—or a response to an anthropogenic environmental change (Pechmann et al. 1991). Natural population fluctuations probably explain some declines that have been observed in the past 50 years, especially in marginal habitat, but they are unlikely to explain synchronous worldwide declines of amphibians. At present there is no evidence for a single causal factor, and most scientists suggest that local effects and global factors probably interact to affect population densities (**Figure 17.25**).

LOCAL CAUSES Habitat destruction, modification, and fragmentation are the leading causes of loss of biodiversity worldwide and are also the major causes of amphibian declines (Collins and Crump 2009). Three other obvious local effects include introduction of predators and competitors, pollution, and overexploitation by humans.

Frogs with multiple, missing, or twisted legs (**Figure 17.26**) have been turning up in high numbers in wetlands in Canada and the United States since the late 1950s (Souder



Figure 17.25 Hypothesized synergistic factors that contribute to amphibian declines. Effects at any given level interact with factors on the same level and affect factors on lower levels, but do not affect higher levels. Tyrone Hayes and his colleagues suggest that the five factors on Level 3—pathogens, environmental pollutants, atmospheric change, habitat modification, and invasive species—affect multiple factors at Level 2. Factors on Level 2 interact with each other and ultimately contribute to population declines through death and decreased recruitment. The depth of color in Level 3 reflect weighted rankings, with factors shown in darker blue considered to have the greatest potential to interact with other factors in ways that amplify one or both factors. (After Hayes et al. 2010.)



Figure 17.26 An American bullfrog (*Rana catesbeiana*) with limb deformity. This bullfrog was found in a wetland in Dickinson County, Iowa, in June 2012. One wonders how it escaped predation for so long, given the awkwardness of jumping with five legs. (Photograph by Rochelle Stiles.)

2000; Lunde and Johnson 2012). In 2013, the results of a 10year assessment of 32 species (48,081 individual frogs) on 462 wetland sites on U.S. National Wildlife Refuges identified localized hotspots, defined as areas where the frequency of amphibian abnormalities was significantly higher than 5% (Reeves et al. 2013). The most commonly observed abnormalities were missing or shortened elements in the digits or limbs. The frequency of abnormalities ranged from 5% to 40% in clusters of sites in the Mississippi River Valley (northeast Missouri, Arkansas, and northern Louisiana), throughout California, and in south-central and eastern Alaska.

The phenomenon of malformed frogs is neither isolated nor rare, and malformations are believed to have three main causes: pollution, parasites (e.g., flatworms, *Ribeiroia*), and predators (Johnson et al. 1999, 2012; Kiesecker 2002; Bowerman et al. 2010; Reeves et al. 2010; Lunde and Johnson 2012). The cause of deformities is a study in progress, and we are still discovering new aspects to the story.

REGIONAL CAUSES Pathogens are another possible cause of amphibian declines, and these often act on a regional basis (Carey et al. 1999). Epidemic diseases of amphibians include a condition called red-leg (caused by the *Aeromonas* bacterium), iridoviruses, and *Saprolegnia* fungi. In the late 1990s a parasitic chytrid fungus—*Batrachochytrium dendrobatidis*, or Bd—was identified as the culprit in the mass death of frogs

in Central America and Australia (Berger et al. 1998). This fungus, now a prime suspect in many amphibian declines that are not attributed to habitat destruction, is found on all continents where amphibians occur (Skerratt et al. 2007). The fungus kills amphibians by disrupting the integrity of the skin (see Figure 17.28), a critical organ for gas exchange, electrolyte balance, hydration, and protection against pathogens (reviewed by Voyles et al. 2009).

GLOBAL CAUSES There is no doubt that the world is experiencing major climatic changes, including higher temperatures, changes in regional precipitation patterns, decreased soil moisture, and increased length of dry seasons (see National Academy of Sciences, http://nas-sites.org/americasclimatechoices, for an excellent summary of the evidence and causes). Amphibians can potentially respond to changing climate in four ways: they can adapt, acclimate, migrate, or die (e.g., Reading 2007; Raxworthy et al. 2008; Todd et al. 2011; Caruso et al. 2014).

Declining populations of many amphibians as well as changes in the distribution patterns of some birds and anole lizards in the area of Monteverde, Costa Rica, may be associated with changing patterns and amount of mist during the dry season (Figure 17.27) (Pounds et al. 1999). The level of the cloud base around Monteverde has risen due to atmospheric warming associated with rising sea surface temperatures. The result is less mist in the cloud forest, creating drier conditions. Shifting climatic conditions (number of dry days, total annual rainfall, and annual mean temperature) are affecting amphibian communities in Italy (D'Amen and Bombi 2009; Salice 2012). Exposure to increased UVB radiation may have detrimental effects for some species of amphibians (Blaustein et al. 1994a; Anzalone et al. 1998), though not all species are affected equally and this hypothesis is controversial (Corn 1998; Crump et al. 1999; Vredenburg et al. 2010).

Changes in rainfall patterns can affect amphibians. Many species of amphibians breed during the spring in temporary pools created by autumn and winter rain and snow, and a decrease in winter precipitation may decrease the abundance of breeding sites for these species. The Australian corroboree frog (Pseudophryne pengilleyi) provides a striking example of this reproductive pattern (Pengilley 1992). In late summer when the breeding sites are dry, male corroborree frogs dig nests several centimeters deep at the edges of depressions that normally fill with water from rain storms. Males call from their nests to attract females, which deposit eggs in the nests. The fertilized eggs develop to hatching stage and then enter diapause (a temporary cessation of development). When the pools are flooded by autumn rains, the tadpoles hatch from the eggs and complete their development in the pools. This mode of reproduction depends on reliable autumn and winter rains to flood the pools, but between 1997 and 2009 southeastern Australia experienced a drought that may have been the most severe since European settlement in 1788. During this drought, the populations of

Figure 17.27 Lack of dry season mist leads to declines of frogs in highland forest. Population declines of four species of frogs in the Monteverde forest of Costa Rica are associated with periods of less moisture (in the form of mist) during the dry season. The population density of all four species drastically declined in 1987, 1994, and 1998—the three years with the largest number of dry days. The chance that these three declines would correspond to the three driest periods by chance is ≤ 0.008 . (After Pounds et al. 1999.)



corroboree frogs at 25 of 60 breeding sites became extinct, in part because the pools did not contain water long enough to allow tadpoles to complete development (Scheele et al. 2012). In 2011 and 2012 the situation reversed—summers in those years were exceptionally wet. The pools filled before the eggs were ready to hatch and the undeveloped tadpoles drowned (Benjamin Scheele pers. comm.).

SYNERGY The synergistic interaction of several factors, none lethal by itself, can be fatal. For example, Cynthia Carey (1993) hypothesized that amphibians stressed by an environmental factor or combination of factors succumb more readily to red-leg disease. Drought and airborne pesticides or other contaminants may be a lethal combination (Pounds and Crump 1994). Increased exposure to excessive levels of ultraviolet radiation increases the susceptibility of amphibian eggs to Saprolegnia fungal infections (Blaustein et al. 1994b; Blaustein and Wake 1995). Temperature, moisture, and the herbicide atrazine act synergistically on larval streamside salamanders (Ambystoma barbouri) (Rohr and Palmer 2013), and pesticides can stress amphibians and enhance the impact of predation (Adeet et al. 2010). The trematode parasites responsible for limb deformities may increase the negative impacts of pesticides (Kiesecker 2002).

Focus: Chytrid fungi and amphibian decline

Because the chytrid fungus *Batrachochytrium dendrobatidis* (Bd) appears to play a major role in many amphibian declines (Skerratt et al. 2007; Collins and Crump 2009), considerable effort has focused on understanding this disease from many different angles—its basic biology, genetic characteristics, distribution, transmission dynamics, and impact on individuals and populations.

LIFE HISTORY AND GENETICS OF BD The life cycle of Bd involves two stages (Berger et al. 2005). The first stage is a motile, short-lived reproductive stage called a zoospore that requires water to disperse. Once a zoospore reaches an amphibian host, it forms a cyst beneath the skin. Fine, threadlike rhizoids that resemble tiny roots grow out, and the fungus develops into the thalus stage: a zoosporangium filled with reproducing zoospores and housed within a covering of vegetative tissue (the fungal covering visible on the frog's skin). Mature reproductive zoospores are released into the water through discharge tubes that form in the zoosporangium (**Figure 17.28**).

Two major hypotheses have been proposed to explain the abrupt appearance of Bd (Berger et al. 1998). The endemic pathogen hypothesis proposes that Bd is a widespread, previously benign organism that has emerged as a pathogen either because of increased virulence of the fungus or increased susceptibility of amphibians. The novel pathogen hypothesis proposes that Bd is an introduced pathogen that is spreading into geographic areas where it did not occur previously and is affecting naive populations. Guillermo Velo-Antón and his colleagues (2012) measured the genetic diversity of Bd in different regions, with results that are consistent with a novel pathogen spreading from North America into Central America (Figure 17.29). A continuous reduction in heterozygosity and increased allele fixation in more recently infected populations revealed that the population genetic composition of Bd has changed during its spread in the New World.

However, Erica Rosenblum and her colleagues (2013) used a genome resequencing approach to address the evolutionary history of Bd and found that the chytrid has a complex evolutionary history that predates recent disease



Figure 17.28 Life cycle of Batrachochytrium dendrobatidis. (1) Zoospores use a flagellum to swim until they locate a frog host. (2) A zoospore penetrates the frog's skin and encysts, reabsorbing its flagellum. Nutrient-absorbing cellular extensions called rhizoids spread, disrupting the structure of the

outbreaks and that lineages of Bd are older, more diverse, and exhibit more heterogeneous and dynamic genomic architecture than had been documented previously. These results suggest that Bd is probably endemic in some parts of its range and novel in others, and that it is premature to identify a geographic location for the origin of Bd. A recent study of museum specimens of Illinois anurans found evidence that Bd was present in that region as far back as 1888 (Talley et al. 2015). This long period of coexistence between amphibians and Bd in Illinois raises questions concerning possible coevolution and the role of the fungus in historic population declines.

Figure 17.29 Genetic analyses of *Batrachochytrium dendrobatidis* **(Bd) in the New World.** The arrow indicates the direction of pathogen spread from North America to Central America. The graph shows that heterozygosity decreased as Bd moved south. (After Velo-Antón et al. 2012.)

frog's skin. (3) The encysted zoospore grows, becoming a zoosporangium within which new zoospores are produced.(4) One or more discharge tubes develop on the zoosporangium.(5) Zoospores are released when the cap on a discharge tube dissolves. Released zoospores swim in search of a frog host.

DEFENSES AGAINST BD Although some species of amphibians experience catastrophic declines when exposed to Bd (e.g., Ryan et al. 2008; Catenazzi et al. 2011), others can coexist with the pathogen (e.g., Retallick et al. 2004;



Briggs et al. 2005). The risk of Bd infection is not randomly distributed taxonomically or geographically. Across Europe, species of *Rana* are less likely and species in the families Alytidae and Bombinatoridae are more likely to be infected than predicted by chance (Baláž et al. 2014). Furthermore, frogs have been found to colonize areas where Bd occurs. After experiencing declines that were probably caused by Bd, whistling treefrogs (*Litoria verreauxii verreauxii*) from Australia re-expanded into 39 new sites where there was a high prevalence of Bd (Scheele et al. 2014). Amphibians are thus not defenseless against this predatory fungus:

- Some amphibians have bacteria on their skin that inhibit growth of Bd (Harris et al. 2006, 2009; Becker et al. 2009). One of these bacteria, *Janthinobacterium lividum*, is found on the skin of red-backed salamanders (*Plethodon cinereus*), four-toed salamanders (*Hemidactylium scutatum*), and mountain yellow-legged frogs (*Rana muscosa*) (Lauer et al. 2007, 2008; Lam et al. 2010; Wiggins et al. 2011).
- Many species of amphibians produce antimicrobial peptides that inhibit the growth of Bd under laboratory conditions (see Rollins-Smith and Conlon 2005). The correlation between documented susceptibility of a species to chytridiomycosis and the production of antimicrobial peptides in the skin is weak, however. In fact, the growth-inhibitory potencies of these peptides are so low that one wonders about their role as protective agents. J. Michael Conlon has suggested that antimicrobial peptides in the skin may provide some immunity in the limited number of species that produce them, but that they may be secondary to symbiotic bacteria on the skin that play a larger role in defense against pathogens (Conlon 2011a,b).
- Amphibians can acquire behavioral or immunological resistance to Bd (McMahon et al. 2014). Exposure of frogs to dead Bd induced as much acquired resistance as did exposure to live Bd. This is good news, as one day we might be able to expose amphibians to Bd antigens to protect pathogen-naive animals, thus facilitating reintroduction of animals to locations where the fungus persists.

Some degree of biocontrol of Bd is also a possibility. A study carried out in the Pyrenees Mountains in southwest Europe revealed that Bd zoospores have predators: microscopic aquatic organisms such as protozoans and metazoans ingest Bd zoospores. In a serious of elegant experiments, Dirk Schmeller and his colleagues (2014) showed that the risk of an amphibian being infected with Bd has a significant site-specific component that is correlated with the aquatic microfauna present at the particular mountain lake. Certain ciliates and rotifers are effective consumers of Bd zoospores, and they reduce the number of free-swimming, infectious zoospores in the water. The lower density of zoospores results in a significantly reduced probability of tadpoles becoming infected with Bd. Although the authors emphasize that more studies are needed to attempt biocontrol safely, they suggest that their study "raises hope that the rate and intensity of Bd infection in amphibian populations can be manipulated by natural means, and that appropriate methods of natural augmentation of predatory microorganisms will significantly decrease the adverse effects of chytridiomycosis on amphibians and ecosystems."

A SECOND CHYTRID FUNGUS PARASITIZES AMPHIB-

IANS As if *Batrachochytrium dendrobatidis* were not bad enough, a second species of pathogenic chytrid responsible for amphibian declines was identified following a dramatic mortality event that nearly extirpated a population of fire salamanders (*Salamandra salamandra*) in The Netherlands. Dead animals were found in the field, and the population declined by 96% between 2010 and 2013 (Martel et al. 2013). After attempts to identify infectious agents (including Bd) yielded negative results, Martel and colleagues discovered, isolated, and characterized a second highly pathogenic chytrid fungus, which they named *Batrachochytrium salamandrivorans*. The species name means "salamander devouring" and refers to the extensive skin destruction and rapid death observed in infected individuals.

B. dendrobatidis and *B. salamandrivorans* appear to have different host ranges and different ecological niches. The newly described chytrid has a lower thermal growth preference than Bd. When the midwife toad (*Alytes obstetricans*, the European species most vulnerable to Bd) was experimentally exposed to *B. salamandrivorans*, it showed no signs of colonization by the new species. It remains to be seen how widespread this new species is, whether it will spread, and how much damage it will do to amphibians worldwide.

17.8 Rediscovery and De-Extinction

Whether described in the professional literature or in the popular media, the litany of population declines and species extinctions can overwhelm us with a sense of helplessness. But there are also some bright spots amid the gloom.

Rediscovery of species

Although amphibians and reptiles are declining worldwide, it occasionally turns out that unseen is not necessarily extinct. More than 100 species of amphibians that were believed to be extinct have been rediscovered (Scheffers et al. 2011). From August to December 2010, Conservation International and the Amphibian Specialist Group of the IUCN supported searches in 21 countries for species of amphibians that had not been seen for more than a decade. The expeditions found only 1 of the top 100 targeted species, but they did rediscover 13 other species of frogs and 1 species of salamander, all of which had been missing for decades. An expedition to the Itombwe Natural Reserve led by Eli Greenbaum and Chifundera Kusamba in 2011 resulted in the rediscovery of four species of frogs, including the Itombwe golden frog (*Chrysobatrachus cupreonitens*; **Figure 17.30A**), which had not been reported since it was described in 1951 (Greenbaum and Kusamba 2012; Eli Greenbaum pers. comm.). The reserve, which lies in the mountains that rise abruptly on the west side of Lake Tanganyika in eastern Democratic Republic of the Congo, was a war zone, and the presence of three different armed militias added to the

(A)



(B)



(C)



usual hazards of fieldwork. The researchers were briefly detained by one militia group but managed to talk their way out of trouble with the assistance of a liberal distribution of beer. Political conditions were better in Burundi, where Greenbaum and David Blackburn rediscovered the Bururi long-toed frog (*Cardioglossa cyaneospila*; **Figure 17.30B**), which had not been seen since 1950.

A few species of amphibians have been found after still longer absences. The webless pygmy treefrog (*Pseudophilatus hypomelas*), Kandyan dwarf toad (*Adenomas kandianus*), and starry frog (*Pseudophilautus stellatus*), all from Sri Lanka, were recently rediscovered 137, 140, and 160 years, respectively, after their last sightings (Wickramasinghe et al. 2012; 2013a,b).

Occasionally a rediscovered species provides new insights. Four decades of searches for the Hula painted frog (originally named *Discoglossus nigriventer*) failed to find any individuals until one was found in Israel's Hula Nature Reserve in October 2011; subsequently ten more frogs were found (Biton et al. 2013). Rebecca Biton and her colleagues not only rediscovered the frog, they reclassified it. Hula painted frogs are the last apparent survivors of an otherwise extinct genus, *Latonia*, whose other members exist only as fossils, and are now known as *Latonia nigriventer* (**Figure 17.30C**).

More than 300 species of reptiles have been rediscovered, some long after they were considered to be extinct (Caut et al. 2013). Examples include the following:

- A Yunnan box turtle (*Cuora yunnanensis*) turned up in a Chinese market 58 years after the species had last been seen (Zhou and Zhao 2004).
- The Clarion Island (Mexico) nightsnake (*Hypsiglena unaocularis*) was rediscovered 77 years after the single known individual was found (Mulcahy et al. 2014).
- The Malagasy blindsnake Xenotyphlops grandieri was found again after 100 years (Wallach et al. 2007).
- The New Caladonian terror skink (*Phoboscincus bocourti*), last seen in 1876, was collected in 2003 (Ineich 2006).
- In India a Jeypore ground gecko (Geckoella jeyporensis) was found after 133 years (Agarwal et al. 2012).

Figure 17.30 Three rediscovered frog species. (A,B) Two species from war-ravaged central Africa that had not been seen since the middle of the 20th century were sighted by a research team in 2011. (A) A pair of Itombwe golden frogs (*Chrysobatra-chus cupreonitens*) in amplexus; the male is much smaller than the female. (B) The Bururi long-toed frog (*Cardioglossa cyane-ospila*) gets its common name from the elongated finger that is present only in males. (C) The Hula painted frog (*Latonia nigri-venter*) from Israel was believed to be extinct. Once found it was studied and reclassified as the last survivor of an extinct genus. (Photographs: A, B, Eli Greenbaum; C © ELIAS/Reuters/Corbis.)



Figure 17.31 A reptilian record for rediscovery. Endemic to the Canary Islands, the Gomera giant lizard (*Gallotia bravoana*) was rediscovered 500 years after it was believed to be extinct. It is remarkable that such a large lizard went undetected for so long in such a small area. (Photograph by Juan Carlos Rando.)

The current record rediscovery is the Gomera giant lizard (*Gallotia bravoana*) (Figure 17.31), which was believed to have become extinct about 500 years ago when humans (and rats and cats) settled in the Canary Islands (Valido et al. 2000).

De-extinction

The most ambitious approach to bringing a species of amphibian back from the dead is de-extinction, an ongoing attempt by Michael Archer and his colleagues at the University of New South Wales, University of Newcastle, and other institutions to resurrect the southern gastric-brooding frog (*Rheobatrachus silus*). The southern gastric-brooding frog was a remarkable species. Females swallowed fertilized eggs that completed development in the mother's stomach and were released after metamorphosis through her mouth (see Figure 8.19) (Tyler and Carter 1981). *R. silus* was last sighted in the wild in September 1981, and the last specimen in captivity died in November 1983. A related species, *R. vitellinus*, has not been seen since March 1985.

Archer's team extracted cell nuclei from tissues of *R. silus* that were frozen in the 1970s and implanted them into nuclei-inactivated eggs of the great barred frog (*Mixophyes fasciolatus*) (Figure 17.32). This frog was chosen because it produces large yolk-filled eggs that may be similar in size and needs to those of *R. silus*. Some of the eggs began to divide, forming multicelled blastulae. To date these blastula have failed to gastrulate. Genetic analysis has confirmed





(B)



Figure 17.32 De-extinction of the southern gastric-brooding frog (*Rheobatrachus silus*). (A) Cell nuclei were extracted from specimens of *R. silus* that had been frozen (without cryoprotection) since the 1970s. (B) The nuclei were implanted in eggs of the great barred frog (*Mixophyes fasciolatus*). (Photographs by Bob Beale, courtesy of Michael Archer.)



that the DNA in most of the cells tested is from R. silus, which means this DNA has been replicating. However, some nuclear DNA of the host frog was also detected, and this may be interfering with embryonic development past the blastula stage. Plans are underway to continue the work after being certain that the host frog's eggs have had their nuclei entirely deactivated (Michael Archer, pers. comm). Archer notes that this is an important advance, because the team has "reactivated dead cells into living ones and revived the extinct frog's genome in the process. Now we have fresh cryopreserved cells of the extinct frog to use in future cloning experiments." Thus, the biological hurdle is in the process of being surmounted. Because the challenges that lie ahead appear to be primarily technological, Archer and his team are increasingly confident of ultimate success (Figure 17.33).

Figure 17.33 A vision of de-extinction. In this view of a hopeful future, a southern gastric-brooding frog (*Rheobatrachus silus*; above right) is giving birth in its pristine mountain habitat in southeastern Queensland. The frog at the lower right is another species that has vanished from the same habitat—the southern day frog (*Taudactylus diurnus*), last seen in 1979. (Art by Peter Schouten, courtesy of Michael Archer.)

SUMMARY

Amphibians and reptiles are declining worldwide.

Amphibian declines are occurring at a rate estimated to be 200 times that of historical extinction levels; the extent of decline varies from region to region and within and among species.

Reptiles may be in even greater danger of extinction than amphibians are, but we do not know much about the population status of many species; more research is needed.

Different cultures perceive amphibians and reptiles differently, and many amphibians and reptiles are viewed both positively and negatively. This dual perception is especially strong regarding snakes, and is important because humans are less likely to protect animals they do not like or find repellent.

Humans impact amphibians and reptiles in many negative ways.

Although extinction is a natural phenomenon, most current extinctions result from human activities. The current rate of extinctions is estimated to be 1,000 times higher than the normal, or background, extinction rate, and future extinction rates may rise to 10,000 times the background rate. The single most important impact of humans on amphibians and reptiles is habitat modification and destruction.

We have introduced animals into areas where they do not naturally occur; many introduced animals and pest species have negative impacts on native amphibians and reptiles.

We pollute the environment with chemicals, noise, and solid waste, particularly plastics.

We harvest huge numbers of amphibians and reptiles for food, leather, and medicine. We also exploit them in other ways, including as pets and in research and teaching.

Climate change can affect amphibians and reptiles in many ways, and it is clear that humans have a hand in bringing about global climate change.

Many factors probably interact synergistically to cause population declines.

■ Certain life-history characteristics are associated with a species' likelihood of decline or extinction.

Long-lived species generally exhibit life-history characteristics that constrain the ability of populations to respond to increased mortality: delayed sexual maturity, low fecundity, and high adult survival rates.

Some amphibians and reptiles have low reproductive rates, which reduces their ability to recover quickly from population declines.

Species with poor dispersal and colonization abilities may be doomed to extinction if their habitat is modified or destroyed.

Species that have extremely restricted distributions and specialized habitats are vulnerable to declines if environmental conditions change.

Many oceanic island endemic species are vulnerable to introduced predators and excessive harvesting by humans because they lack efficient antipredator defenses.

Species that congregate for breeding are vulnerable to exploitation by humans and to predation by mammals associated with humans.

Amphibians and reptiles that migrate long distances are vulnerable to declines because they often are exposed to a greater range of environmental problems than are more sedentary species. Additionally, species that migrate between countries might be protected in one country but not the other.

The most successful conservation programs identify and address the reason a species is endangered and at the same time provide benefits to local people.

The most important conservation action we can take for amphibians and reptiles is to protect habitat. Many species can coexist with people if we modify our behavior to share critical habitat.

We need more research to understand the basic biology of declining or endangered amphibians and reptiles.

Education is needed at all levels, from the local people who share the environment with species of conservation concern to policymakers and the general public.

Legislation is needed at national levels to protect amphibians and reptiles.

International trade must be controlled.

Populations can be reestablished through repatriations, translocations, relocations, captive propagation, and head-starting.

Rearing animals in captivity for harvest reduces the number of wild animals that are harvested for food, skins, or the pet trade. If we do exploit wild populations, we must harvest them sustainably.

Thirty percent of amphibian species are classified by the IUCN as Critically Endangered, Endangered, or Vulnerable.

The chytrid fungus *Batrachochytrium dendrobatidis* has caused the decline of many amphibian species.

There is some good news (but not much).

A few amphibians and reptiles that were believed to have become extinct have been rediscovered.

It is possible that sophisticated biotechnological methods may be able to resurrect extinct species using DNA from frozen specimens; this research is ongoing.

Go to the *Herpetology* Companion Website at sites.sinauer.com/herpetology4e for links to videos and other material related to this chapter.

Glossary

A

- **acrodont** Referring to the type of dentition in which the teeth have a bony attachment to the crest of tooth-bearing bones and are not continually replaced throughout life.
- advertisement signals Signals used by animals to advertise their presence to other individuals.
- aestivation Long-term dormancy that occurs during periods of heat or drought.
- aggressive signals Signals used by animals to indicate aggressive intent.
- aglyph Referring to the type of dentition, characteristic of many colubrid and lamprophiid snakes, in snakes in which the maxillary teeth show little variation in size or shape.
- akinetic Referring to the condition in which there is no movement among the bones of the skull, other than movement between the mandibles (lower jaw) and the rest of the skull.
- alarm signals Signals used by animals to communicate alarm to other animals.
- ammonotely Excreting nitrogenous wastes in the form of ammonia. Most species of amphibians excrete nitrogenous wastes as ammonia and urea (uricotely). Many reptiles adjust the proportion of ammonia, urea, and uric acid (uricotely) in their nitrogenous wastes as their hydration state changes.
- **amphibian papilla** An inner-ear organ unique to amphibians that detects low-frequency sounds.
- amphicoelous Referring to the condition of the vertebral centrum (body)

in which both the anterior and the posterior ends are convex.

- **amplexus** A mating behavior of frogs in which the male grasps the female before fertilizing her eggs The three general amplexus positions are axillary, cephalic, and inguinal.
- ampullary organs In amphibian larvae and adults of aquatic species, electroreceptors that are located on the head and body and are part of the lateral line system. Ampullary organs sense weak, low-frequency electric stimuli and appear to facilitate prey capture and predator avoidance in some species.
- **ancestral character** Any feature of an organism that has been inherited unchanged from an ancestral form. *See also* plesiomorphy.
- **apomorphy** Any feature of an organism that differs from the ancestral form of that character. Also called a derived character. *See also* synapomorphy.
- apomorphy-based definition A taxonomic definition referring to members of a group that all share a specific apomorphy.
- aposematic coloration Bright color or striking color pattern of toxic species that acts as a warning to predators.
- **assemblage** A subset of a community, as in an assemblage of amphibians breeding in a pond.
- associated (prenuptial) gonadal cycle A reproductive pattern in which both males and females exhibit maximum sex hormone secretion and gametogenesis immediately before mating, and fertilization occurs shortly thereafter.
- autotomy See caudal autotomy.

axillary amplexus The form of amplexus in which the male grasps the female immediately behind her forelimbs.

В

- **balancers** In pond-dwelling larvae of some salamander families, rodlike structures on the region of the jaw joint that provide physical support. Balancers also secrete adhesive mucus that allows the larvae to adhere to the substrate.
- **ballistic motion** The condition in which movement is governed only by the initial acceleration and the forces of gravity and air resistance. Also called projectile motion.
- **basilar papilla** An inner-ear organ of amphibians that detects high-frequency sounds.
- **behavioral mating system** The pattern of mating within a population as defined by the number of mates obtained by an individual (e.g., monogamy, polyandry, polygamy).
- **bioaccumulation** A progressive increase in the concentration of a substance in an organism's body during its lifetime or in progressively higher levels of a food web. *See also* biomagnification.
- **biodiversity** The level of local or global diversity, often expressed as the number of different species.
- **biogeography** The scientific field that combines information about natural history, phylogeny, geology, and climate to interpret the past and present distributions of taxa.
- **biological species concept** A widely used species concept that identifies populations as the same species if they

actually or potentially interbreed. Populations that cannot interbreed, and are therefore reproductively isolated, are considered separate species.

- **biomagnification** The increasing concentration of a compound in the tissues of organisms as the compound passes up the food chain.
- **biophysical ecology** The study of the exchange of energy and matter between an organism and its environment.

branches See sister lineages.

- **branchial arches** The gills and their supporting tissues. This term is often used to refer more narrowly to the skeletal supports for the gills, which are generally cartilaginous in amphibians. A few of the branchial arch supports are retained in adult tetrapods, and generally are associated with the hyoid skeleton. *See also* hyobranchium.
- **breeding glands** In many amphibians, specialized glands that develop during the breeding season. Breeding glands may be concentrated into nuptial pads.
- **buccopharyngeal** Referring to both the mouth (buccal, or oral, cavity) and throat (pharynx).

С

- **camber** Curvature of a hydrofoil or airfoil (wing).
- **captive propagation** A reestablishment effort that involves maintaining and breeding animals in captivity and releasing their offspring, with the ultimate goal of establishing self-sustaining populations in the wild.
- **carapace** The dorsal half of a turtle shell, formed primarily by costal and neural bony plates, which are continuous with the underlying thoracic ribs and vertebrae, respectively.
- **cardiac shunt** A pattern of blood flow in the heart in which the blood shifts between the systemic and pulmonary circuits within the ventricle (intracardiac shunt) or between the left and right aortas (extracardiac shunt).
- **casque** Prominent ossified outgrowths of the skull found in some frogs and lizards.
- caudal autotomy Spontaneous breaking off of the tail, used by many squamates as a defensive mechanism. In intravertebral autotomy, the tail breaks at specific fracture planes within the vertebrae and can be regenerated. In intervertebral autotomy, also called

pseudoautotomy, the tail breaks between vertebrae and cannot be regenerated.

- **center of gravity** The single point on a solid body where gravitational force can be considered to act.
- **cephalic amplexus** The form of amplexus in which the male grasps the female by her head.
- character Any heritable trait, including morphology, behavior, physiology, DNA sequences, and virtually anything else observable about an organism. Characters are used to determine the branching order of phylogenies and to define clades.
- **chromatophores** Color-producing cells in the skin of amphibians and reptiles (and many other animals). The three major types of chromatophores are iridophores, melanophores, and xanthophores.
- **clade** A monophyletic taxonomic group comprising a common ancestor and all of its descendants.
- cladistics See phylogenetic systematics.
- cladogram See phylogeny.
- **climatic niche** For a species, an aggregate index that describes the range of climatic conditions over which the species can occur.
- **cohort** In research studies, a group of individuals identified at oviposition or birth and followed until the last member has died.
- **common ancestor** The hypothetical taxon from which two or more lineages diverged; usually represented by a node in a phylogeny.
- **community** Any ecologically integrated group of species of microorganisms, plants, and animals inhabitating a given area.
- **community structure** The number of species present, their relative abundance, and the spatial and temporal arrangement of those species within a community.
- compensatory suction Suction produced when reduced pressure is generated by expansion and forward movement of the mouth and pharynx. In contrast to inertial suction, compensatory suction moves the mouth and pharynx over the water, rather than drawing water into the mouth.
- concertina locomotion A form of limbless locomotion in which a region of the elongate body is drawn into a series

of tight loops, which provide a static platform allowing another region of the body can be extended forward or drawn up from behind.

- **contact signals** Signals used by animals to maintain contact with other individuals, as in social groups of crocodylians.
- **continental island** An island that has a geologic connection to a landmass, and a terrestrial connection to that landmass that emerges and submerges as sea level changes.
- Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) An international treaty that regulates trade based on assessment of the status of each species of concern. CITES mandates that international trade in species (and products thereof) listed by the convention is unlawful unless authorized by permit.
- **convergent evolution** The independent evolution of phenotypically similar characters in two or more lineages (e.g., the alkaloid toxins in the skin of mantellid and dendrobatid frogs).
- cornified See keratinized.
- **corpus luteum** A secretory structure formed from the walls of a ruptured ovarian follicle after release of the ovum.
- **costal grooves** The vertical grooves of a salamander's body that facilitate water movement over the body surface.
- **countercurrent heat exchange** Transfer -of heat between two closely juxtaposed streams of fluid flowing in opposite directions.
- **courtship signals** Signals used by male or female animals to stimulate a partner during courtship.
- cranial kinesis The condition in which there is movement (kinesis) between the bones of the skull in addition to movement of the mandibles (lower jaw) against the rest of the skull.
- **crown group** A taxonomic group that contains the common ancestor to all living members of that group and that ancestor's descendants. A crown group contains extant species and also any lineages that arose after the common ancestor but subsequently became extinct. *See also* node-based definition.
- cryptic species A species that is morphologically indistinguishable from other species but is distinguishable using genetic data.

D

- debt-for-nature swap A method of preserving habitat whereby land is set aside as a reserve in exchange for release of a national government from its international loan debts.
- demography The statistical properties of populations, including population size (i.e., the number of individuals), birth and death rates, age structure, and population growth rate.
- **denticles** In tadpoles, toothlike structures formed by keratin on the jaw sheath that are used to scrape food from the substrate.
- derived character See apomorphy.
- **dermophagy** The behavior of eating skin. The larvae of some herpelid and siphonpid caecilians consume the lipidrich skin from the mother.
- **diapophysis** One of a pair of lateral projections from the vertebrae, often bearing an articular surface for a rib. Plural, diapophyses.
- differentiation The process whereby originally similar cells follow different developmental pathways to form different tissues and organ systems.
- **direct development** A transition from the embryo to the adult body form without a larval stage or metamorphosis.
- **direct fitness** The component of fitness that results from an individual producing its own offspring. *See also* inclusive fitness.
- disassociated (postnuptial) gonadal cycle A reproductive pattern in which mating is uncoupled from maximum sex hormone secretion and gametogenesis, and fertilization occurs after a period of sperm storage in the reproductive tract of males, females, or both.
- dispersal (1) The movement of animals from natal areas to different habitats, followed by return to the natal areas for breeding (as in pond-breeding amphibians or sea turtles). (2) Permanent movement to a new home range and breeding area distant from the natal area (as in many lizards).
 (3) Permanent colonization of a new geographic area (as by rafting from the mainland to an island, or by movement between continents, as in transcontinental dispersal between North America and Asia via the Bering land bridge).
- **drag** A force that acts against the movement of a hydrofoil or airfoil.

- **dry adhesion** A form of attachment in which the opposing surfaces attach to one another without any intervening fluid, such as water or mucus.
- **durophagous** Referring to the behavior of consuming hard-surfaced foods, such as molluscs.

Ε

- **ecomorphs** Species with the same structural habitat and ecological niche that are similar in morphology and behavior but not necessarily closely related phylogenetically.
- ectothermy A form of body temperature regulation in which the heat energy used to raise the body temperature comes primarily from outside the organism (e.g., from sunlight or a warm substrate).
- eft An immature terrestrial stage of the life history of some species of salamandrids.
- **emissivity** The ability of a surface to radiate heat energy.
- endemic Inhabiting only a specific geographic area.
- endocrine-disrupting contaminants

(EDCs) Compounds with molecular structures so similar to that of estrogen that they act as estrogen when they enter an animal's body. EDCs can alter sexual differentiation. Also called endocrine disruptors or environmental estrogens.

- endothermy A form of body temperature regulation in which the heat energy used to raise the body temperature comes primarily from inside the organism (i.e., from metabolism).
- epicontinental sea A shallow sea that covers part of the landmass of a continent.
- equitability The proportions of different species in an assemblage or community.
- explosive mating aggregation A mating system characterized by the highly synchronized arrival of large numbers of males and females at a breeding site. Explosive mating aggregations are characteristic of species in which the breeding period is short and the temporal and spatial distribution of females is limited.

F

facultative metamorphosis Metamorphosis in which the timing is governed by environmental conditions.

- facultative parthenogenesis Spontaneous parthenogenesis in individuals of species that normally reproduce sexually.
- fenestrae Openings in the temporal region of the skull. Anapsids lack fenestrae; synapsids have a single fenestra; and diapsids have two fenestrae, although this condition has been secondarily lost in squamates and turtles.
- field metabolic rate (FMR) The energy an animal uses when it is engaged in its usual behaviors in its natural environment.
- **folivores** Leaf-eating animals, such as iguanas.
- **footfall pattern** The order in which the feet are placed on the substrate during terrestrial tetrapod locomotion.
- **free fall** The condition in which the only force acting on a falling object is its own weight.
- freeze resistance The ability of an organism to remain unfrozen at sub-freezing temperatures.
- **freeze tolerance** The ability of an organism to withstand freezing and thawing without damage.

G

- **gene flow** The movement of genes from one population to another population through mating.
- genetic mating system The pattern of mating within a population (e.g., monogamy versus polygamy). It is often identified by DNA sequencing of parents and offspring.
- **genotypic sex determination (GSD)** A form of sex determination in which an individual's sex is a function of the individual's genotype at fertilization.
- **gliding** A form of unpowered aerial locomotion in which lift exceeds drag, allowing the animal to travel horizon-tally more rapidly than it descends. As a result, the angle of descent is shallower than 45°, and the animal travels farther horizontally than vertically.
- **good genes hypothesis** The hypothesis that certain traits are favored by sexual selection because they are indicators of the genetic quality of a mate.
- granular glands Toxin-producing glands in the skin of amphibians.
- Great American Biotic Interchange (GABI) A series of momentous dispersal events among South, Central, and

G-4 Glossary

North American biotas that occurred with the closure of the Isthmus of Panama. The GABI included all groups of plants and animals throughout the Americas.

н

- halfway technology Technology characterized by measures that address the effects but not the underlying causes of a problem.
- **head-starting** A reestablishment effort that involves collecting eggs from a nesting site, raising the eggs in captivity, rearing the hatchlings to a size that will reduce their vulnerability to predators, and releasing the young into the wild.
- **heliothermy** The use of heat from the sun to raise body temperature.
- **hemipenes** The paired, evertable copulatory organs of male squamates. Singular, hemipenis.
- **heterochrony** A change in the timing of embryonic and juvenile development that affects the sexually mature adult phenotype. One common result of heterochrony is the morphologically juvenile state referred to as paedomorphosis.
- **heterozygosity** The proportion of genetic loci for which an average individual is heterozygous.
- **heterozygosity index** The estimation of how much of a species' total genetic diversity is due to within-population variability and how much is due to among-population variability.
- hibernation Long-term dormancy that occurs during periods of cold and food scarcity.
- **holotype** The physical example of a single species that possesses all the characters of that species. When a new species is formally described, the researcher designates a holotype specimen.
- **homologous** Referring to two or more structures that evolved from the same ancestral structure. For example, the forelimb of a salamander and the forelimb of a bird are homologous because they are both modifications of the same ancestral tetrapod limb structure.
- **homoplasy** A derived character that has evolved in two groups that do not share a recent common ancestor. *See also* convergent evolution.

- **Hox genes** Regulatory genes whose products are expressed in specific locations along the body axis of an embryo.
- **hybridogenesis** A reproductive system, exhibited in some amphibians, in which the genome of the female parent passes unchanged from one generation to the next. Hybridogenetic genotypes are reconstituted in each generation, and the maternal genome is inherited clonally.
- **hydrofoil** A relatively thin body that generates lift as it travels through water, often exhibiting camber (curvature).
- **hydroperiod** The length of time a site contains water.
- **hyobranchium** The term used to refer collectively to the hyoid apparatus (of the tongue) and branchial (gill) skeleton.
- **hyoid apparatus** The skeletal elements that support the tongue and related structures. Often these elements are closely associated with the skeletal supports for the branchial, or gill, arches, in which case they are referred to collectively as the hyobranchium.

I

- **inclusive fitness** The sum of an individual's genetic contribution to subsequent generations both by production of its own offspring and by its influence on the survival of relatives who are not direct descendants. *See also* direct fitness.
- inertial suction Suction produced by reduced pressure that generates a flow of water into the mouth and pharynx, which remain relatively stationary. In contrast to compensatory suction, inertial suction imparts motion to the water, drawing food into the mouth rather than moving the mouth and pharynx over the water.
- inguinal amplexus The form of amplexus in which the male grasps the female immediately in front of her hindlimbs.
- intercalary cartilages Small cartilaginous elements located between the terminal and penultimate phalanges of the toes in some frogs. The purpose of intercalary cartilages is unknown, but they may influence the forces acting on the toe pad.
- **iridophore** A type of chromatophore that reflects white, silver, or blue coloration, depending on the size of purine granules in the cell.

к

- **keratanized** The condition of being covered by a layer of keratin, the structural protein found in human hair and fingernails, as well as the beaks of anuran larvae (tadpoles), the jaws of turtles, and the outer layer of reptilian scales. Also referred to as cornified.
- kleptogenesis A reproductive system, exhibited in some salamanders, in which females "steal" genomes from males of other species. Unlike hybridogenesis, there is not a common genome that is inherited clonally.
- **kleptothermy** The use of heat from another organism to raise body temperature.

L

- **labial lobe** One of a pair of fleshy extensions along the side of the mouth, on the upper and sometimes also the lower jaw. The labial lobes of some aquatic salamanders limit the escape of water from the sides of the mouth during suction feeding, thereby increasing the pressure with which water is drawn into the mouth and reducing escape by the prey.
- **lamellae** The enlarged, transverse scales that make up the scansors of some lizards, including many geckos and *Anolis* lizards. Singular, lamella.
- **lateral line system** In larval amphibians and adults of aquatic species, a system of mechanoreceptors (neuromasts) and electroreceptors (ampullary organs) that are arranged singly or in rows on the head and body and that detect water flow and other stimuli. *See also* ampullary organs and neuromasts.
- **lateral undulation** A form of limbless locomotion in which an elongate body moves in horizontal waves that pass from anterior to posterior.
- **lecithotrophy** A developmental pattern in which embryos are nourished by materials deposited in the yolk of the ovum.
- **lek** A display ground where male animals gather to compete for females and defend small display areas as a means of demonstrating territorial prowess and winning opportunities to mate.
- **lenticular sense organs** Small, circular mechanoreceptors that detect vibration. They are embedded in the scales of most squamates and in the head scales of crocodylians. Also called scale organs.

- **life history** The sequence of major events (development, growth, reproduction, and death) during an individual's life. A complex life history includes a larval stage that undergoes metamorphosis to the adult stage.
- **life table** A tabular summary of agespecific survival and fecundity for a cohort or for individuals of different ages during several years.
- **lift** A force generated by a hydrofoil or airfoil that acts at an angle of 90° to drag.
- **limb girdles** *See* pectoral girdle; pelvic girdle.

M

- mark–recapture studies Studies that trace the movement of animals by marking, releasing, and then recapturing or otherwise locating them after time has passed.
- mass-specific energy requirement The amount of metabolic energy required by a unit of mass (e.g., gram) of an organism.
- **matrotrophy** A developmental pattern in which embryos are nourished directly by the mother through the placenta rather than indirectly through yolk in the ovum.
- maximum aerobic speed The rate of locomotion by an animal that requires the highest rate of aerobic metabolism the animal can attain. Moving faster requires the addition of anaerobic metabolism.
- **melanophore** A type of chromatophore that contains the pigment melanin, which gives rise to shades from brown to black.
- **mental glands** Glands on the chins of male salamanders that produce courtship pheromones.
- mesokinesis A form of cranial kinesis, found in many lizards, in which there is movement across the transverse suture between the frontal and parietal bones. Mesokinesis may increase the gape (size of the open mouth), the force of the bite, or both.
- **metakinesis** A form of cranial kinesis, found in many lizards, in which there is movement between the parietal and the supraoccipital bones, resulting in movement of the skull roof relative to the braincase.
- metamorphosis The process of transformation from a larval form to an adult form.

- **metapopulation** A network of populations connected by dispersal among habitat patches. Sometimes a large patch, such as a pond, serves as a source of dispersers to other patches, such as smaller ponds.
- **microhabitat** The location in which a organism is normally found (e.g., beneath loose bark on a fallen tree).
- **migration** Directed movement between habitats that is not influenced by local resources, such as migration to a specific breeding site.
- minimum viable population (MVP) The smallest number of individuals required for a population to have a 99% chance of surviving for the next 1,000 years in spite of the effects of environmental, demographic, and genetic stochasticity and natural catastrophic events.
- **monophyly** A taxonomic group that includes a common ancestor and all of its descendants. Only monophyletic groups (also called clades) are given formal taxonomic names.

N

- **nasolabial grooves** In plethodontid salamanders, grooves that run from the nasal cavity to the upper lip and that transport chemicals to the vomeronasal organ.
- **natal philopatry** The tendency for animals to return to their place of birth, especially for breeding.
- **nectivory** The behavior of feeding on nectar.
- neuromasts In amphibian larvae and aquatic adults, mechanoreceptors that are located on the head and body and are part of the lateral line system. Neuromasts respond to directional changes in water currents at the skin surface and appear to facilitate prey capture and predator avoidance in some species.
- **node** A point in a phylogeny at which a common ancestor gives rise to two sister lineages, or branches.
- **node-based definition** A taxonomic definition referring to a group comprising the most recent common ancestor of at least two taxa (called specifiers) and all of the descendants of that common ancestor.
- **nuptial pads** In many amphibians, large clusters of breeding glands that develop on the hands and/or forearms of breeding males that allow them to

better grasp females during amplexus. Nuptial pads may be highly keratinized and may be ornamented with spines used in male combat.

0

- oceanic islands Islands that do not have terrestrial connections to the mainland, even during periods of low sea levels. These islands are commonly formed from uplifted limestone or volcanic activity.
- **oogenesis** The process by which haploid ova are produced from primordial germ cells by way of mitosis and meiosis.
- **oophagy** The behavior of eating eggs.
- **operculum** In salamanders and frogs, a bony or cartilaginous structure that attaches to the ear capsule and is connected to the suprascapula via the opercular muscle. Functionally, the operculum allows ground vibrations to be transmitted from the forelimb to the inner ear. This structure is not homologous with the operculum that covers the gills in fish.
- **opisthocoelous** Referring to the condition of the vertebral centrum (body) in which the anterior end is rounded and the posterior end is convex.
- **opisthoglyph** Referring to the type of dentition in snakes in which enlarged, grooved fangs are located on the posterior portion of the maxilla. This dentition is characteristic of some colubrids and lamprophilds. Also called rearfanged.
- osteoderms In many reptile groups, layers of bone that develop within the dermis, providing rigidity to the skin.
- **oviparity** Reproduction in which eggs are released by the female and develop outside the female's body.

Ρ

- paedomorphosis The retention, in sexually mature adults of a derived species, of characteristics found in juveniles of an ancestral species. Paedomorphosis is a type of heterochrony.
- **paleoendemism** The phenomenon of ancient taxa that were once widespread being limited to small, isolated areas.
- **parachuting** A form of unpowered aerial locomotion in which surface drag is greater than the lift generated by the airfoil. As a result, the animal descends more rapidly than it travels in the horizontal plane, and the angle of descent

is greater than 45° (but still less than 90°, as in a free fall).

- **paraphyletic** Referring to a group that contains only some, but not all, of the descendants of a common ancestor. For example, a definition of Reptilia that does not include birds is paraphyletic because birds evolved from dinosaurian reptiles. Paraphyletic taxa are not given formal taxonomic names.
- **parotoid glands** Concentrations of toxin-producing granular glands that occur behind the eyes or on the neck or shoulders of bufonid toads.
- **parthenogenesis** A form of asexual reproduction in which a female produces female offspring through a process not involving the fusion of gametes from two individuals.
- **pectoral girdle** In tetrapod vertebrates, the bony structures that support the forelimbs, including but not limited to the scapula, suprascapula, cleithrum, clavicle, and sternum. The pectoral and
- , pelvic girdles are collectively referred to as the limb girdles.
- **pelvic girdle** In tetrapod vertebrates, the bony structures that support the hind limbs, including the pubis, ilium, and ischium. The pelvic and pectoral girdles are collectively referred to as the limb girdles.
- **phallodeum** The protrusible copulatory organ of male caecilians.
- **phenotypic plasticity** The ability of one genotype to express phenotypes that vary as a function of environmental conditions.
- **pheromones** Chemicals secreted by an animal and used as communication signals that impact the behavior (particularly mating behavior) of the receiving animal.
- **phylogenetic systematics** A system of classification that uses shared derived characters (apomorphies) to place organisms into taxonomic groups that represent evolutionary history. Also called cladistics.
- **phylogeny** A diagrammatic representation of the evolutionary history of a particular group of organisms. Also called a cladogram. Phylogenies are increasingly inferred from DNA data, but features of the phenotype may also be used.
- **pit organs** Specialized sensory structures in the face of some boas, pythons, and vipers that detect infrared radiation (heat).

- **pivotal temperature** The incubation temperature that produces equal numbers of males and females in species with temperature-dependent sex determination (TSD).
- **placenta** A juxtaposition of the uterus and extraembryonic membranes that facilitates the exchange of nutrients and gases between maternal and fetal tissues.
- **placentotrophy** A form of matrotrophy in which nutrients for embryonic development are provided by the mother through some form of placentation.
- **plastron** The ventral half of a turtle shell, formed primarily from the fusion of the clavicle and other elements of the pectoral girdle and endochondral bone, and typically covered by keratinous scutes.
- **plesiomorphy** The ancestral form of a character. Modifications of ancestral characters are called apomorphies, or derived characters.
- **pleurodont** Referring to the type of dentition in which the teeth have a bony attachment to the lingual (inner) side of the tooth-bearing bone and are replaced continually.
- **polyandry** A mating system in which a female mates with more than one male.
- **polygyny** A mating system in which a male mates with more than one female.
- **polymorphism** (genetic) The percentage of loci for which the frequency of the most common allele is less than some arbitrary threshold, often 95%.
- **polymorphism** (phenotypic) The coexistence within a population of two or more distinct traits.
- **polyphyly** A taxonomic group that does not contain the most recent common ancestor of all the members of that group. Polyphyletic taxa are not given formal taxonomic names.
- **polyploidy** The possession of more than two paired sets of chromosomes (diploid, or 2*n*). Most amphibians and reptiles are diploid, but some polyploid species are triploid (3*n*), tetraploid (4*n*), or even dodecaploid (12*n*).
- **polytomy** A taxonomic group in which three or more lineages share a common ancestor but the phylogenetic relationships among these lineages cannot be determined.
- **population** A group of conspecific individuals living in an arbitrarily defined area.

- **population dynamics** Changes in population size and the processes that influence those changes.
- **procoelous** Referring to the condition of the vertebral centrum (body) in which the anterior end is convex and the posterior end is rounded.
- **production efficiency** The proportion of assimilated food that is used by the consumer to produce new biomass.
- projectile motion See ballistic motion.
- **prokinesis** A form of cranial kinesis, found in most alethinophidian snakes, in which the bones of the snout move relative to those of the braincase.
- **prokinetic** The joint formed between the frontal and nasal regions of the skull in snakes that permits downward movement of the snout relative to the braincase.
- **proteroglyph** Referring to the type of dentition in some colubroid snakes in which the anterior end of each maxilla bears a single hollow fang (and smaller teeth posteriorly) that is not erected by rotation of the maxilla. This dentition is seen in elapids and in the lamprophild *Homoroselaps*.
- pseudoautotomy See caudal autotomy.

R

- ranging behavior Movement beyond the normal home range in search of new resources or habitat patches.
- rank-free taxonomy A system of categorizing organisms into hierarchicāl taxonomic groups without using Linnaean rank labels such as phylum, order, class, and so on.
- rectilinear locomotion A form of terrestrial limbless locomotion in which bilaterally synchronized waves of muscular contraction sequentially lift, protract, and fix the ventral scales.
- **Red List of Threatened Species** A catalog of the conservation status of species maintained by the International Union for the Conservation of Nature (IUCN). Usually referred to as simply "the Red List."
- **refugia** An area in which a population of organisms has been able to persist through a period of unfavorable environmental conditions.
- **relocation** A reestablishment effort that attempts to protect a population by moving animals from areas where they are threatened to areas where they will be less vulnerable.

- **repatriation** A reestablishment effort that involves releasing animals into areas that were formerly or are currently occupied by that species.
- **reproductive cycle** The sequence of gonadal maturation (spermatogenesis, oogenesis, and vitellogenesis), mating, fertilization, embryogenesis, and hatching or birth that results in the production of offspring.
- resource partitioning The differential use of resources by sympatric species (i.e., species occupying the same area).
- rhinokinesis A form of cranial kinesis, found in some colubroid snakes, in which there is movement among the bones of the snout (in addition to the movement of the snout against the braincase at the prokinetic articulation).

runaway selection Sexual selection that favors exaggerated traits.

S

- scale organs See lenticular sense organs.
- scales Thickened layers of epidermal and dermal tissue that form by folding of the integument during embryogenesis.
- scansors The adhesive pads of certain lizards, including many geckos and *Anolis* lizards. Scansors consist of elongated, transverse scales (lamellae) that bear keratinous spines (setae) with flattened tips that generate dry adhesion.
- scleral ossicles A circle of thin overlapping bony plates embedded in the sclera, surrounding the pupil of the eye.
- scramble competition A mating system in which males compete to locate and mate with females as quickly as possible.
- **scutes** Units of thickened, keratinized epithelial tissue that overlie the bony shell of most turtles.
- senescence The deterioration of organismal function with age.
- sensory exploitation hypothesis The hypothesis that sexually selected traits are favored because they exploit the sensory biases of females (e.g., a preference for red coloration).
- **sensu lato** "In the broad sense," Latin term used to describe usage of an outdated taxonomic name, typically one that has undergone major taxonomic revision that has reduced the scope of taxa included.

- **sensu stricto** "In the strict (narrow) sense," Latin term used to describe a taxonomic name that has been revised to narrow the scope of taxa included.
- **setae** The fine keratinous spines that occur on the lamellae of lizards that possess scansors, such as many geckos and species in the genus *Anolis*. The setae terminate in one or more minute, flattened tips that make intimate contact with the substrate, producing dry adhesion.
- **sexual selection** A form of selection that acts on traits through their effects on mating success.
- **sexy sons hypothesis** The hypothesis that sexually selected traits are favored because they make the sons of females attractive to other females.
- shared derived character See synapomorphy.
- shell membrane The inner proteinaceous layer of an eggshell.
- **shell units** Discrete mineral aggregates that form the outer layer of the eggshell in some reptiles.
- sidewinding A form of limbless terrestrial locomotion in which sections of the body are sequentially lifted from the substrate, drawn forward, and then placed back on the substrate. Because force is exerted downward rather than laterally, sidewinding is effective on loose substrates such as sand dunes.
- sister lineages Two lineages that descend from a common ancestor and thus are each other's closest relatives. Also called branches.
- **sky islands** Biogeographically isolated mountaintops in which populations evolve without gene flow from other mountaintops (much as happens with oceanic islands).
- **solenoglyph** Referring to the type of dentition in some colubroid snakes in which the maxilla is reduced and bears only a single hollow fang. The fang can be rotated by moving the maxilla. This dentition is characteristic of vipers and the lamprophild *Atractaspis*.
- spatial ecology The study of patterns of movement and habitat use in animals.
- speciation The formation of new species, usually by splitting of a population into two or more reproductively isolated populations.
- **species richness** The total number of species in an assemblage or community.

- **specific dynamic action** The increase in metabolic rate, above the basal rate, that is associated with the digestion of food.
- **spermathecae** In salamanders that have internal fertilization, spermstoring clusters of tubules in the female that connect to the cloaca. In some species, the walls of the spermathecae provide nutritional secretions that sustain the sperm for some time.
- **spermatophore** A typically mushroomshaped, sperm-containing capsule deposited on the substrate by male salamandroid salamanders.
- **spermiogenesis** The process by which haploid spermatazoa are produced from primordial germ cells by way of mitosis and meiosis.
- **spiracle** In tadpoles, the structure through which water exits after it passes through the mouth and branchial basket.
- **squamulae** Mineralized nodules that top the collagenous fibers of a caecilian scale.
- **stapes** The bone that directly transmits vibrations to the middle ear. Also called the columella.
- **station-keeping** The tendency to remain in one location, such as a home range.
- **stegokrotaphy** The condition of having an akinetic skull that is entirely roofed by bone.
- **stem** The region of a phylogeny between two nodes that represents unsampled lineages.
- **stem-based definition** A taxonomic definition referring to a group comprising lineages more closely related to at least one taxon than another taxon.
- **stem lineages** Lineages that diverged before the crown group.
- **streptostyly** A form of cranial kinesis that involves movement of the quadrate bone.
- subdentary glands Pheromone-secreting glands on the chins of tortoises.
- **subterminal** When referring to the mouth, opening beneath the tip of the snout, as in sharks. *See also* terminal.
- **supercontraction** The condition in which a muscle can generate force even after being greatly stretched.
- **supercooling** Cooling a fluid below its freezing point without freezing it.
- sustainable harvesting Removing individuals from a population in such a

way that the resource is renewable, that is, so that the population can continue indefinitely.

synapomorphy An apomorphy shared by two or more taxa. Synapomorphies are evidence that a group of taxa form a clade and all descended from a common ancestor with this apomorphy. Also called a shared derived character.

т

- taxon Any named group of organisms.
- **taxonomy** The science of categorizing, or classifying, Earth's living organisms.
- **temperature-dependent sex determination (TSD)** A form of sex determination in which an individual's sex is a function of the temperatures it experienced as an embryo during the middle third of development.
- **tentacle** In caecilians, a specialized chemosensory organ composed of muscles, glands, and ducts that can be protruded through an aperture in the skull. The tentacle may also incorporate some structures from the eyes.
- **terminal** When referring to the mouth, located at the tip of the snout. *See also* subterminal.
- thermoconformer An organism that assumes the temperature of its external environment. See also thermoregulator.
- **thermogenesis** The process of heat production by an organism.
- **thermoregulator** An organism that maintains a body temperature different from the temperature of its external environment. *See also* thermoconformer.
- **thigmothermy** The use of heat from contact with a warm surface to raise body temperature.
- **translocation** A reestablishment effort that involves moving animals into areas that were not historically occupied by that species.

trochlear process A bony structure that acts like a pulley, redirecting force from one direction to another. In the case of turtle skulls, the trochlear process allows the jaw-closing muscles, which in many species originate well behind the lower jaw, to turn downward and insert almost vertically on the mandibles.

tympanic membrane The eardrum.

U

- unken reflex A defensive posture of some species of frogs and salamanders whereby they contort their body to reveal otherwise obscured bright coloration.
- **ureotely** Excreting nitrogenous wastes in the form of urea. Most species of amphibians excrete nitrogenous wastes as ammonia (ammonotely) and urea. Many reptiles adjust the proportion of ammonia, urea, and uric acid (uricotely) in their nitrogenous wastes as their hydration state changes.
- **uricotely** Excreting nitrogenous wastes in the form of uric acid. Only a few species of amphibians are known to be ureotelic. Many reptiles adjust the proportion of ammonia (ammonotely), urea (ureotely), and uric acid in their nitrogenous wastes as their hydration state changes.
- **urostyle** A rod-shaped bone in frogs formed from the fusion of caudal vertebrae.

٧

- **venom** Toxins that are delivered to the interior tissues of a prey item or predator.
- vicariance The process by which a new barrier fragments what had been a continuous geographic distribution of organisms into two or more discontinuous distributions.
- visual noise Movement in the environment, such as windblown vegetation,

that interferes with communication signals.

- vital rate Information about age-specific reproduction and survival.
- vitellogenesis The process of yolk formation via deposition of nutrients in the oocyte.
- viviparity Reproduction in which fertilization of eggs and development of the embryos occur inside the female's body.
- vomeronasal organ (VNO) A chemicalsensing nasal organ found in many amphibians and reptiles. The VNO is located in paired outgrowths of the olfactory organ that open via a duct in the roof of the mouth. Scent molecules are delivered to the VNO by the tongue.

W

Wallace's Line A biogeographic line drawn in the mid-nineteenth century by Alfred Russel Wallace, dividing the Indo-Australian Archipelago (IAA) into two portions with dramatically different flora and fauna. The line corresponds to a deep-water channel that would have blocked the movement of terrestrial organisms between the islands of Bali and Borneo on the west and Lombok and Sulawesi on the east, even when sea level was low during the Pleistocene glaciations.

х

xanthophore A type of chromatophore that contains pteridine or carotenoid pigments, which are responsible for red, yellow, and orange colors.

Z

zygokrotaphy The condition of having a skull characterized by open fenestrae. Zygokrotaphy is characteristic of rhinatrematid, scolecomorphid, and typhlonectid caecilians.

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Chapter 4

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Chapter 6

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Chapter 7

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Chapter 9

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Chapter 12

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Chapter 14

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Chapter 15

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