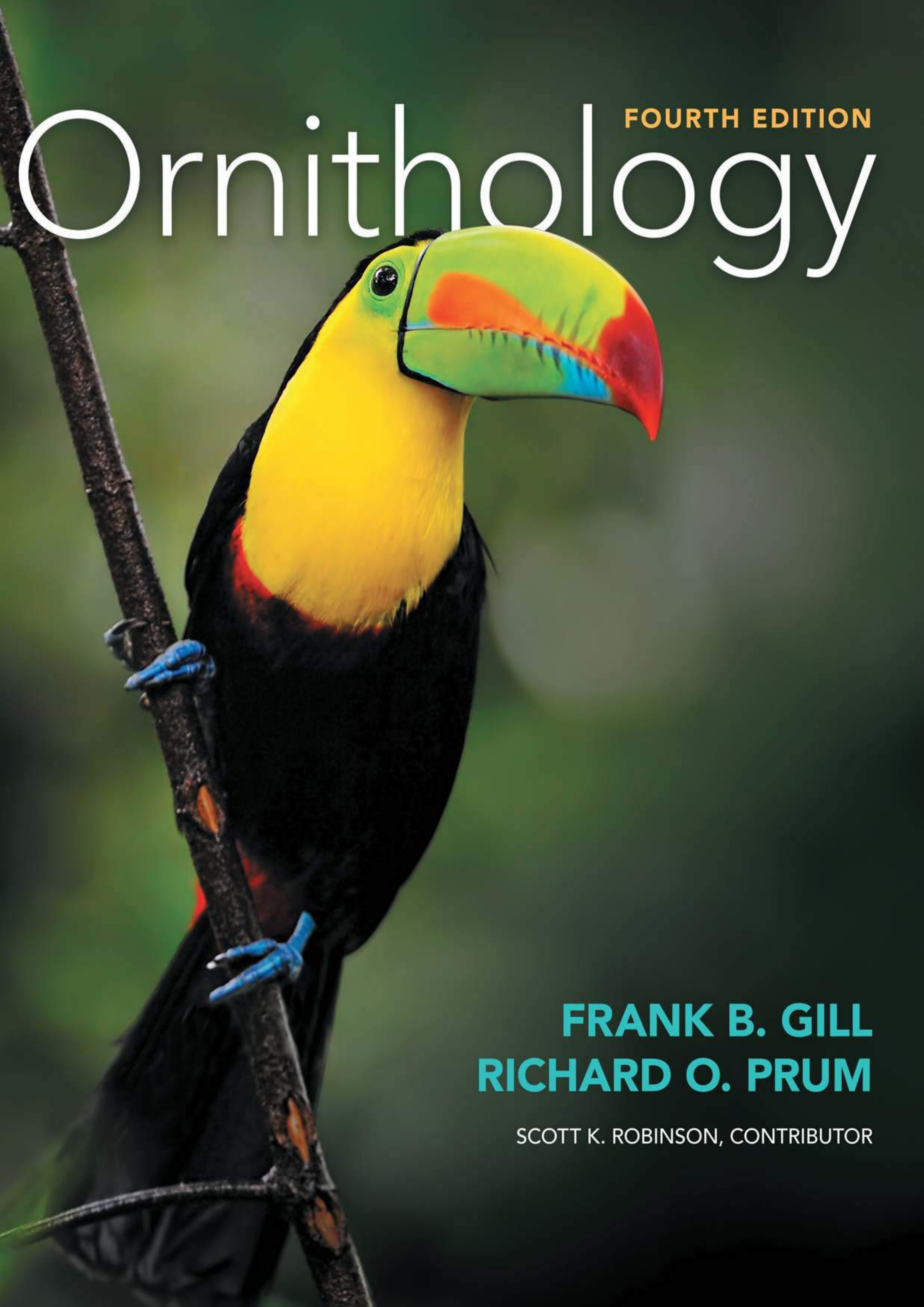


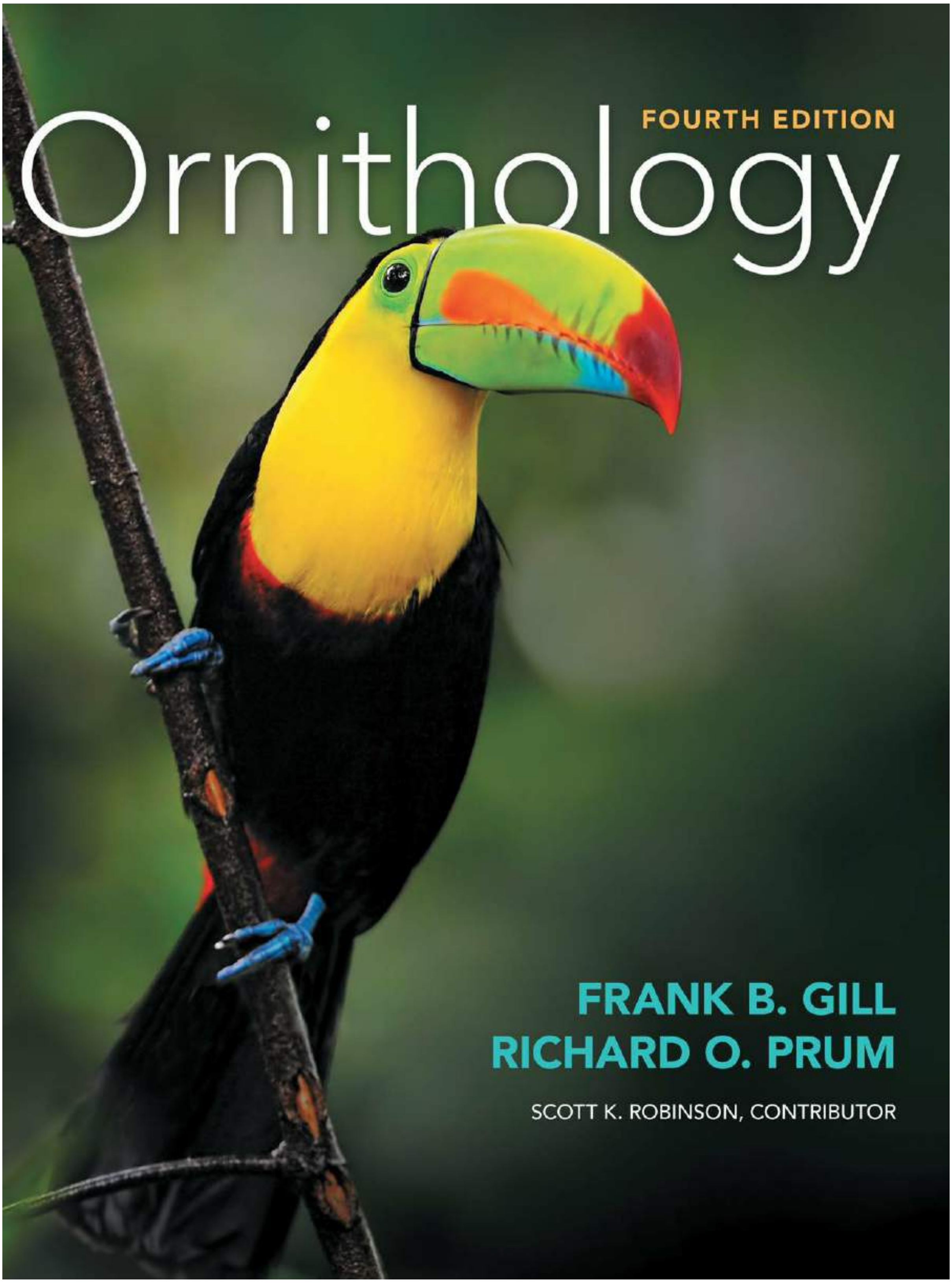
FOURTH EDITION

Ornithology

FRANK B. GILL

RICHARD O. PRUM

SCOTT K. ROBINSON, CONTRIBUTOR



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Frank B. Gill

Academy of Natural Sciences of Drexel University

Richard O. Prum

Yale University

With Contributions by

Scott K. Robinson

Florida Museum of Natural History

w.h.freeman
Macmillan Learning
New York

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To the late Wesley “Bud” Lanyon, our beloved mentor and friend

BRIEF CONTENTS

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Hoatzin [© Geoff Jones 2010/barraimaging.com.au]

Indian Peafowl [apiguide/
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PREFACE

This fourth edition of *Ornithology* strives to capture the vital features of the biology of birds from a contemporary ornithological perspective. As in the preceding editions, we designed it primarily for undergraduate students, but we also have in mind bird enthusiasts young and old who simply want to know more about birds.

This edition, like the earlier ones, avoids theory for theory's sake. It stresses discovery rather than the mathematical models that may guide discovery. To make the book accessible to readers who are not specialists, we highlight technical terms when they are first used and list them at the end of that chapter. Additionally, the enhanced, comprehensive index refers the reader to the first use of a term and its definition.

The power of evolution by natural selection is a central theme of this book. The adaptations of birds ranging from morphology and physiology to migration and mating systems are testimony to the pervasive role of Darwinian evolution in action through the millennia. Evolution is responsible for the transformation of birds from a single dinosaurian ancestor to the great diversity of over 10,000 species with great variety of plumages, songs, ecologies, and intelligences.

Conservation is an increasingly strong theme of this textbook. Once a sideline of ornithology, conservation science is now a central focus of interest of students and faculties alike. As barometers of environmental quality and ecosystem health, birds engage scientists and the public in the stewardship of landscapes and waterscapes. Most chapters of this book include specific examples of conservation challenges and successes. Chapter 21 provides a broad overview of conservation matters facing birds, with an emphasis on hope rather than despair.

The ornithological literature is a huge and growing enterprise due in part to the major contributions of birds to biological understanding. The advances in ornithology in the last decade have been diverse and substantial. The revisions and updates, therefore, are now a team effort with contributions by coauthor Richard Prum and guidance by Scott Robinson. Topics that feature new in-depth explorations include the paleontology and evolution of bird ancestors, the taxonomic classification of modern birds, the microstructures of feathers, the aerodynamics of flight, and the diversity of bird nests.

This fourth edition of *Ornithology* includes much that will be familiar to those who used the third edition, but it also is dramatically different in design and content. Macmillan Learning, our publisher, invested in many redesigns, including new artwork, lots of color photos, vibrant sonograms, and sets of teaching tools, all while embracing the flavor of professional ornithology. We hope this approach will help students to identify and fully appreciate the diversity and delights of birds.

The chapters in this edition are packaged into five sections instead of the six sections in the third edition. Chapters 1 to 3 introduce the diversity of birds, their evolutionary history, and their phylogenetic relationships. Chapters 4 to 6 address the fundamentals of avian form and function, including feathers, flight, and physiology. Chapters 7 to

11 broadly repackage the behaviors of birds, including their senses and vocalizations, their annual cycles and seasonal migrations, and their social behavior. Chapters 12 to 17 look broadly at reproduction from the basics of bird sex to breeding systems, raising young, and overarching life histories. Chapters 18 to 21 shift the focus from reproductive biology to the ecology of bird populations, their communities, and the evolution of species. Chapter 21 celebrates the conservation of birds and the power of citizen science.

Students and faculty alike responded favorably to the use of boxes to separate particular examples, important technical information, and recent discoveries from the text. This edition continues that innovation to call attention, for example, to the discovery of melanin coloration in fossil feathers (Box 4–3), understanding the complex web of competition among cavity nesters (Box 15–3), and the embryonic controls of beak shape diversification in Galapagos finches (Box 15–4).

Possible supplements to this textbook abound in both bookstores and on the Web. *Sibley's Guide to Bird Biology and Behavior* (2009) is an excellent introductory complement to *Ornithology*, complete with a glossary and links to David Sibley's wonderful field guides. Encyclopedic accounts of individual species are available in *The Birds of North America, Life Histories for the 21st Century* (https://bna.birds.cornell.edu/BNA) and in the *Handbook of the Bird of the World* (https://www.hbw.com).

This edition has benefited greatly from comments by many colleagues and students. The next edition will do so also. We sincerely invite creative suggestions, corrections of errors, updates, and reprints containing interesting, new ornithological information.

Thank you.
Frank and Rick ☺

ABOUT THE AUTHORS

Frank B. Gill, Author

PHOTO CREDIT: JOHN THAXTON

Frank Gill is an American ornithologist with worldwide research interests and birding experience. Expeditions to remote corners of the globe are one of his favorite pastimes. Gill’s projects include innovative leadership and engagement of the public in ornithology. He directed the encyclopedic work *The Birds of North America* (BNA), now online. He pioneered the use of the internet for citizen science initiatives, including eBird with the Cornell Lab of Ornithology. He now leads an international effort to maintain an up-to-date classification of the birds of the world (http://www.worldbirdnames.org).

Gill was a full-time staff member of the Academy of Natural Sciences in Philadelphia from 1969 to 1995. He served the National Audubon Society from 1996 to 2010 in various roles, including chief scientist and interim president. Gill was president of the American Ornithologists’ Union from 1998 to 2000 and received the Union’s prestigious William Brewster Award.

Richard O. Prum, Author

PHOTO CREDIT: RUSSELL KAYE

Richard O. Prum is the William Robertson Coe Professor of Ornithology at Yale University and curator of ornithology at the Yale Peabody Museum of Natural History. Prum is an evolutionary ornithologist with broad interests in avian evolution, behavior, systematics, color production, color vision, feather development and evolution, and more. Prum has received the MacArthur, Guggenheim, and Fulbright fellowships. His first book, *The Evolution of Beauty* (Doubleday, 2017), was named a Top Ten Book of 2017 by the *New York Times* and a 2018 Pulitzer Prize Finalist in General Non-Fiction. Prum's popular writing on birds has been published in *The New Yorker,* the *New York Times,* the *New York Times Book Review, Natural History,* and *Scientific American.* A lifelong bird-watcher, Prum has done fieldwork on every continent.

Scott K. Robinson, Contributor

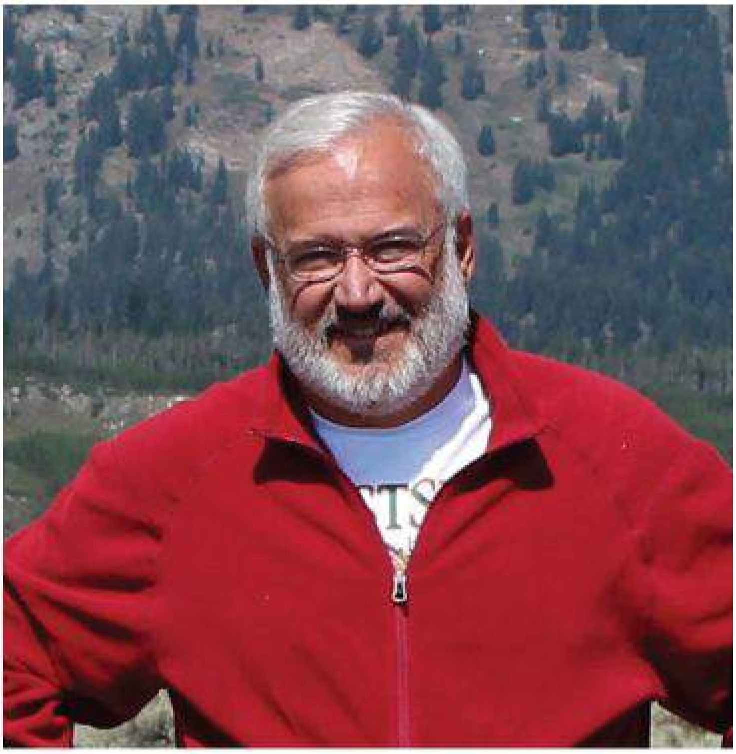

Photo credit: Glendy C. Vanderah

Scott K. Robinson is the Ordway Professor of Ecosystem Conservation in the Florida Museum of Natural History of the University of Florida. Robinson received his bachelor's degree from Dartmouth College, where he worked in the northern hardwoods forests of New

Hampshire, and his doctorate from Princeton University, where he began his lifelong work in bird communities of tropical forests, especially in the Neotropics. Robinson began his career at the Illinois Natural History Survey and the University of Illinois (1984–2003), where he studied mainly the effects of habitat fragmentation on bird communities. Since 2003, he has been at Florida, where he studies the community ecology of birds, especially along environmental gradients. He has trained more than 30 PhD students who work around the globe. Robinson is also a fanatical bird-watcher.

ACKNOWLEDGMENTS

In addition to the many friends who contributed to the preceding editions of *Ornithology*, we thank with greatest appreciation those who evaluated the third edition, reviewed draft chapters of this edition, provided photographs, and patiently responded to our queries. Among the many who helped were K. Able, F. Ammer, M. Baldwin, G. Barrowclough, B. Beason, S. Beissinger, J. Berv, B.-A. Bhullar, R. O. Bierregaard, H. Bilger, C. Blem, K. Bostwick, J. Brawn, P. Brennan, S. Bush, W. Buskirk, G. Butcher, C. Caffrey, J. Cecil, C. Clark, D. Clayton, J. Cracraft, R. Crawford, D. Cristol, K. Dial, R. Dooling, J. Dosch, S. Doucet, R. Dudley, M. Ellison, J. Erritzoe, A. Feduccia, T. Feo, D. Field, J. Fitzpatrick, J. Gauthier, D. Gill, R. Gill, F. Goller, P. Grant, R. Grant, J. Grantham H. Greeney, J. Groth, J. Hagan, T. Hanson, J. Hengeveld, S. Hengeveld, F. Hertel, G. Hill, M. Huber, G. Hunt, H. James, E. Jarvis, J. Johnson, G. Jones, L. Joseph, H. Karten, L. Kiff, D. Klein, S. Kress, D. Kroodsma, D. Lank, S. Lanyon, G. LeBaron, R. Lein, D. Lentink, D. Levey, M. Mace, J. Madden, J. Marks, G. Martin, L. Mertz, J. Musser, D. Niven, M. Norell, R. Payne, I. Pepperberg, S. Peters, T. Piersma, J. Podos, D. Pratt, S. Pruett-Jones, R. Ricklefs, G. Ritchison, M. Rowe, P. Ryan, J. Sauer, S. Senner, F. Sheldon, S. Sillett, B. Slikas, T. Smyth, P. Stettenheim, C. Sturdy, R. Suthers, R. Telfair, C. Thébaud, J. Thaxton, D. Varricchio, G. Wagner, C. Walcott, G. Waring, F. Wasserman, A. Wheeler, K. Winker, D. Winkler, C. Witt, J. Wunderle, R. Zink, and K. Zyskowski. L. J. Friesen drafted the end-of-chapter learning questions. Special and enthusiastic thanks go also to H. McCoy, E. Dionne, J. MacMillan, R. Fox, M. McAdams, and A. Dunaway of the W. H. Freeman team who greatly improved the book’s content, accuracy, and clarity.

From Frank—My wife, Sally Conyne, contributed her editorial and bibliographic expertise. Equally appreciated has been the advice and memory of my three primary mentors in ornithology—Wesley E. Lanyon, Robert W. Storer, and Harrison B. Tordoff—no longer with us.

From Rick—I would like to thank Frank Gill for his kind invitation to coauthor the fourth edition of *Ornithology* and his persuasive energy to see the project through to completion. I would like to thank my wife, Ann Johnson Prum, for her unflagging support over many years.

ORNITHOLOGY: A SHORT HISTORY

In my hand I held the most remarkable of all living things, a creature of astounding abilities that elude our understanding, of extraordinary, even bizarre senses, of stamina and endurance far surpassing anything else in the animal world. Yet my captive measured a mere five inches in length and weighed less than half an ounce, about the weight of a fifty-cent piece. I held that truly awesome enigma, a bird. [Fisher 1979, p. 154]

*W*ith no other animal has our relation been so constant, so varied, so enriched by symbol, myth, art, and science, and so contradictory as has our relation with birds. Since earliest records of humankind, birds have served as symbols of peace and war, as subjects of art, as objects for study and for sport. Birds and their eggs range from the most exotic to the common. Their command of our imagination is not surprising because they are astonishing creatures, most notably for their versatility, their diversity, their flight, and their song.

Birds are conspicuous and found everywhere: Snowy Owls in the Arctic Circle, Black-bellied Sandgrouse in the deserts of the Middle East, the White-winged Diuca Finch at the highest elevations of the Peruvian Andes, and Emperor Penguins hundreds of meters beneath Antarctic seas. Huge eagles and bright parrots course over the rain forests of the world, and bustards, plovers, and larks stride and scurry across the arid plains.

These highly mobile creatures are travelers of the long distance and the short. Some birds, such as the Nicobar Pigeon in Indonesia, move incessantly from island to island, whereas others are master navigators, traveling phenomenal distances. The Sooty Shearwater migrates from islands off Australia to the coasts of California and Oregon, the Arctic Tern from New England to Antarctica, and the Rufous Hummingbird from Alaska to Mexico.

And birds please the eye and the ear. Little in nature is more extravagant than the Twelve-wired Bird-of-Paradise, more subtly beautiful than the Evening Grosbeak, more stylish than the Horned Sungem hummingbird, or more improbable than the Javan Frogmouth. No other sounds in nature can compare in exuberance and complexity to the song of a Wood Thrush or a White-rumped Shama.

Birds as Cultural and Religious Symbols

All these qualities seem to have provoked wonder and a sense of mystery since the dawn of human existence. Indeed, in almost every early culture, birds were divine messengers and agents. To understand their language was to understand the gods. To interpret the meaning of the flight of birds was to foretell the future. Our words *augury* and *auspice* literally mean “bird talk” and “bird view.” By the time Greek lyric poetry was flourishing (fifth and fourth centuries B.C.E.), the words for *bird* and *omen* were almost synonymous, and a person seldom undertook an act of consequence without benefit of augury and auspice. This practice still prevails in parts of Southeast Asia and the western Pacific.

As symbols of ideology and inspiration, birds have figured largely in many religions and in most cultures. The dove was a symbol of motherhood in Mesopotamia and was especially associated with Aphrodite, the Greek goddess of love. For the Phoenicians, Syrians, and Greeks, the dove was the voice of oracles. In Islam, it is said to call the faithful to prayer. In Christianity, it represents the Holy Spirit and is associated with the Virgin Mary. Bearing an olive branch in its bill, the dove continues to be a potent symbol of peace. In contrast, the dove was a messenger of war in early Japanese culture.

The eagle appeared as a symbol in Western civilization as early as 3000 B.C.E. in the Sumerian city of Lugash. In Greek mythology, the eagle was the messenger of Zeus. At least since Roman times, the symbolic eagle in Europe was the Golden Eagle, and that species also was the war symbol of many North American natives at the time of early English settlement. In 1782, the Bald Eagle became the symbol of the fledgling United States.

Less common than the eagle but prevalent in myth and legend is the raven. As Apollo’s messenger, the raven reported a nymph’s infidelity, and, as a consequence, Apollo changed the bird’s color from white to black. After 40 days, Noah sent forth both a dove and a raven to discover whether the floodwaters had receded. The faithless raven, according to some accounts, did not return and so earned Noah’s curse and, once again, a color change from white to black. The belief in the raven’s color change appears in a Greenland Eskimo legend in which the Snowy Owl, long the raven’s best friend, poured sooty lamp oil over him in the heat of a disagreement.

In other legends, the raven plays a more favorable role. Native North American folklore described the raven’s generosity in sharing its food with men stranded by floodwaters. Norse sailors, like Hindu sailors half a world away, carried ravens, which they released to lead them to land. Two ravens are said to have guided Alexander the Great through a dust storm on his long journey across the Egyptian desert to consult the prophet at the Temple of Ammon.

Diversity of Human Interest in Birds

Not only is our association with birds as old as human society, it is characterized by the diversity of our interest in them. We can do no more here than to consider a few examples of that diversity and, through those examples, come finally to the rich and varied science of ornithology.

The earliest records indicate that eggs have always been part of the human diet. The domesticated chicken, a form of the Red Junglefowl, existed in India before 3000 B.C.E. and was known in China by 1500 B.C.E. and in Greece by 700 B.C.E. Mallard ducks and geese were domesticated in the Far East nearly 1,000 years before the time of Christ, and domestication of the turkey in Mexico appears to be very ancient. The Romans developed large-scale breeding and raising of poultry for food, but the practice on that scale disappeared after the fall of the Roman Empire and did not reappear in Europe until the nineteenth century.

The first American poultry exhibition was held in Boston in 1849, and, in 1873, the American Poultry Association (APA) was founded, the oldest association of livestock breeders and growers in the United States. In 1905, the APA published the *American Standard of Perfection.* Now in its forty-fourth edition, published in 2015, the book is a wonderfully informative and entertaining illustrated guide to the ideal characteristics of more than 100 domestic fowl, ducks, geese, and turkeys.

The pigeon has had a dual role as a carrier and as a prized food. There were ancient pigeon posts in Babylon, and the bird was used as a carrier in early Egyptian dynasties. The use of carrier pigeons as messengers was common in Roman times and continued into the twentieth century until the invention of the radio and widespread use of the telegraph and telephone.

Falconry is enjoying a modest renaissance. Originating perhaps as long ago as 2000 B.C.E., the sport flourished in Europe in the Middle Ages, and the Crusaders introduced Islamic techniques that increased and refined European falconry. After a sharp decline in Peregrine Falcons and several small accipiters in Europe and North America in the 1960s, breeding and release programs arose; and now the ancient sport, with its historical tradition of studying and protecting birds of prey, is being revived.

The use of feathers as ornamentation was widespread among North and South American peoples, in Africa, and in the western Pacific from the earliest known times. The elaborate feather capes of the Hawaiian kings and the feather mosaics of the Mayas and Aztecs were extraordinary works of art. Among native North Americans, particular uses of feathers as badges of rank and status were common. Feather clothing was also common for protection from weather, much as goose down is widely used today.

Birds have always been influential in the arts. The earliest piece of English secular music of which we know, “Sumer Is Icumen In,” is a canon for four voices, and the words are those of the thirteenth-century lyric in which the cuckoo welcomes summer with its song. The cuckoo, nightingale, and quail are heard in Beethoven’s Sixth Symphony. The eighteenth-century composer Boccherini wrote a string quintet called “The Aviary,” perhaps the first complex composition in which a number of birds are imitated. Composers Maurice Ravel, Béla Bartók, and Olivier Messiaen used bird songs in their works for orchestra, voice, and piano.

Birds as subject and as metaphor are found frequently in opera. Wagner wrote an aria about owls, ravens, jackdaws, and magpies for *Die Meistersinger.* In Puccini’s *Madama Butterfly,* a character sings of a robin, and, in *La Bohème,* another sings of swallows. In what is probably the most popular aria in the most popular opera of all time, the “Habanera” in Bizet’s *Carmen,* the opening words are “Love is a rebel bird that no one is able to tame.”

An interesting confluence of the name of a musician—in this instance, the nickname—and the name of the music brought together one of the most memorable of American jazz musicians and one of the most memorable tunes: Charlie “Bird” Parker and “Ornithology.”

The role of birds in painting and sculpture is impressively large. Birds appeared in paleolithic cave paintings in France and Spain as early as 14,000 B.C.E. and in neolithic cave paintings in eastern Turkey 8,000 years later. In Egyptian tombs at Thebes, very accurate bird paintings appeared before 2000 B.C.E. In Knossos, on Crete, a well-known Minoan fresco of a partridge and a hoopoe survives from about 1800 B.C.E. Among the most vibrant and brilliantly colored Roman mosaics are those of birds, from Pompeii.

A remarkable work is an assemblage of bird species in a thirteenth-century illuminated manuscript of the Book of Revelation. Hieronymus Bosch’s *Garden of Delights* (about 1500) is filled with birds. Among twentieth-century artists, Matisse and Picasso showed recurring interest in birds, and Brancusi’s sleek birds in both chrome and stone are memorable.

Birds are ubiquitous in literature. For its perfect matching of avian and human characteristics, Aristophanes’ comedy *The Birds* has been described as an “ornithomorphic view of man.” Birds are prominent enough in Shakespeare’s plays and poems to have led the scholar James Harting to write an entire book on the subject, *The Ornithology of Shakespeare,* first published in 1871.

Some lyric poets were excellent ornithologists, notably the seventeenth-century Englishmen Michael Drayton and Andrew

Marvell, whose descriptions of birds are very precise. More recently, Shelley’s skylark, Keats’s nightingale, and Yeats’s swan have become the best-known birds in English literature.

Beginning as early as the fifteenth century, books with numerous bird illustrations began to appear. Bird illustrations continued through the centuries, with the Englishmen Mark Catesby and Thomas Bewick (both in the eighteenth century) and the American John James Audubon, whose four-volume work titled *The Birds of America* (1827–1830) is among the most prominent. By the turn of the twentieth century, a great flourishing that continues to this day was under way and served as an impetus to the rise of modern ornithology and field guidebooks.

Among the finest illustrators of the early twentieth century were Bruno Liljefors of Sweden, Archibald Thorburn of England, and Louis Agassiz Fuertes of the United States. Fuertes, with his unerring eye and his faultless sense of the remarkable characteristics of any bird, is believed by many to have made his birds more dazzlingly alive than any other painter. Standing on the shoulders of their predecessors, a host of brilliant and talented bird artists have created works that prevail in beautiful books, in wildlife art shows, and in modern field guides that continue to get better and better. Now supplementing the rich modern treasury of twentieth-century bird illustrations are amazing digital photographs and videos that Liljefors, Thorburn, and Fuertes could never have envisioned.

Early Ornithology

With all the disparate appeal of birds, it is little wonder that many human beings have chosen to study them, a study that has evolved into the modern science of ornithology. Aristotle’s fourth-century B.C.E. *History of Animals* is the first known effort in Western culture to systematically account for what we observe in nature, and the writing records the first organized scientific research. Birds figure prominently in all of Aristotle’s work in natural history. Alexander of Myndos, in the first century C.E., wrote a three-volume work on animals, two of which are about birds. Only fragments survive in quotation. Pliny the Elder (C.E. 23–79) produced an elaborate natural history encyclopedia in 37 volumes, all of which survive. He summarized the work of some 500 ancient authors and offered his own critical point of view. Aelian (C.E. 170–235), a Roman who wrote in Greek, gave much attention to birds in *On the Characteristics of Animals.*

Until the Renaissance, our knowledge of the natural history of birds depended largely on these and other ancient Greek and Roman writers. They told us much that was reliable, but they also left us with many erroneous notions. The quotations from Alexander’s work are based on close and accurate observation, but Aelian was steadfastly uncritical of his sources and perpetuated two remarkably wrong notions about the behavior of cranes: one, that they flew against the wind and swallowed a stone for ballast so as not to be swept off course; the other, that they posted sentinels at night, requiring them to stand on one foot while holding a stone in the other, thereby ensuring that, if the sentinel fell asleep, it would drop the stone and be awakened by the noise.

A major step toward modern ornithology was the growth of field observation in the eighteenth century. In 1789, Gilbert White, an English clergyman, published a natural history of his parish, gathered over 40 years’ time. His observations of birds were marvelously precise and beautifully expressed. But he also asked incisive questions about the basic biology of birds, about species, ecological niches, physiology, and migration. Many of his curiosities still pertain to research in ornithology. Contemporary ornithology has benefited from years of careful field observation by devoted amateurs who followed Gilbert White as well as by professional ornithologists.

Ornithology Today

Our knowledge of birds is more complete than that of most other classes of animals. Due in part to this wealth of information and in part to their attributes, birds feature prominently in primary biological studies. By the middle of the 1980s, birds provided more textbook examples of biological phenomena than any other class of vertebrates.

Advances in ornithology have been honored with some of the highest awards. The pioneering works of Niko Tinbergen on the evolution of behavior with gulls and of Konrad Lorenz with ducks and geese earned them a Nobel Prize in physiology or medicine. In cell biology and medicine, the discovery of B vitamins and their roles in nutrition came from studies of chickens, which readily reveal dietary deficiency. Albert Szent-Györgyi was awarded a Nobel Prize in physiology or medicine for the elucidation of the Krebs cycle from studies of pigeon breast muscle, as did Payton Rous for studies of avian sarcoma that linked viruses to cancer for the first time.

Broadly speaking, birds have been central to advances in speciation theory and the deciphering of historical relations. The greatest contribution of bird studies has been their role in increasing our knowledge of population and community ecology. Their contributions to evolutionary ecology and to behavioral ecology follow as a close second. Birds increasingly play central roles in advanced studies of breeding systems, including the dynamics of sexual selection, the roles of kinship and cooperation, and the often-subtle strategies employed to maximize lifetime reproductive success.

Grabbing headlines also are the regular revelations about how birds use their extraordinary senses. We cannot see color differences in the near ultraviolet without special equipment. Birds, on the other hand, use ultraviolet color differences to choose an attractive mate, to select the best foods, and to congregate with other members of the same species.

Birds have starred in the study of the interplay between inheritance and learning, mediated by the central nervous system. The early development of birdsong provides one of the best working models of how a complex, learned motor skill develops. Neurobiologists can track how specific parts of the brain’s song system participate in the process of song development. Research on neural pathways that control song and spatial memory in birds led to a major discovery: the fine structure of the adult brain is dynamic, not static. Adult songbirds can form new neurons, replace old ones, and reallocate brain space appropriately to seasonal efforts, whether relocating hidden seeds in the fall or learning new songs in the spring. The fundamental discovery of neural plasticity in birds ultimately contributed to medical research on new therapies for stroke in humans.

Birds have enormous conservation power. Their public appeal motivates millions of people to take time to observe them, to count them, to care about their well-being, and to act on their behalf. Added to their public appeal and economic power is their potential political power. Birds are sensitive barometers of the environment. Recall Rachel Carson's *Silent Spring* (1962), which ignited the modern era of positive environmentalism. Failures of seabird reproduction also heralded the El Niño phenomenon of the Pacific Ocean, which meteorologists now recognize as a driving force of annual climate events. More important now than ever before, birds are one of our best barometers of global climate change.

The science of ornithology is diverse, and so are ornithologists. Ornithology is a global science, which has been enriched by the contributions of ornithologists from every country and continent in the world. Throughout its history, ornithology has benefited from the critical scientific contributions of women. In 1931, the American ornithologist Florence Merriam Bailey (1863–1948) received the American Ornithologists' Union Brewster Award for her book *Birds of New Mexico.* Margaret Morse Nice (1883–1974), another Brewster Award winner, pioneered many of the approaches of modern behavior ecology with her close studies of the reproductive biology of Song Sparrows.

Throughout this book, we point out areas of exciting, recent progress in ornithology, and outstanding problems in our understanding of the biology of birds. Our highest hope is that students of the fourth edition of *Ornithology* will be inspired to make their own future contributions to our science and to conservation of birds in the decades to come. The future of ornithology is in *your* hands.

PART I *Origin and Diversity*

Hoatzin [© Geoff Jones 2010/barraimaging.com.au]

CHAPTER 1 *The Diversity of Birds*

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The hummingbirds (Trochilidae) are a diverse family of more than 300 species of hovering nectarivores that are found in North and South America. Hummingbirds evolved from within an adaptive radiation of nocturnal insectivores (Caprimulgiformes).

> It is easy to understand why so many of us are

> so fond of birds. They are lively; they are lovely; and they are everywhere.
> [Attenborough 1998, p. 7]

Millions of years ago, a bipedal theropod dinosaur evolved a novel and empowering structure—the feather. Feathered insulation enhanced its ability to control its high body temperature, thereby increasing its activity and endurance. Feathers evolved into diverse and complex structures, which lead to the evolution of flight. Mastery of flight opened a world of ecological opportunities, and a new group of vertebrates—the Class Aves—evolved, and then thrived. Today, the birds constitute the most species-diverse class of four-limbed vertebrates.

The biggest conservation challenge facing the world is that of maintaining the global fabric of biodiversity. As author David Quammen writes in his *Song of the Dodo* (1996), the global tapestry of life on Earth is in danger of unraveling as key ecological threads are broken. Birds are one of those threads. Birds move in vast numbers across the hemispheres, playing essential roles as consumers of insects, pollinators of flowers, and dispersers of seeds. Birds are pivotal players in ecosystem dynamics and provide essential services to human societies. Birds also serve as barometers of the health of ecosystems, pristine and altered, that serve mankind. Understanding their diversity, their ecology, their history, and their future will serve us well.

This chapter previews the major features of the diversity of birds: their basic form, function, and biology; their major kinds; and their geographical distribution. Chapter 2 examines the evolutionary origin of birds among the theropod dinosaurs and the diversification of birds from the oldest known fossil bird, *Archaeopteryx lithographica*, to modern birds themselves. Chapter 3 briefly considers the reconstruction of the phylogenetic relationships among living birds and recent advances in their classification.

1.1 Basic Characters of Birds

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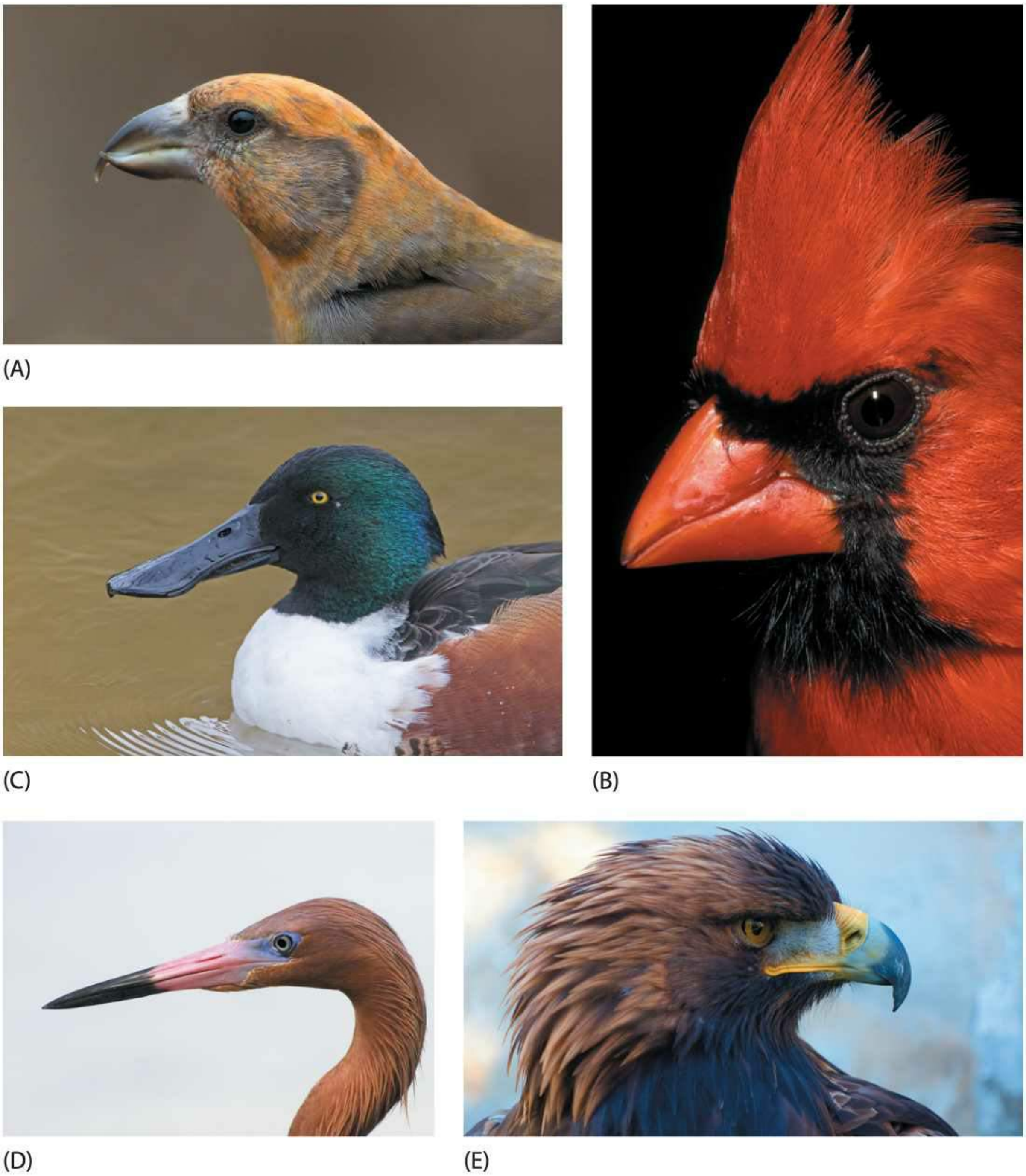
Figure 1–1 The King of Saxony Bird-of-Paradise displays its elaborate, flexible, enamel-blue head plumes.

Birds are two-legged (bipedal) vertebrates—the group of animals with backbones that also includes mammals, amphibians, other reptiles, and fishes. Despite their diversity of form, birds are a well-defined group of vertebrates. They are distinguished from other (living) vertebrates by feathers, which are unique outgrowths of the skin. Compared with the scales of reptiles, **feathers** are filamentous, soft in texture, flexible, lightweight structures with extraordinarily diverse functions (Figure 1–1). No comparable structures exist in other living vertebrates. Feathers are dead structures that wear easily, and they must be replaced regularly through molt. Feathers are essential for both temperature regulation and flight. They insulate the body, repel water, and help birds to maintain their high body temperature. Lightweight and strong, the long feathers of the wing generate lift and thrust for flight. The wide variety of feather colors and coloration patterns are used by birds for camouflage and for social and sexual communication.

All birds have beaks, or bills, a distinctive attribute that facilitates instant recognition. The avian **beak** varies greatly in form and function but is always toothless and covered with a horny sheath (Figure 1–2).

The avian beak has no exact parallel among other living vertebrates; it is approximated only by the snout of the duck-billed platypus, a strange, egg-laying mammal of Australia. However, beaks evolved convergently in Mesozoic birds, such as *Confuciusornis*, and in theropod dinosaurs, such as *Oviraptor*.

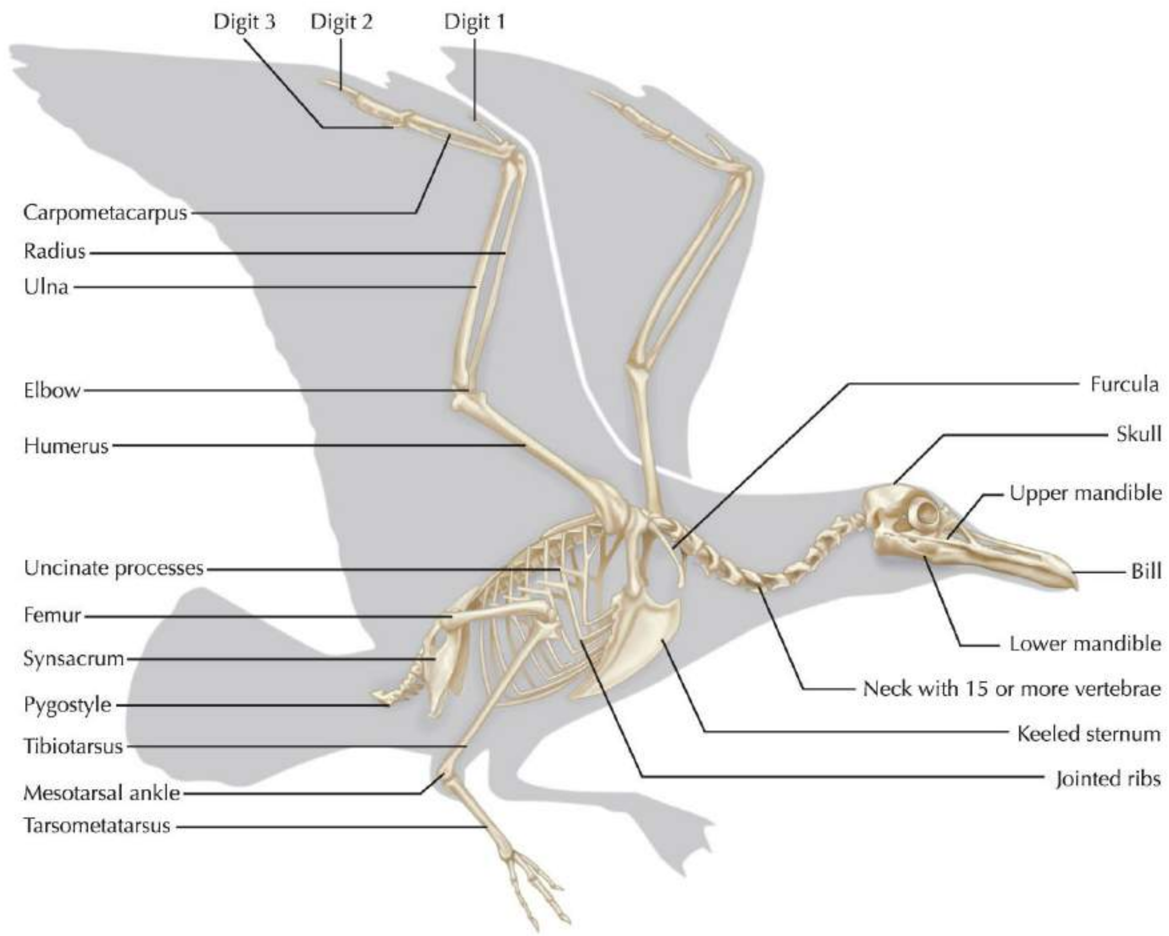


(A) Tom Kruissink/AGE Fotostock. (B) Doug Wechsler/VIREO. (C) FLPA/Paul Sawer/Getty Images. (D) Avalon/Picture Nature/Alamy stockphoto. (E) Jan Kovarik/EyeEm/Getty Images

Figure 1–2 The beaks of birds have evolved as adaptations to their dietary specialties. (A) Red Crossbills extract seeds from pine cones. (B) Northern Cardinals crack large, hard seeds. (C) Northern Shoveler ducks strain food from the mud. (D) Reddish Egrets either seize fish with a forceps grip or impale fish like a spear. (E) Golden Eagles tear apart the flesh of their prey.

Birds lack teeth that chew food before swallowing. Consequently, the avian digestive system is specialized to process unmasticated food. Instead of teeth, birds have a gizzard. The avian **gizzard**—a functional analogue of mammalian molars—is a large, strong, muscular structure used primarily for grinding and digesting tough food. The gizzards of grain eaters and seed eaters, such as turkeys, pigeons, and finches, are especially large and have powerful layers of striated muscles. Turkey gizzards can pulverize English walnuts, steel needles, and surgical lancets. The internal grinding surfaces of the gizzard are covered with a rough pleated or folded surface with many grooves and ridges. In some pigeons, it has strong, tooth-shaped projections. The gizzard can also contain large quantities of grit, which grinds food. The gizzards of moas, extinct ostrichlike birds of New Zealand, have been found to contain as much as 2.3 kilograms of grit. Gizzard stones are also common in nonavian dinosaurs, crocodiles, and alligators. The existence of gizzard stones probably allowed living birds to lose their teeth. The gizzard is not so muscular in birds that eat softer foods, such as meat, insects, or fruit, and in raptors and herons, it may take the form of a large thin-walled sac.

Birds are feathered flying machines (Figure 1–3). Wings and the ability for powered flight evolved convergently in extinct pterosaurs, the bats, and the insects, but the feathered wings of birds provide them with an extraordinary flight capacity.



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DATA FROM PASQUIER 1983

Figure 1–3 Avian skeletal anatomy and flight adaptations. Supporting the wings of the Herring Gull is a strong but lightweight skeleton. An enlarged, keeled sternum houses and anchors the large breast muscles that empower the wings. The bones of the hand and wrist, which support and maneuver the primary flight feathers, are reduced in number and fused for extra strength. Similarly, the pygostyle, made of fused tail vertebrae, supports and controls the tail feathers, which are used for braking and steering. Strengthening the body skeleton are fusions of the pelvic bones and associated vertebrae to form the synsacrum, and horizontal rib projections called uncinate processes. The furcula, or wishbone, compresses and rebounds like a powerful spring in rhythm to the beat of the wings.

The structure of the avian body has extensively evolved for flight. Bird bones, for example, are typically lightweight structures, being spongy, strutted, and hollow. The skeleton generally is strengthened and reinforced through fusions of the bones of the hands, head, pelvis, and feet. Horizontal, backward-curved projections—called **uncinate processes**—on the ribs overlap other ribs and so strengthen the walls of the body. The **furcula,** or wishbone, compresses and rebounds like a powerful spring in rhythm to the beat of the wings. The wing itself is a highly modified forelimb that, with a few remarkable exceptions, is nearly incapable of functions other than flight. The **carpometacarpus,** or fused hand bones, supports and maneuvers the large and powerful primary flight feathers.

Like other dinosaurs, the avian ankle joint is positioned in the middle of the foot (or tarsal) bones. On either side of the ankle, birds have unique, fused leg bones called the **tibiotarsus** and **tarsometatarsus.** For stable balance on land, a bird’s center of gravity is positioned directly over and between its feet, particularly when the bird perches, squats, or rises (Figure 1–4). The equal length of the tibiotarsus and tarsometatarsus of long-legged birds ensures this relation. Foot-propelled diving birds, such as loons and grebes, have much shorter upper leg bones (femurs), giving them considerable swimming abilities but greatly compromising their balance on land. For efficient propulsion, they have powerful legs situated at the rear of a streamlined body, placing their center of gravity far forward of their feet when on land.

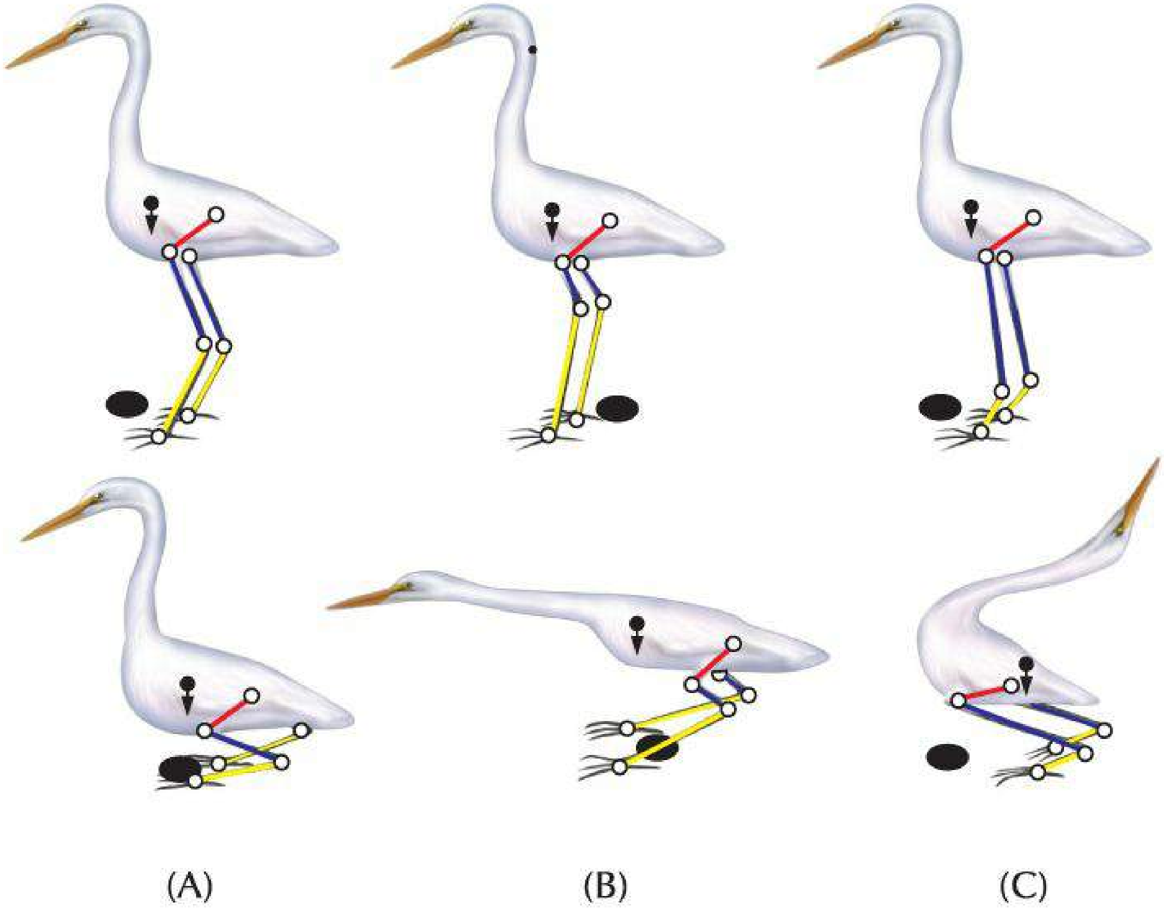

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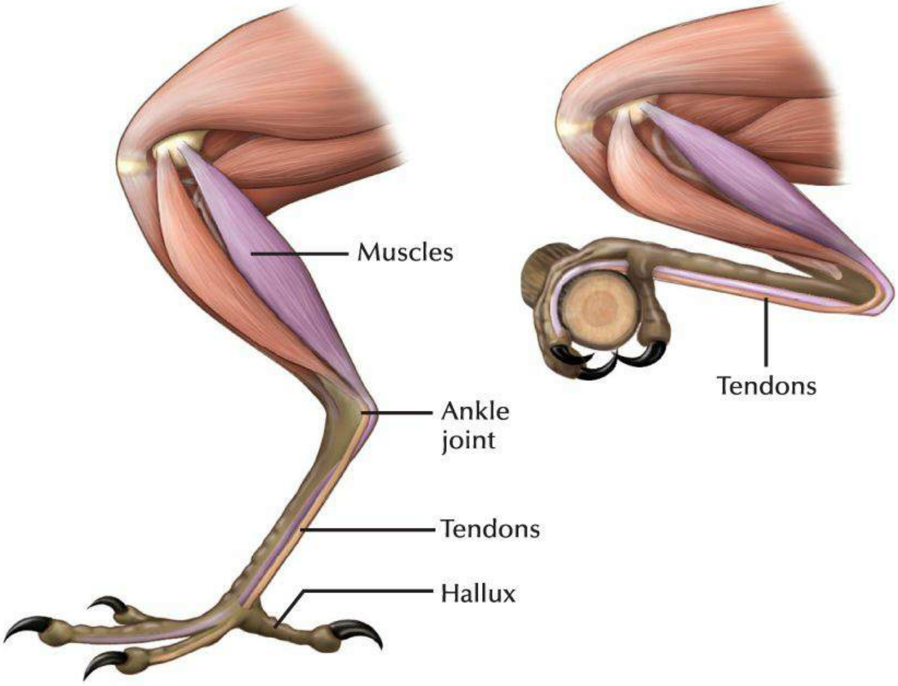
Figure 1–4 (A) Leg bones of equal lengths contribute to the balance of long-legged birds. When a bird crouches to incubate its egg, for example, leg bones of different lengths (B and C) would displace the center of gravity (↓). What appears at first glance to be a backward-bending knee joint is really the ankle joint. In birds, the foot bones (three tarsals) are fused both to one another and to the metatarsals, thereby creating a long, strong, single leg element, the tarsometatarsus, which enables birds to walk on their toes rather than on the whole foot.

Birds do not have very fleshy feet. Instead, the muscles that move the feet and toes of birds are all located on the upper leg. The muscles control the feet with long tendons that pass around the backside of the ankle joints. When a bird bends its joints to squat, the tendons automatically flex, locking the toes around the branch (Figure 1–5). When a bird stands, the tension relaxes and the toes open. The foot of the perching birds—Order Passeriformes—is perhaps the most advanced in this respect. A special system of ridges and pads between the tendons that flex the toes and the insides of the toe pads acts as a natural locking mechanism and permits birds to sleep while perching. The large, reversed, opposable first rear toe, or **hallux,** enhances the ability of birds to grip a branch or prey item and is unique among vertebrates.



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DATA FROM WILSON 1980

Figure 1–5 When a perching bird squats, the leg tendons, which are located on the rear side of the ankle, automatically cause the toes to grip.

Avian physiology accommodates the extreme metabolic demands of flight and temperature regulation. The red fibers of avian flight muscles have an extraordinary capacity for sustained work and can produce heat by shivering (Chapter 6). Birds are **endothermic**; that is, they are warm-blooded and maintain high body temperatures (40°–44°C) over a wide range of ambient temperatures. The circulatory and respiratory systems of birds include a powerful four-chambered heart and efficient, unidirectional lungs, which deliver fuel and remove both waste and heat produced by metabolic activities.

The reproductive systems of birds also are unusual. Birds produce large, external **eggs** that are richly provisioned with a large yolk and protected by a hard shell of calcium carbonate. Avian eggs are the most elaborate reproductive cells of any animal. Unlike all other classes of vertebrates, no bird species bears live young. Nurturing the growth of the embryos in the eggs and of the young after they hatch requires dedicated parental care. Most birds form monogamous pair bonds, some for life, but many, it turns out, engage in additional sexual liaisons. As a result, the eggs in one nest may be of mixed paternity or, more rarely, mixed maternity. Mating systems, spacing behavior, and cooperation afford varied solutions to the challenges of successful reproduction in a highly competitive and unpredictable social and ecological world.

Birds have large, well-developed brains, six to 11 times as large as those of like-sized reptiles, and are more intelligent than many mammals. Bird brains and primate brains exhibit functional lateralization, with left-hemispheric dominance associated with learning and innovation in vocal repertoires. Substantial learning by birds guides the mastery of complex motor tasks, social behavior, and vocalizations.

Highly developed neural systems and acute senses in birds mediate feats of communication and navigation. Birds, particularly the songbirds, have the greatest sound-producing capabilities of all vertebrates. The **syrinx** of birds is a unique sound-producing structure, and it provides birds with more complex and diverse sound production capabilities than any other animals. In contrast with the syrinx, the sound-producing larynx of mammals constrains mammalian vocalizations by its structural simplicity. The larynx is homologous with the avian hyoid apparatus, which became the bony tongue of birds. The syrinx evolved only after the evolution of the avian bony tongue led to selection for a new vocal sound production apparatus.

Birds can navigate by using the Earth’s magnetic field and celestial cues. The highly developed color vision of birds reaches into the near-ultraviolet range of the spectrum and provides birds with an entirely new dimension of color perception, including complex colors that humans cannot even imagine, like ultraviolet-yellow and ultraviolet-green. The broad hearing range of various birds encompasses both infrasound and ultrasound—frequencies below and above the hearing range of humans.

1.2 Adaptive Radiation of Form and Function

Roughly 300 billion birds now inhabit the Earth. The variety of birds is the grand result of millions of years of evolutionary change and adaptation. The current classification of living birds arranges 40 orders, 247 families, 2,312 genera, and at least 10,699 species (Table 1–1). Yet this number is only a small fraction of the number of species that have existed since the age of dinosaurs. The earliest birds in the Mesozoic era more than 150 million years ago had feathers and probably could fly after a fashion. Responding to ecological opportunities, subsequent birds diversified in form and function. From the fundamental anatomy of their common ancestor evolved terrestrial game birds, such as quail and tinamous; aquatic divers, such as penguins; oceanic mariners, such as albatrosses; shoreline waders, such as plovers; diurnal predators, such as hawks, vultures, and falcons; terrestrial predators, such as seriemas; perching songbirds, such as robins; nocturnal forest hunters, such as owls and nightjars; and large, flightless ground birds, such as the ostrich and emus (Figure 1–6). Birds range in size from only two grams (hummingbird) to 100,000 grams (ostrich).

Table 1–1 *A Higher Classification of Modern Birds*

Order	Members (Species No.)	Comments
Paleognathae	Ratites	The paleognaths are the sister group to the rest the living birds.
Struthioniformes	Ostriches (2)	

Rheiformes	Rheas (2)	
Apterygiformes	Kiwis (5)	Kiwis are sister to tinamous/emus and cassowaries.[1,2]
Casuariiformes	Emus, cassowaries (4)	
Tinamiformes	Tinamous (47)	Tinamou relationships with the ratites are uncertain[3,4,5] but are treated provisionally as sister to emus and cassowaries.[2]
Neognathae		The neognaths are the sister group to the paleognaths.
Galloanseres		Landfowl (Galliformes and waterfowl (Anseriformes) togethe (Galloanseres) are siste to all other neognath birds (Neoaves).
Galliformes	Landfowl: grouse, quail, pheasants, francolins, guineafowl, moundbuilders (300)	Landfowl (Galliformes are sister to the waterfowl (Anseriformes).
Anseriformes	Waterfowl: ducks, geese, swans, screamers	Waterfowl (Anseriformes) are siste to the landfowl (Galliformes).

	(177)	
Neoaves		Neoaves includes three major components: (1) basal unresolved polytomy of at least nin orders, (2) a core waterbird clade (Aequornithes) and (3) core land bird clade (Telluraves).[2,6]
Caprimulgiformes	Nightjars, frogmouths, potoos, oilbirds, owlet-nightjars, swifts, hummingbirds (602)	The Caprimulgiform nightbirds define a spectacular adaptive radiation of nocturnal and diurnal Neoaves. Swifts and hummingbirds were previously placed in the Apodiformes.
Musophagiformes	Turacos (23)	Turacos are sister to bustards (Otidiformes) and cuckoos (Cuculiformes)[2] or to th bustards alone.[7]
Otidiformes	Bustards (26)	Now in their own order the bustards are sister group to the turacos (Musophagiformes)[7] or the cuckoos (Cuculiformes).[2]
Cuculiformes	Cuckoos (149)	Cuckoos are sister to th bustards (Otidiformes)[2] or the turacos (Musophagiformes).[7]

Mesitornithiformes	Mesites (3)	Now in their own order the Mesites of Madagascar are sister t sandgrouse (Pterocliformes) and, i turn, pigeons (Columbidae).[2,3,7]
Pterocliformes	Sandgrouse (16)	Sandgrouse are sister t the Malagasy mesites (Mesitornithiformes).[2,
Columbiformes	Pigeons (344)	Pigeons are the sister group to an Old World clade consisting of sandgrouse (Pterocliformes) and th mesites (Mesitornithiformes). Together they form the clade Columbimorphae at or near the base of Neoaves.[2,3,7]
Gruiformes	Diverse terrestrial marshbirds: rails and allies, flufftails, finfoots, cranes, limpkin, and trumpeters (188)	The revised monophyletic Gruiformes now includes seven families rails (Rallidae), flufftai (Sarothuridae), finfoots (Heliornithidae), crane (Gruidae), Limpkin (Aramidae), and trumpeters (Psophiidae).[2,3]
Podicipediformes	Grebes (23)	Grebes and flamingos (Phoenicopteriformes) are ancient sister taxa

		and members of the basal polytomy, or potentially related to shorebirds (Charadriiformes).[2,3,8]
Phoenicopteriformes	Flamingos (6)	Flamingos and grebes (Podicipediformes) are ancient sister taxa, potentially related to shorebirds (Charadriiformes).[2,3,8]
Charadriiformes	Shorebirds and relatives: sandpipers, plovers, phalaropes, stilts, jacanas, painted-snipes, pratincoles, gulls and terns, seedsnipes, sheathbills, skimmers, skuas, auks (383)	Shorebirds and diving birds in the Charadriiformes are an extraordinary adaptive radiation of waterbirds.
Eurypygiformes	Sunbittern, Kagu (2)	The Sunbittern and Kag are removed from the Gruiformes to a new Order Eurypygiformes, which is sister to the tropicbirds (Phaethontiformes). Th combined group is siste to the core waterbird clade.[2,3]

Phaethontiformes	Tropicbirds (3)	Tropicbirds together with Sunbittern and Kagu (Eurypygiformes) are sister to the core waterbird clade.[2]
Aequornithes	Core waterbirds	
Gaviiformes	Loons (5)	Loons are the sister group to penguins (Sphenisciformes) + tube-nosed seabirds (Procellariiformes).[2]
Sphenisciformes	Penguins (18)	Penguins are sister to th tube-nosed seabirds (Procellariiformes).
Procellariiformes	Tube-nosed seabirds: petrels, shearwaters, albatrosses, storm petrels, diving petrels (147)	The tube-nosed seabird are sister to penguins (Sphenisciformes). Albatrosses are the siste group to all other tubenoses.[2,3] The two families of storm petrel and the diving petrels a embedded within other petrels.
Ciconiiformes	Storks (19)	The Ciconiiformes includes only the storks (Ciconiidae). Ibises and spoonbills (Threskiornithidae) and

		herons (Ardeidae) are members of the Pelecaniformes.[2,3,7]
Suliformes	Totipalmate water and diving birds: frigatebirds, cormorants, anhingas, boobies (61)	The Suliform waterbird are sister to the wading birds and pelicans (Pelecaniformes).[2]
Pelecaniformes	Ibis, herons, pelicans, Hammerkop, Shoebill (118)	The relationships amon Pelecaniform families remain uncertain.[2,3]
Opisthocomiformes	Hoatzin (1)	The Hoatzin is one of t most ancient, living bir lineages.[2]
Telluraves	Core land birds	
Accipitriformes	Raptors including New World vultures (266)	Raptors (Accipitriformes) are basal members of the core land birds clade. New World vultures ar the sister group to all other Accipitriformes.[2]
Strigiformes	Owls (243)	Owls are basal member of the core land birds.
Coliiformes	Mousebirds (6)	Mousebirds are basal members of the core land birds.
Leptosomiformes	Cuckoo Roller	Formerly placed in the

	(1)	Coraciiformes, the Cuckoo Roller is the only member of an ancient lineage of land birds that is the sister group to the Trogoniformes, Bucerotiformes, Coraciiformes, and Piciformes.[2,3]
Trogoniformes	Trogons, quetzals (43)	Trogons are embedded in the core land birds as the sister group to Bucerotiformes, Coraciiformes, and Piciformes.[2]
Bucerotiformes	Hornbills, hoopoes, wood hoopoes (74)	Separation of the hornbills and hoopoes from the Coraciiformes as the Order Bucerotiformes maintains monophyly o the Coraciiformes.[2,3]
Coraciiformes	Kingfishers and allies: rollers, todies, motmots, bee-eaters (177)	The kingfishers, rollers and allies form the siste group to the monophyletic Piciformes.[2]
Piciformes	Woodpeckers and allies: jacamars, puffbirds, honey guides, puffbirds, honeyguides, barbets,	The diverse, monotypic Piciformes includes woodpecker relatives worldwide.[2,3]

	toucans (445)	
Australaves	Terminal land bird clade	
Cariamiformes	Seriemas (2)	Seriemas are removed from the traditional Gruiformes to their ow order and sister group t the large land bird clad Australaves.[2,3,7]
Falconiformes	Falcons (67)	The falcons and caracaras (Falconiformes) are no close relatives of other raptors (Accipitriforme but rather a separate lineage that is sister to the parrots (Psittaciformes) and perching birds (Passeriformes).[2,3,7]
Psittaciformes	Parrots (398)	Parrots (Psittaciformes are the sister group to t perching birds (Passeriformes).[2,3,7]
Passeriformes	Perching birds (6,456)	The perching birds (Passeriformes) include the majority of all bird species. The New Zealand wrens (Acanthisittidae) are th sister group to all other passerines, including th suboscines and oscines.

Data from: [1]Cracaft (2013); [2]Prum et al. (2015); [3]Hackett et al.

(2008); [4]Baker et al. (2014); [5]Haddrath and Baker (2012); [6]Suh. (2016); [7]Jarvis et al. (2014); [8]Mayr (2011).

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Figure 1–6 Birds have evolved a great diversity of body types in response to natural selection for a variety of ecologies and modes of life, including (A) terrestrial gamebirds, such as quail and tinamous; (B) wing-propelled aquatic divers, such as penguins; (C) oceanic mariners, such as albatrosses; (D) shoreline waders, such as plovers; (E) diurnal predators, such as hawks, vultures, and falcons; (F) terrestrial predators, such as seriemas; (G) perching songbirds, such as jays; (H) nocturnal forest hunters, such as owls and nightjars; and (I) large, flightless ground birds, such as the emus and ostrich.

The diversity of birds is due to the evolution of various species adapted to different ecologies and behaviors, a phenomenon called **adaptive radiation.** Beak sizes and shapes evolve in relation to the types of food in the diet. Leg lengths evolve in relation to habits of perching or terrestrial locomotion, and wing shapes evolve in relation to modes of flight. For example, from a single ancestral species of shorebird evolved aerial pirates, such as skuas, and plunging divers, such as terns, as well as a host of long-legged wading birds, including sandpipers, plovers, turnstones, stilts, jacanas, snipes, stone curlews, woodcocks, curlews, and godwits, each with characteristic leg lengths and beak lengths, shapes, and curvatures. As varied as the habitats that they occupy, shorebirds also include aerial pratincoles, gulls, and skimmers, deep-water divers such as puffins, and the grouselike seedsnipes of South American moorlands. All these related species are members of the Order Charadriiformes (Figure 1–7).

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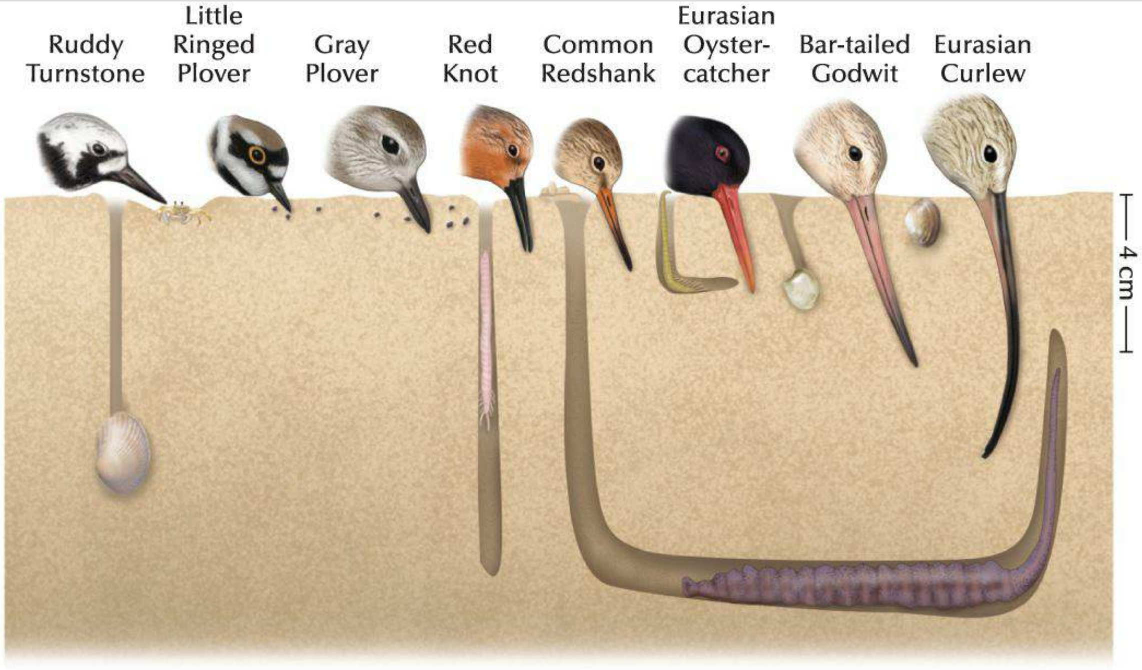
Figure 1–7 Shorebirds, gulls, and allies (Order Charadriiformes): (A) Pheasant-tailed Jacana (Jacanidae); (B) Snowy Sheathbill (Chionidae); (C) Eurasian Woodcock; (D) Eurasian Curlew (Scolopacidae); (E) Blacksmith Lapwing (Charadriidae); (F) Collared Pratincole (Glareolidae); (G) Ring-billed Gull (Laridae); (H) Black Skimmer (Rynchopidae); and (I) Atlantic Puffin (Alcidae).

The varied diets of modern birds include invertebrates of all sizes; vertebrates of many kinds, including carrion; and fruits, nectar, seeds, buds, and leaves. Insects, seeds, and fruits nourish the majority of bird species, especially the passerine land birds. Few birds are specialized herbivores; perhaps mammals have usurped most of the terrestrial grazing and browsing niches. In the absence of mammals in New

Zealand, numerous species of flightless, herbivorous moas evolved. Efficient digestion of low-calorie plant matter often involves the evolution of large body size, which may limit the flying abilities of avian herbivores or favor flightlessness, as in ostriches, emus, rheas, and moas.

Corresponding to a diversity of diets is a diversity of beak shapes (see Figure 1–2). A bird’s beak is a key adaptation for feeding. The size, shape, and strength of the bill prescribe the potential diet. The land carnivores—eagles, hawks, falcons, and owls—have strong, hooked beaks with which they tear flesh and sinew. Other beak types tear meat, spear fish, crack seeds, probe crevices, or strain microscopic food from the mud. The broad, flat beak of a duck is suitable for straining mud, whereas the chisel-like bill of a woodpecker is suitable for digging into trees to reach insects. Marine predators, such as penguins and cormorants, have internal mouth cavities with curved projections that direct fish toward the esophagus. The varied lengths and curvatures of shorebird beaks determine which prey they can reach by probing into the mud (Figure 1–8). Nectar feeders, such as hummingbirds, probe their long, thin beaks into floral nectar chambers and draw up nectar through tubed tongue tips. Their beak shapes coevolve with the lengths and curvatures of preferred flowers, which depend on the birds for pollination (Figure 1–9). Even slight differences in beak dimensions influence the rate at which food can be consumed.



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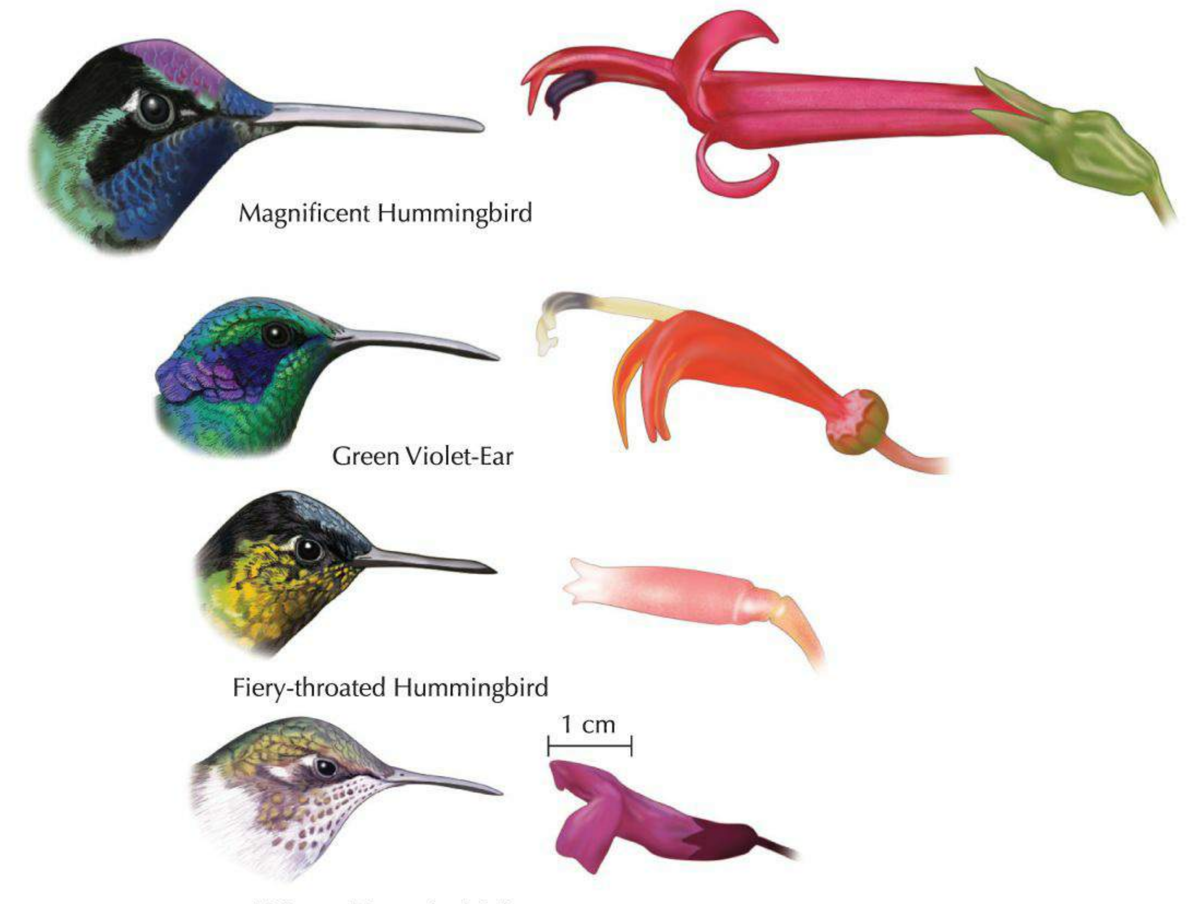
DATA FROM GOSS-CUSTARD 1975

Figure 1–8 Varied bill lengths enable shorebirds to probe to various depths in the mud and sand for food. Plovers feed on small invertebrates, mainly by surface pecking with their short bills. Common Redshanks and other species of waders with moderate bill lengths probe the top four centimeters of the substratum, which contain many worms, bivalves, and crustacea. Only the long-billed birds, such as curlews and godwits, can reach deep-burrowing prey, such as lugworms.



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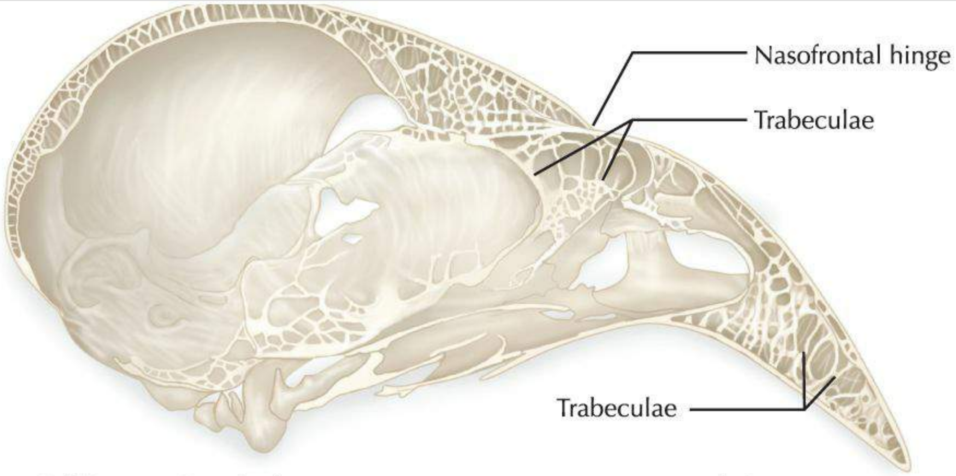
DATA FROM WOLF ET AL. 1976

Figure 1–9 The lengths and shapes of hummingbird bills coevolve with those of their preferred flowers.

The bones of the avian beak, jaws, and palate are an engineer's delight. The upper mandible, or **maxilla,** is a flattened, hollow, bony cone reinforced internally by a complex system of bony struts called **trabeculae** (Figure 1–10). These struts make the beak much stronger than a hollow mandible but add little weight. The lower mandible is composed of three bones fused together. Covering both jaws is a horny sheath, or **rhamphotheca,** which may have sharp cutting edges (as in boobies), numerous toothlike serrations (as in mergansers), or well-developed notches (as in falcons and toucans). The beak is not rigid.

Many birds can flex or bend the upper half of the bill at the nasofrontal hinge (see Figure 1–10), an ability called **cranial kinesis** (Zusi 1984). Woodcocks can open just the tip of their bills to grasp earthworms deep in the mud. The flexible lower mandibles of pelicans bow like a seine net for scooping fish into its gular pouch (Figure 1–11).



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DATA FROM BOCK 1966

Figure 1–10 The form of their large bills enables finches such as the Northern Cardinal to bite hard seeds without straining the nasofrontal hinge (located between bill and skull) with excessive shear forces. Shown here is a cross section of a cardinal skull, revealing the bony struts (trabeculae) in the upper jaw and forehead. Lower jaw is not shown.

ZIMMYTWS/SHUTTERSTOCK.COM

Figure 1–11 The pelican uses its flexible lower mandible, which bows as its gular pouch extends, like a seine net for scooping fish.

The diversity of beak shapes that can evolve through adaptive radiation is exemplified by the Hawaiian honeycreepers, which apparently evolved from a single flock of small cardueline finches that strayed out over the Pacific Ocean from Asia or North America more than 5 million years ago. The finches made landfall on one of the more ancient Hawaiian Islands, then flourished and spread throughout the growing archipelago. Isolated populations changed in genetic composition and appearance, at first imperceptibly and then conspicuously. Subtle changes in bill shapes and sizes led to a proliferation of bill types and their related feeding behaviors: from heavy grosbeak-like bills for cracking large legume seeds to long sicklelike bills for sipping nectar from flowers or probing bark crevices for insects (Figure 1–12). Various lineages of honeycreepers diversified along with different groups of flowering plants that also dispersed to the Hawaiian Islands from distant continents.

Figure 1–12 A classic example of an explosive adaptive radiation. As a result of natural selection for a diversity of diets in isolation on the Hawaiian Islands, Hawaiian honeycreepers have evolved bills that range from thin warblerlike, insect-feeding bills to long, sicklelike nectar-feeding bills to heavy, seed-cracking grosbeak-like bills.

Different modes of locomotion further expand the ecological opportunities of birds. Shorebirds, as already mentioned, include aerial, wading, and wing-propelled diving species. Birds soar through the sky, scurry and stride across the land, hop agilely from branch to branch, hitch up or down tree trunks, and swim powerfully to great depths in the sea with their feet or with their wings. The combination of forelimbs adapted for flight and hindlimbs for bipedal locomotion gives birds a tremendous range of ecological options.

There are specialized flying birds, as well as specialized swimmers, runners, waders, climbers, and perchers. Wing shapes and modes of flight range from the long, narrow wings of the albatross, adapted for soaring over the oceans, to the short, round wings of wrens, adapted for agile fluttering through dense vegetation. At another extreme are the adaptations of wing-propelled diving birds, such as penguins, which use their flipperlike wings to move underwater (Figure 1–13).

(A) Paul Souders/Corbis Documentary/Getty Images. (B) Cagan H. Sekercioglu/Getty Images. (C) James Hager/robertharding/Getty Images. (D) Steve Bloom Images/Alamy Stock Photo. (E) Khoroshunova Olga/Shutterstock.com

Figure 1–13 Penguins have wing adaptations for wing-propelled diving: (A) Chinstrap Penguin; (B) Rockhopper Penguin; (C) African Penguin; (D) King Penguin, juvenile (*left*), adult (*right*); and (E) Little Blue Penguin.

Like the structures of bills and wings, the anatomy of feet and legs corresponds to different lifestyles (Figure 1–14). At one extreme are the long, powerful legs of wading and cursorial (or running) birds, such as storks and ostriches. At the other extreme are the tiny feet and short legs of aerial specialists, such as swifts. The long toes of herons and jacanas spread the bird’s weight over a large surface area and facilitate walking on soft surfaces. Sandgrouse scurry on soft desert sands, and ptarmigan can walk on snow by virtue of feathery, snowshoelike adaptations of their feet. Lobes on the toes of coots and webbing between the toes of ducks aid swimming. Climbing birds, such as woodpeckers, have large, sharply curved claws; nuthatches climb downward by gripping a tree’s bark with a large claw on the hind toe.

(A) Duck (B) Blue-footed Booby (C) Coot

(D) Ostrich (E) Pheasant

(F) Ptarmigan (G) Heron (H) Woodpecker

(I) Eagle (J) Warbler

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DATA FROM WILSON 1980

Figure 1–14 The feet of birds reveal their ecological habits. Many waterbirds have (A) partially webbed, (B) completely webbed, or (C) lobed toes for swimming; terrestrial birds have toes specialized for (D) running, (E) scratching in dirt, (F) walking on snow, or (G) wading. Other land birds have feet designed for (H) climbing trees, (I) holding prey, or (J) perching.

1.3 Life Histories

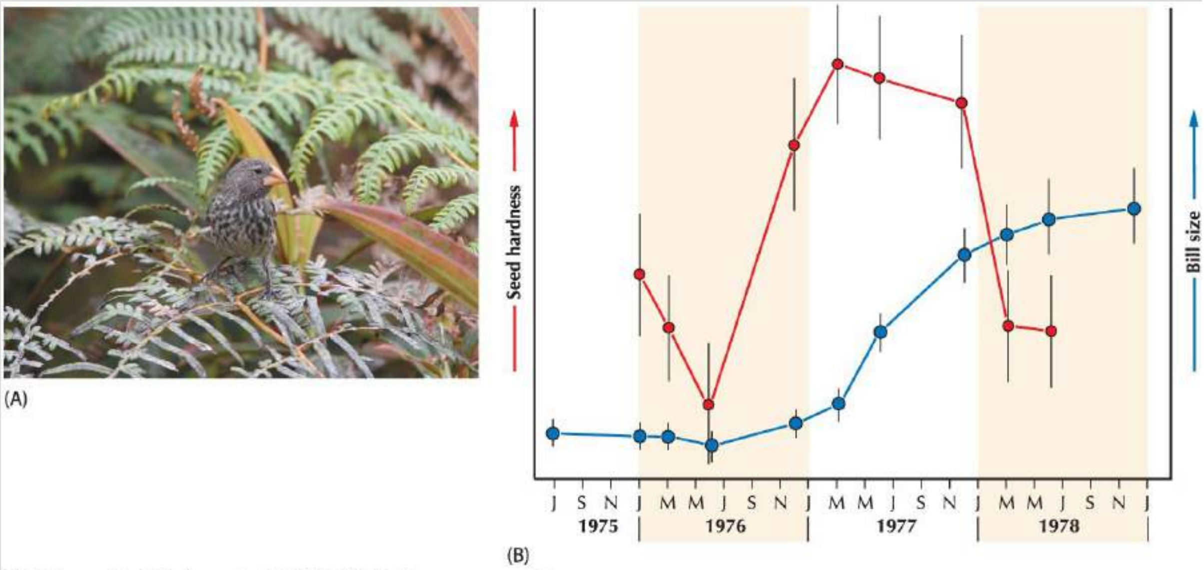
In addition to their form and function, birds have diversified in all aspects of their seasonal and social biology. Reproductive rate, adult life span, and age at maturity differ more than 10-fold among species (Ricklefs 2000a). Large albatrosses are long-lived, lay only one egg at a time, and breed only every other year. In temperate climates, small songbirds, instead, tend to have short life spans and to raise many young together. Some species lay large eggs for their body size; other species lay small and lightly provisioned eggs. Newly hatched young may be helpless or agile. Parental care may be minimal or prolonged. Such attributes of life history contribute to an individual bird's lifetime reproductive success. They are as subject to evolutionary molding by the environment and by population dynamics, as are the shapes of bills and wings.

1.4 Natural Selection and Convergence

The close fit between the form and function of the organism and its environment, portrayed so vividly by the diversity of birds and their life-history traits, is the product of evolutionary **adaptation** through natural selection. As set forth by Charles Darwin in 1859 and confirmed subsequently through experiment, independent observation, and comparative analysis, **natural selection** is simply the differential survival of individual organisms with advantageous traits. If the advantageous traits that contribute to survival are heritable, then natural selection will result in adaptive evolutionary change among generations. Well-adapted individuals live longer and leave more offspring than other individuals. Camouflaged chicks are more likely to escape predation and to reproduce themselves than are boldly colored chicks. To be favored by natural selection, however, traits need not be dramatically better. Subtle or slight advantages will increase in prevalence within a local population. Adaptation by natural selection is a process without plan or purpose—a process that can transform the appearances and abilities of organisms.

A classic example of adaptive evolution by natural selection is the evolution of beak shape in Darwin’s Finches, first proposed by Charles Darwin and confirmed by observation of natural experiments by Peter and Rosemary Grant and colleagues. A large finch bill can be so advantageous in times of food shortage that the average bill size in a population increases from one year to the next (Boag and Grant 1981). In 1976 and 1977, a severe drought gripped Daphne Island in the

Galápagos archipelago. Plants failed to produce new crops of seeds, and seed densities dropped sharply, especially the densities of small seeds. Many finches starved. In the Medium Ground Finch (*Geospiza fortis*), individual birds with large, deep bills survived in greater numbers than did those with small bills because these large-billed birds could more easily crack the remaining larger, harder seeds. The result was the evolution of a dramatic increase in average bill size over only one year's time due to natural selection (Figure 1–15). This intense natural selection was later reversed by the improved survival of small-billed birds during wet years, when small seeds were again plentiful.



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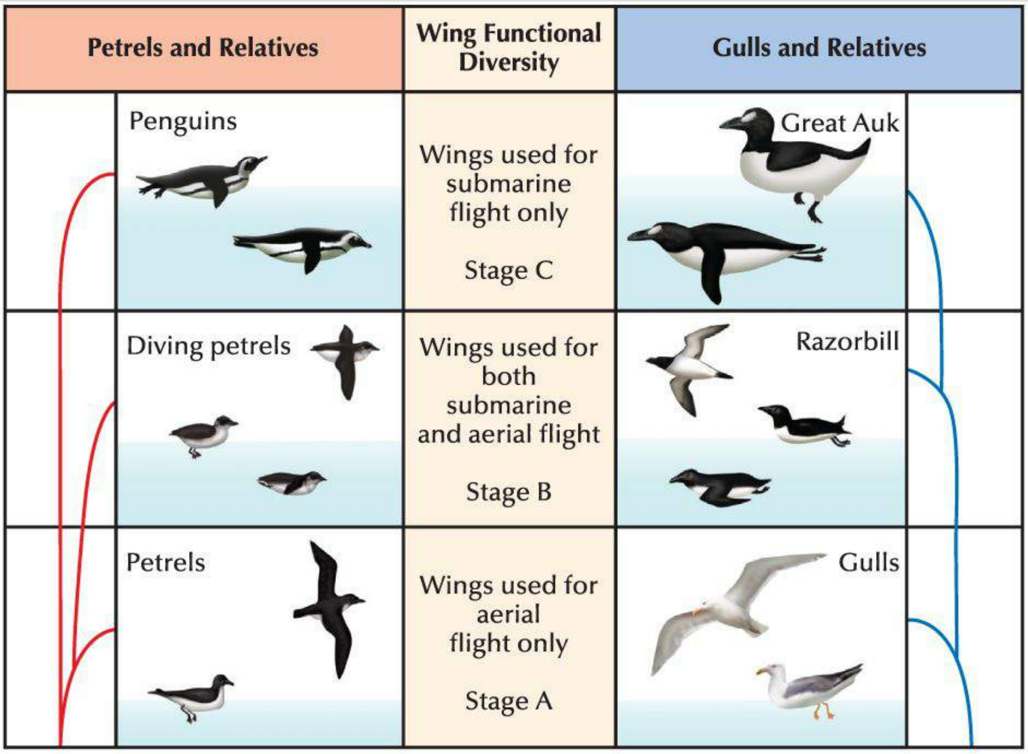
(A) © Geoff Jones/barraimaging.com.au. (B) Data from Boag and Grant 1981

Figure 1–15 Evolution of beak shape in Medium Ground Finch on the Galápagos Islands. (A) Medium Ground Finch. (B) Drought caused a failure of the usual seed crop on Daphne Island leading to a rapid increase in seed hardness (red). Large bill size of the Medium Ground Finch evolved rapidly in reponse to intense natural selection (blue). Abbreviations, starting at left on *x*-axis: J, June; S, September; N, November; J, January; M, March; M, May.

The power of natural selection is perhaps best demonstrated through

convergence—the independent evolution of similar adaptations in unrelated organisms. Adaptation to similar ecological roles causes unrelated species of birds to become superficially similar (i.e., to converge) in details of appearance and behavior. For example, large, seed-eating, finchlike beaks have evolved convergently and independently in numerous different families of perching birds, including New World sparrows, Old World sparrows, cardinals, tanagers, weaver birds, larks, parrotbills, and manakins. Another classic case of convergence is that of the auks of the northern oceans and the penguins of the southern oceans. From different aerial ancestors, species of compact black-and-white seabirds have evolved in both ocean regions, including flightless forms that use their wings to propel themselves underwater to capture marine crustaceans and fish (Figure 1–16).



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DATA FROM STORER 1960

Figure 1–16 Convergent evolution of wing-propelled divers. Adaptive stages in the parallel evolution of two independent origins of wing-propelled diving in birds, in the petrels and penguins, and the gulls and auks, respectively.

1.5 Biogeography

Biogeography is the study of the geographical distributions of plants and animals. For more than a century, biogeographers have divided Earth into six major faunal regions corresponding roughly to the major continental areas (Figure 1–17). Each faunal region has its characteristic birds: so-called **endemic** taxa or species, which are found nowhere else, and other birds that represent major adaptive radiations of more widespread taxa. Waxwings and loons are restricted to North America and Eurasia, the Nearctic and Palearctic regions, respectively. The birds that are endemic to tropical Africa, or the Afrotropical region, include guineafowl, mousebirds, and turacos. Australia and New Guinea, the Australasian region, have emus, honeyeaters, and birds-of-paradise. Tropical South Asia, the Indomalayan region, has fairy-bluebirds and leafbirds. South and Central America, the Neotropical region, have toucans, tinamous, trumpeters, and the Hoatzin.

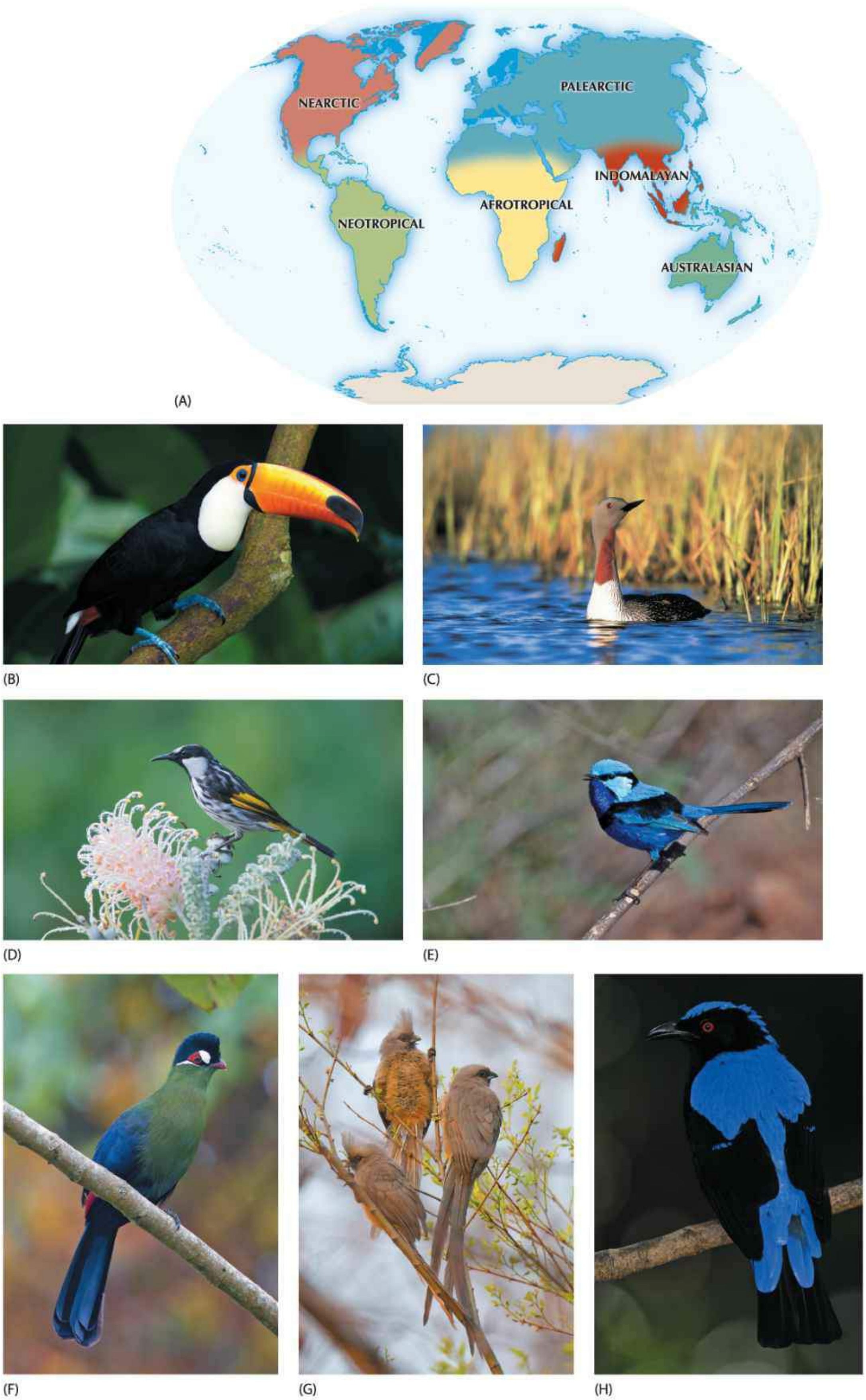

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Figure 1–17 The six major faunal regions (A) and some of their bird specialties: (B) toucans (Neotropical region); (C) loons (Nearctic and Palearctic regions); (D) honeyeaters and (E) fairywrens (Australasian region); (F) turacos and (G) mousebirds (Afrotropical region); and (H) fairy-bluebirds (Indomalayan region).

Avifaunas—regional assemblages of bird species—are mixtures of species of varied ages and origins. Some groups have radiated in isolation on particular continents or island regions. Other species have arisen in recent colonizations of new islands or continents. The history of bird distributions can be understood as a series of waves of adaptive radiations, dispersal events, imposed isolation events, and extinctions. The birds of North America include old and new colonists from Asia and South America, remnants of ancient avifaunas, plus diverse species groups that radiated extensively on that continent—for example, the colorful wood warblers.

Early avian colonists on each continent or major group of islands diversify locally in response to the ecological opportunities available to them. The diversity of finches on the Galápagos Islands and of honeycreepers on the Hawaiian Islands inspired the evolutionary theories of Charles Darwin. Just as dramatic is the diversity of the tyrant flycatchers of South America, which radiated to include new species that look and function like shrikes, wheatears, tits, warblers, pipits, or thrushes from other parts of the world. Australian land birds, related genetically most closely to one another, matched so well the external attributes of shrikes, flycatchers, and small insect-eating warblers that, until 1990, they were misclassified with superficially similar species native to Europe and Asia.

REVIEW KEY CONCEPTS

1.1 Basic Characters of Birds

Birds are bipedal, feathered vertebrates. They have evolved a host of novel anatomical features that are directly or indirectly associated with the evolution of flight. Living birds are toothless and feed using their beaks and bony tongues. Birds have also evolved a unique vocal apparatus—the syrinx—which provides them with the most complex and diverse vocal capabilities of any animals. Like mammals, birds are also endothermic, or warm-blooded, which influences many aspects of their anatomy, physiology, and ecology. Birds lay eggs, and most species of birds provide their young with extensive parental care. Birds are intelligent with large and complex brains.

Key Terms: feathers, beak, gizzard, uncinate processes, furcula, carpometacarpus, tibiotarsus, tarsometatarsus, hallux, endothermic, eggs, syrinx

1.2 Adaptive Radiation of Form and Function

Since their origin in the Mesozoic, modern birds have evolved into a diverse adaptive radiation including more than 10,000 species with a tremendous variety of morphologies, diet, ecologies, and breeding systems. The ecological diversification of birds is most visible in the variation in beak shape, which is associated with underlying variation in the structure and function of the cranium. The morphology of bird feet is highly variable, as a result of adaptation for perching, swimming, wading, running, grasping, and climbing.

Key Terms: adaptive radiation, maxilla, trabeculae, rhamphotheca, cranial kinesis

1.3 Life Histories

Birds have a great diversity of life history traits, which include the details of growth and maturation, the life span, the rate of reproduction, and the nature of parental care. The adult life span and age at maturity differ among bird species by more than 10-fold.

1.4 Natural Selection and Convergence

The adaptive radiation in avian morphology, ecology, and life history is the result of the process of natural selection. A result of natural selection is adaptation—the enhanced fit between the organism and its environment. Birds provide some of the best-studied and historically most important examples of adaptation by natural selection, such as the adaptive radiation in beak shape of Darwin’s Finches. Another common result of natural selection is convergence in which similar adaptations have evolved in different lineages in response to similar forms of natural selection. For example, stout, seed-eating, finchlike beaks have evolved many times in different families of birds.

Key Terms: adaptation, natural selection, convergence

1.5 Biogeography

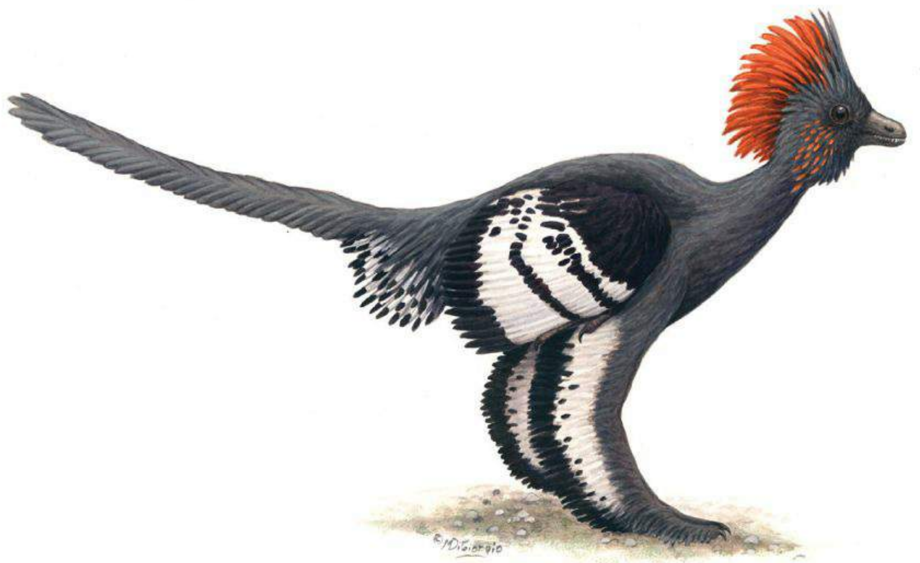
Biogeography is the study of the geographical distributions of plants and animals. A few species of birds are very broadly distributed, but most bird species and families are restricted, or endemic, to a specific, limited region of the planet. The uneven distributions of higher taxonomic categories of birds among the continents and oceans of the world create distinct avifaunas in different biogeographic regions.

Key Terms: biogeography, endemic, avifaunas

APPLY YOUR KNOWLEDGE

1. Define the modern bird. Using anatomical structures unique to modern birds, describe those features that contribute to increased power, reduced weight, and balance.
2. How has high body temperature contributed to the success of birds, and how has it influenced their diets?
3. Bipedal dinosaurs had long, muscular bony tails for balance. Explain how modern birds have been able to eliminate the tail and maintain the center of gravity over the legs.
4. Define "adaptation" and describe specific adaptations for flight, walking, perching, swimming, and feeding.
5. Adaptation by natural selection is described as "a process without plan or purpose." Support this statement using the evolution of bills of Darwin's Finches and Hawaiian honeycreepers and the convergent evolution of the wings and colors of auks and penguins.
6. Describe the factors that have led to "avifaunas" on continents and islands, incorporating the concepts of endemism and adaptive radiation.

CHAPTER 2 *Evolutionary Origin*



MICHAEL DIGIORGIO, COURTESY OF RICHARD O. PRUM

Anchiornis huxleyi was a fully feathered theropod dinosaur closely related to the ancestor of *Archaeopteryx* and living birds. Its plumage color patterns have been reconstructed from the fossil melanosomes of its feathers (Box 4–3 in Chapter 4).

2.7 Evolution of Flight

> The evidence supporting the hypothesis that birds are derived maniraptoran theropod dinosaurs is overwhelmingly convincing in its sheer quantity and interdisciplinary breadth. [SMITH ET AL. 2015b]

Avian history starts more than 150 million years ago with the evolution of feathered theropod dinosaurs with limited flying abilities. Birds then diversified in form and function during the Mesozoic era and then again into modern taxa in the Cenozoic era (Table 2–1). The evolution and adaptive radiation of living birds paralleled the independent evolution and rise of placental mammals to their own modern prominence. Increases in atmospheric oxygen over this same period of Earth history, with rapid increases in the early Jurassic and the Eocene periods, potentially favored the success of these two principal groups of highly active land vertebrates with aerobic metabolism (Falkowski et al. 2005).

During the late twentieth century, the hypothesis of the evolution of birds from dinosaurs generated intense debate (section 2.4; see also Box 2–2). However, after more than a century focused on ***Archaeopteryx lithographica,*** the earliest known fossil bird, a wealth of well-preserved new fossils of both early birds and dinosaurs began to appear from northeastern China in 1998. This continuing wave of revolutionary discoveries has provided decisive evidence to support the theropod dinosaur origin of birds and insights into the early evolutionary radiation of birds.

Major episodes of extinction punctuated the long history of life on Earth. Birds participated in several of them, starting in the late Cretaceous. In another episode, climatic changes caused the extinction of at least 25 percent of the existing bird species at the beginning of the Pleistocene epoch about 3 million years ago. Recurrent climatic changes continued to alter habitats and, in turn, the distributions and viabilities of bird populations. Human colonization of island archipelagos in the Pacific Ocean, Indian Ocean, and Caribbean Sea over the last few thousand years led to the extinction of an estimated 2,000 species, or nearly one-fifth of all the world's bird species (Steadman 1995). In the past century, humans have become the primary force changing and threatening the natural world, including global climates. Birds now face major new risks of species extinctions.

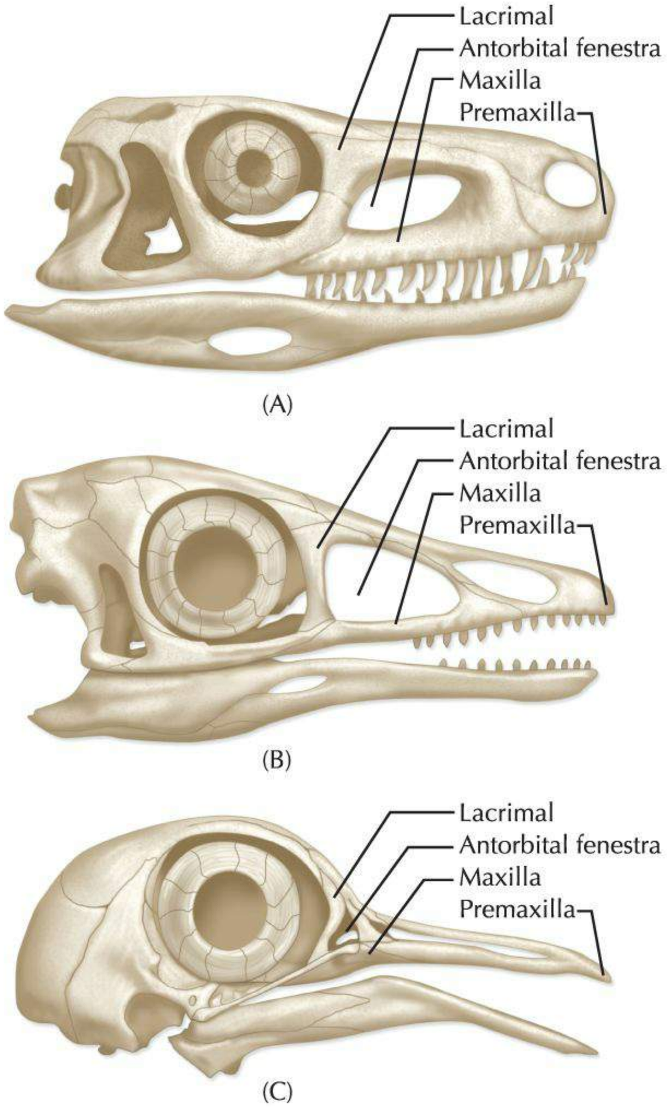
This chapter first examines the reptilian features of birds and then *Archaeopteryx lithographica*, the earliest known bird. The evolutionary origin of birds is a question of where birds fit in the Tree of Life—or **phylogeny.** So, next, this chapter examines the basic logic of reconstructing phylogeny and the evidence that birds are living dinosaurs. The stage is then set for Chapter 3, which examines the phylogeny, diversity, and classification of living birds.

2.1 Birds Are Reptiles

Thomas H. Huxley, the great evolutionary biologist of the nineteenth century, asserted that birds were "merely glorified reptiles" and accordingly classified them together in the taxonomic category Sauropsida (Huxley 1867). Indeed, birds and modern reptiles have many characters in common. The skulls of both articulate with the first neck vertebra by means of a single ball-and-socket device—the **occipital condyle;** mammals evolved two of them. The lower jaws, or mandibles, of both birds and modern reptiles are composed of three or more bones on each side; mammals have only one mandibular bone. Birds and reptiles have a simple middle ear with only one ear bone—the **stapes.** Mammals have three middle-ear bones; the two unique middle ear bones evolved from bones of the lower jaws. The ankles of both birds and modern reptiles are located in the middle of the foot, or the **tarsal bones** (see Figure 1–3), not between the long lower leg bones, or tibia, and the tarsi as in mammals. The scales on the legs of birds are similar in structure to the body scales of modern reptiles. The scales and feathers of birds and other reptiles are made of a distinctive protein called beta-keratin (Chapter 4). Both birds and modern reptiles lay yolked, polar eggs in which the embryo develops by shallow divisions of the cytoplasm on the surface of the egg.

In his influential 1926 book *The Origin of Birds*, Gerhard Heilmann established that birds are members of a specific group of reptiles that are called Archosauria. The **archosaurs** also include the alligators and crocodiles, the dinosaurs, and the pterosaurs—the extinct reptiles that flew on batlike wings made of skin. All archosaurs share an **antorbital**

fenestra, a distinctive hole in the side of the skull in front of the eye socket (Figure 2–1). Thus, among living reptiles, birds are most closely related to the alligators and crocodiles. Interestingly, like birds, alligators and crocodiles are distinct from most other reptiles in having advanced parental care behavior. This breeding system likely evolved in the common ancestor of all archosaurs.



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DATA FROM HEILMANN 1926

Figure 2–1 Skulls of (A) the nondinosaurian Triassic archosaur *Euparkeria*, (B) *Archaeopteryx lithographica*, and (C) a pigeon showing the antorbital fenestra between the lacrimal bone and the maxilla. The antorbital fenestra is a shared, derived feature of archosaurian reptiles.

The similarities between birds and reptiles leave no doubt of their evolutionary relationship to each other. Yet we are not content with that. We want to know which reptiles gave rise to birds and how that evolutionary transformation proceeded. For this knowledge, we must turn to the fossil record.

2.2 Archaeopteryx: The Original Link Between Birds and Reptiles

For more than 130 years, the extinct creature *Archaeopteryx lithographica* provided most of the relevant evidence on this critical question. Since 1998, however, the historical importance of *Archaeopteryx* to the study of avian evolution has been eclipsed by an explosion of new fossil discoveries. Yet *Archaeopteryx* remains a critical and iconic piece of this evolutionary story.

Fine-grained limestone deposits in central Europe contain a record of creatures that occupied that region during the age of dinosaurs—in the late Jurassic period, from 155 million to 135 million years ago (Table 2–1). At that time, central Europe was tropical, sporting palmlike plants. Great warm seas and lagoons covered parts of the European continent. The coastal lagoons attracted pterodactyls, some as small as sparrows and others as large as eagles. Sometimes they perished in the lagoons, where gentle fossilization in the fine calcareous sediments preserved their features in exquisite anatomical detail. Also preserved in the same lagoons were the remains of the feathered reptile now called *Archaeopteryx*.

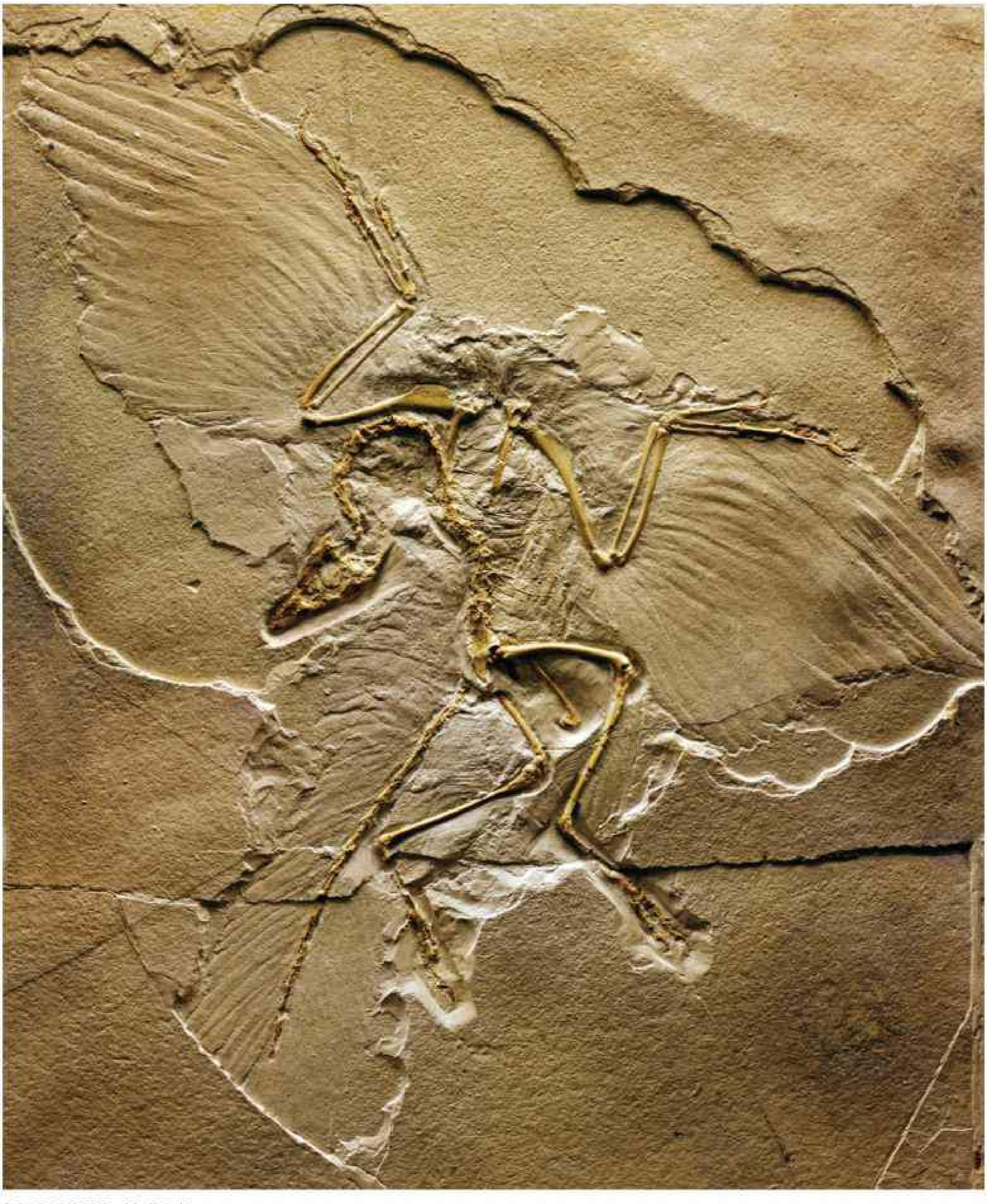
Table 2–1 *Geologic Time Scale*

Era	Period	Epoch	Million Years Before Present
Cenozoic	Quaternary	Holocene	0.01
		Pleistocene	2.6–0.01
	Neogene	Pliocene	5–2.6

		Miocene	23–5
	Paleogene	Oligocene	34–23
		Eocene	56–34
		Paleocene	66–56
Mesozoic	Cretaceous	Late	100–66
		Early	145–100
	Jurassic	Late	164–145
		Middle	174–164
		Early	200–175
	Triassic		250–200

Sources: Geological Society of America Time Scale (v.5.0); Walker et al. (2013).

The first fossil evidence of the origin of birds was an impression of just a single feather found in a quarry in Solnhofen in Bavaria, Germany, from which Jurassic limestone was mined for lithographic slabs. The fossil impression was brought to the attention of German naturalist Hermann von Meyer of Munich, and in 1861 von Meyer named it *Archaeopteryx* (*archaios*, “ancient”; *pteryx*, “wing”) *lithographica*. A complete skeleton of a small reptilelike animal with feathers also was found and brought to von Meyer’s attention just a few months later. The discovery of a second complete specimen of *Archaeopteryx* in another quarry near Eichstätt, Germany, followed in 1877 (Figure 2–2). It is fully articulated, revealing details of the wing bones, flight feathers, and the pairs of feathers attached to each vertebra of its long tail. These feathers are indistinguishable from modern bird feathers.



McPHOTO /AGE FOTOSTOCK

Figure 2–2 This fully articulated skeleton of *Archaeopteryx lithographica* was found in 1877 near Eichstätt, Bavaria. It is now known as the Berlin specimen.

Now known from 12 specimens and that first feather, *Archaeopteryx* was a crow-sized bipedal reptile that bore a mosaic of primitive, reptilian and derived avian features. For example, the blunt snout held many small, reptilian teeth. Like reptiles, *Archaeopteryx* also had a long, bony tail and free belly ribs, called gastralia. Yet it bore feathers on both wings and tail and probably also over most of its body, like modern birds. And the first toe pointed backward like modern birds.

Like the modern guans (Cracidae), *Archaeopteryx* may have been a strong-running, terrestrial "bird" that could leap into trees, jump among large branches, and make short flights between trees. Most paleontologists agree that *Archaeopteryx* was capable of gliding and weak flapping. The **vanes,** or planar surfaces on either side of the shaft, of *Archaeopteryx*'s primary wing feathers were asymmetrical, a character common to nearly all flying birds and most pronounced in strong fliers (Feduccia and Tordoff 1979). However, the absence of a modern, birdlike shoulder joint indicates that *Archaeopteryx* was not capable of long, sustained flights or rapid wing beaks, at least not like a modern bird.

The discovery of *Archaeopteryx* was extremely timely and provided powerful evidence of the complex history of evolutionary change. Only two years before, in the *Origin of Species* (Darwin 1859), Darwin had predicted the existence of "intermediate forms," and *Archaeopteryx* fulfilled that prediction precisely.

2.3 Putting Birds on the Tree of Life

In the *Origin of Species,* Charles Darwin hypothesized that the evolutionary history of organisms could be understood as a “great Tree of Life.” Biologists now refer to this tree of evolutionary relationships as a phylogeny. To understand the origin of birds, we need to discover where birds fit in the phylogeny of all vertebrates—animals with backbones.

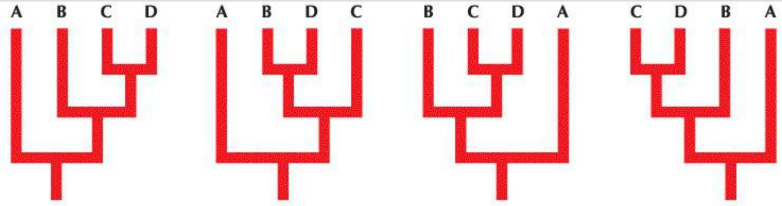
Since the origin of life, all organisms share common ancestry. We depict the history of shared evolutionary relationships among organisms diagrammatically as a branching, **phylogenetic tree.** The branches in a phylogeny represent historic species evolving through time. The branching events, or nodes, in a phylogeny depict speciation events, or the creation of new species in the past. The pattern of relationships in the tree represents the history of evolutionary events that gave rise to the diversity of those organisms (Box 2–1).

Box 2–1

Phylogeny and Tree Thinking

Discovering the full details of the entire Tree of Life is a major goal in biology because the phylogenies of organisms are fundamental to understanding the patterns and mechanisms of evolution and ecological differentiation of all biodiversity. Depicting phylogenies are an important kind of scientific communication, but understanding these tree diagrams is not always straightforward. This introduction to how to “read” phylogenies can help in understanding them throughout this book.

The lines of a phylogeny depict lineages, or interbreeding populations, of organisms in the past. The branching points, or nodes, in a phylogeny depict speciation events that produced new, descendant lineages of organisms. The pattern of branching events communicates the history of shared ancestry among organisms. The pattern of branching events on a phylogeny always depict the relative timing of different speciation events to each other. Some phylogenies can also be time calibrated so that the lengths of the branches reflect hypotheses about the geological ages of each of the branches in the tree. However, the order of the names at the tips of the branches does not provide any information. You can rotate the branches around any node without changing any of the information in the tree.



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One of these trees is not like the other. The information within a phylogenetic tree is contained in tree shape—the relative order of the branching events—and not in the linear order of names of the taxa. All of these trees are identical except for one. Can you spot it?

To discover the phylogeny of a group of organisms, we use evidence we can observe from extant organisms and the fossil record to reconstruct the ancient, unobserved history of evolutionary relationships. Our goal is to identify groups of organisms that include all the descendants of a single common ancestor. Such natural groups are described as monophyletic because they constitute a single, entire branch on the phylogeny. A monophyletic group is also called a **clade** (from the Greek *klados,* “branch”).

We identify clades by discovering shared, evolutionarily derived character states. For example, among living vertebrates, feathers are a **derived character state** that tell us that all birds share a common ancestor, exclusive of other living vertebrates, in which feathers evolved. In contrast, a **primitive character state** cannot tell us which organisms are more closely related. Since all birds have feathers, feathers are primitive to living birds. Consequently, the presence of feathers will not tell us whether ducks are more closely related to chickens or to sparrows. Thus, whether a specific character state is primitive or derived depends on which branch of the phylogeny we are trying to resolve.

We can interpret the direction of the evolution, or polarity, of a character by comparison of variation within a group to other, more distantly related organisms, a method called out-group comparison. For example, the wings of all birds are **homologs,** or similarities inherited from a common ancestor. The penguins (Spheniscidae) are flightless, wing-propelled diving birds (Figure 2–3; see also Figure 1–16). Penguins use their flipperlike wings to swim. The flipperlike wings of penguins are a distinct kind of avian forelimb. To understand whether swimming wings or flying wings bird are primitive or derived within the diving birds, we must compare penguins and other diving birds—the **in-group**—to other, more distantly related birds—the **out-groups.** We see that almost all other birds have flying wings. As a result, we can conclude that having flying wings is the primitive character state among living birds and diving birds and that the flipperlike wings of penguins are evolutionarily derived. Accordingly, we have evidence that penguins are a monophyletic group that is diagnosed by the presence of a shared derived morphological character state—flipperlike wings.

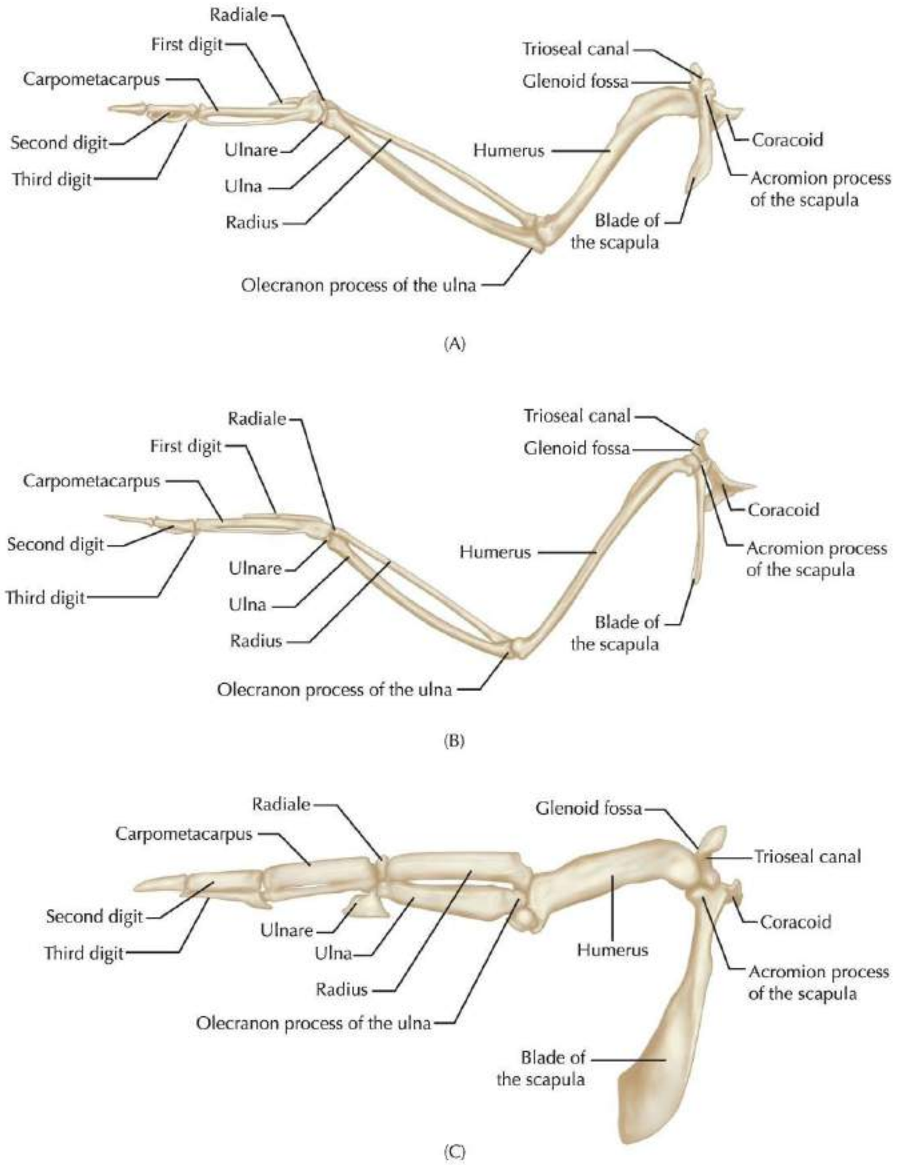

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Figure 2–3 Comparison of the wing bones of (A) a Ferruginous Hawk, (B) a Common Loon, and (C) a King Penguin. The flipperlike wing bones of the penguin are derived in shape from the wings bones of their flying ancestors.

In real data sets, different characters will inevitably conflict in what specific clades they support. Resolving character conflict requires analyzing comparative data using various criteria and models of evolution (Chapter 3).

Investigating the evolutionary origin of birds requires that we apply this phylogenetic method to the diversity of living birds, Mesozoic fossil birds, and other archosaurs, especially the dinosaurs.

2.4 Birds Are Dinosaurs

Birds are living dinosaurs. So, to investigate the origins of birds, we need to explore the diversity of dinosaurs—or reexplore—since this is an activity that most children do. The dinosaurs included three main, monophyletic groups, each of which includes iconic and familiar creatures (Figure 2–4). The **ornithischian** dinosaurs were mostly quadrapedal vegetarians, including *Ankylosaurus, Stegosaurus, Triceratops,* and *Parasaurolophus.* The saurischian dinosaurs are the sister group to the ornithischians, and include the sauropods and theropods. The **sauropods** were the long-necked vegetarian dinosaurs, which included the largest animals to have ever lived. Well-known sauropods include *Brachiosaurus, Brontosaurus,* and *Titanosaurus.* The phylogenetic sister group to the sauropods are the bipedal, meat-eating dinosaurs called **theropods,** which include the famous *Allosaurus, Tyrannosaurus rex, Oviraptor,* and *Velociraptor.* Birds are living theropod dinosaurs that are most closely related to the dromaeosaurs like *Deinonychus* and *Velociraptor* and to *Troodon* (see Figure 2–4).

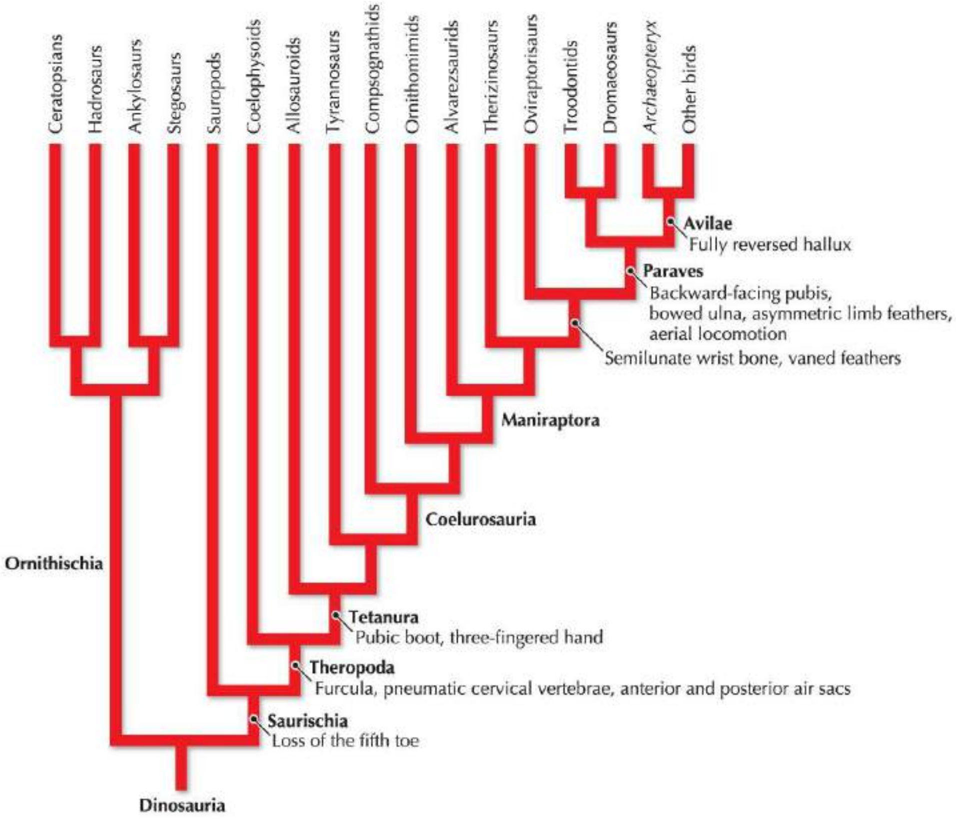

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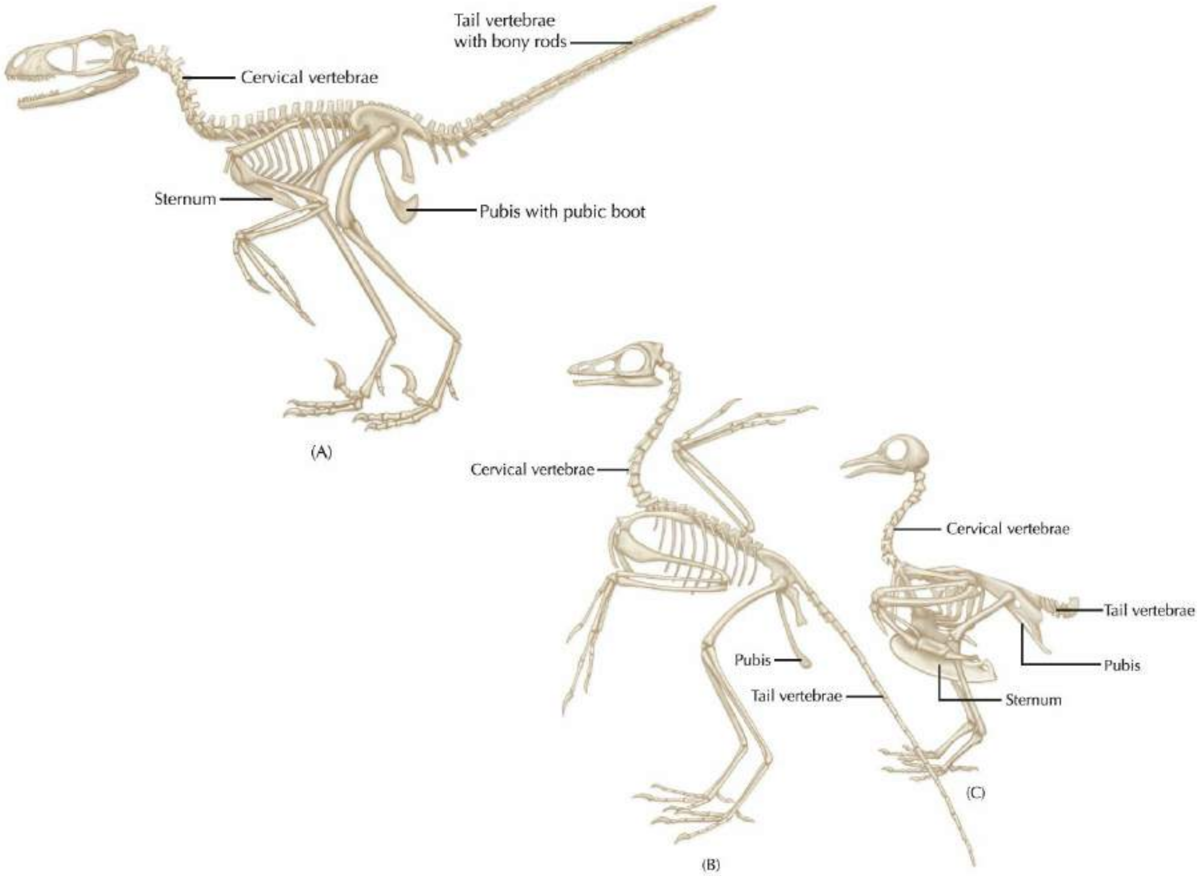
Figure 2–4 Phylogeny of dinosaurs with the names of major dinosaur clades (bold) and shared derived characters supporting some monophyletic groups.

Although the feathered, flying, and warm-blooded birds have long been thought of as strikingly distinct from all other extant vertebrates, analysis of the theropod origin of birds documents that there were no huge leaps, or revolutionary changes, in morphology (Brusatte et al. 2014). Rather, the rate of evolutionary change was quite gradual. The more we discover about theropod dinosaurs, the more difficult it has become to actually distinguish birds from the continuum of evolutionary change within the theropods.

The shared derived character states that support the theropod origin of birds can be found throughout the body (Figure 2–5). Starting with the hindlimb, the fifth toe of the foot was lost in the most recent common ancestor of sauropod and theropod dinosaurs (Figure 2–6). The first toe, or **hallux,** later evolved to point backward in the most recent common ancestor of *Archaeopteryx* and living birds—a group called Avialae. In the hips, the long pubis bone evolved a broad expansion on the end, which is called the **pubic boot** (Figure 2–7) in the tetanurans, the theropod group that evolved from the most recent common ancestor of the carnosaurs, like *Allosaurus,* and the birds. Later, the pubis bone evolved to point backward in Paraves, the group including the troodontids, dromaeosaurs, and the birds.



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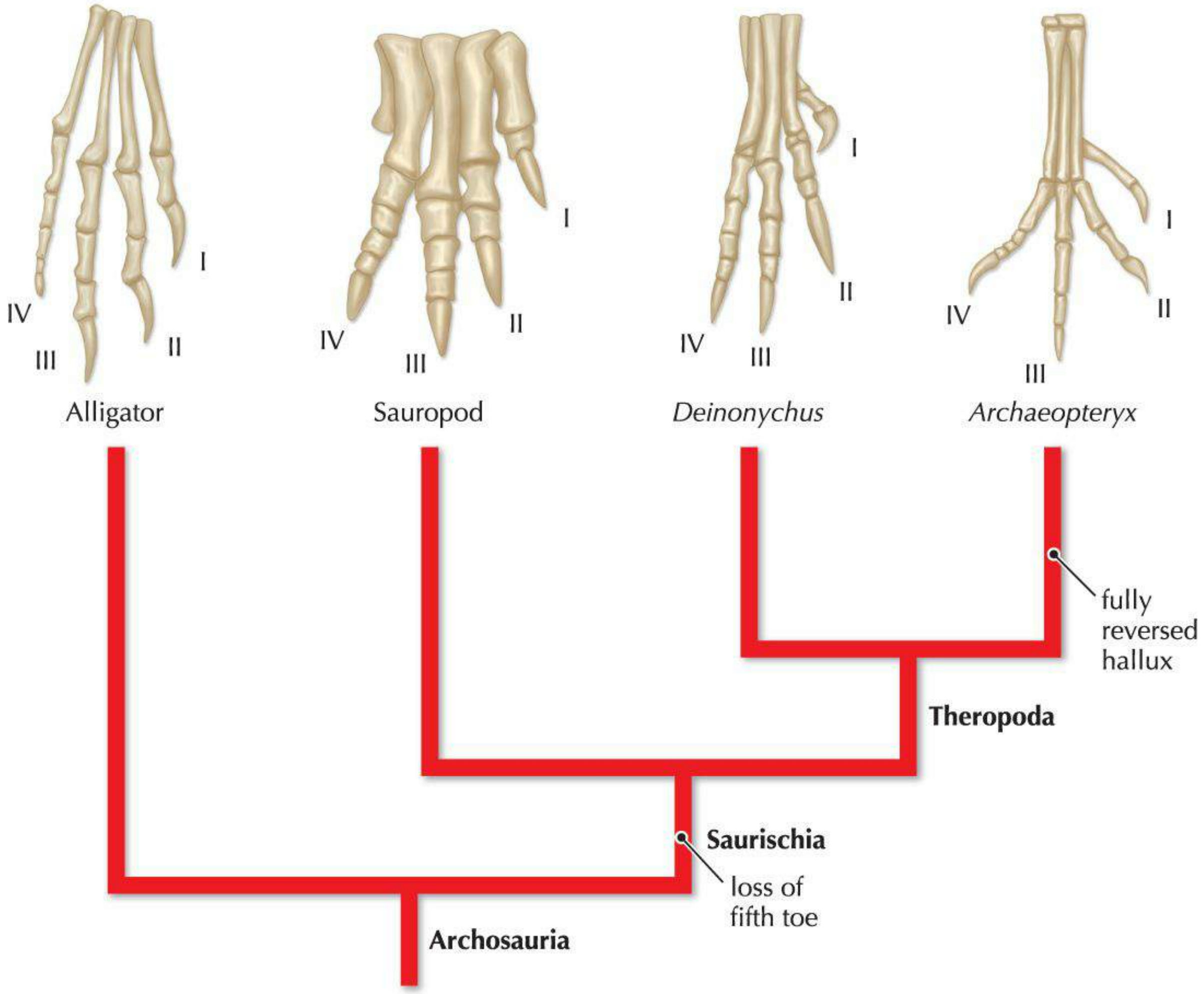
(A) Data from Burnham et al. 2000. (B, C) Data from Colbert 1955

Figure 2–5 The skeletons of (A) *Bambiraptor*, (B) *Archaeopteryx*, and (C) a pigeon.



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DATA FROM CURRIE AND PADIAN 1997

Figure 2–6 Toe evolution in archosaurs. Comparison of the right hind feet of an American Alligator, a sauropod, *Deinonychus*, and *Archaeopteryx*.

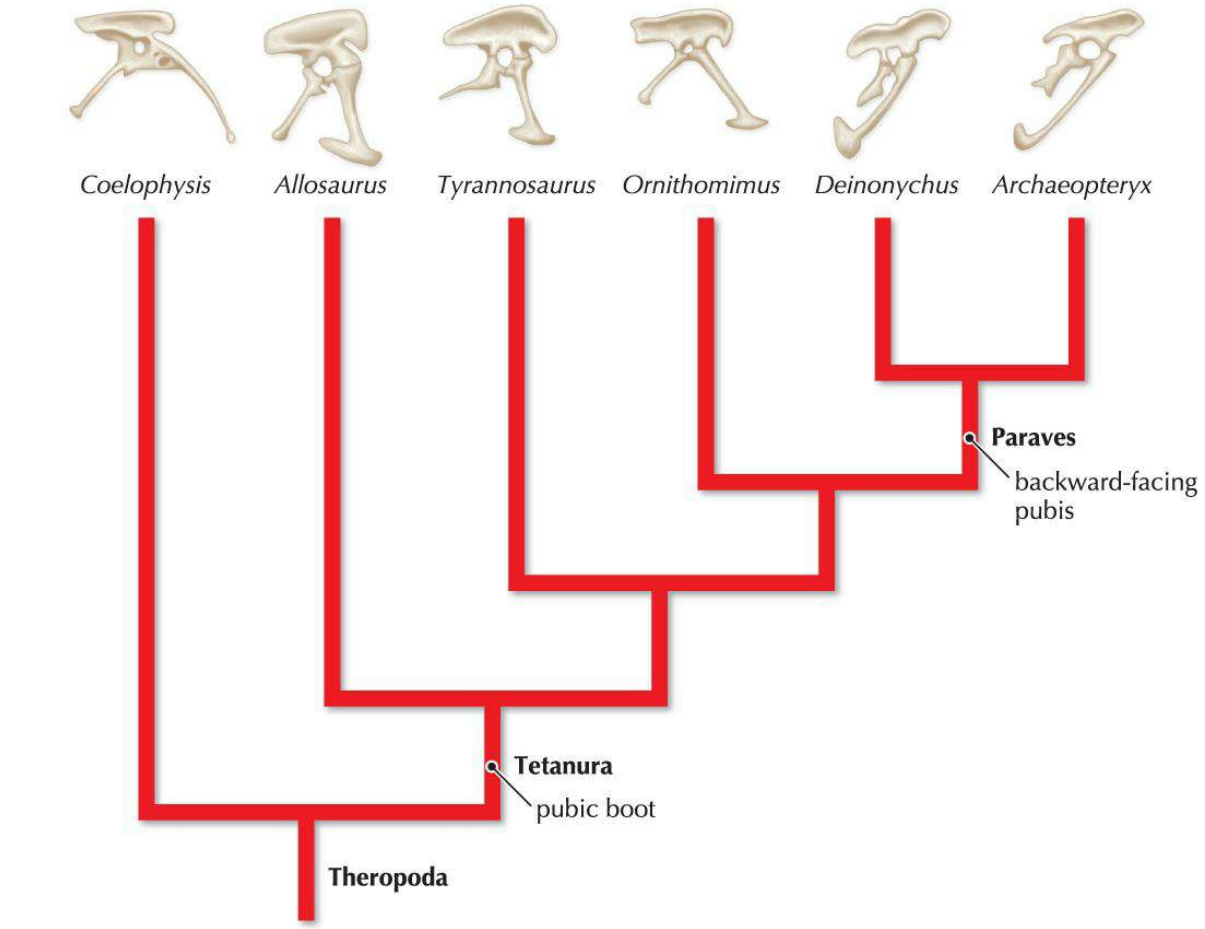

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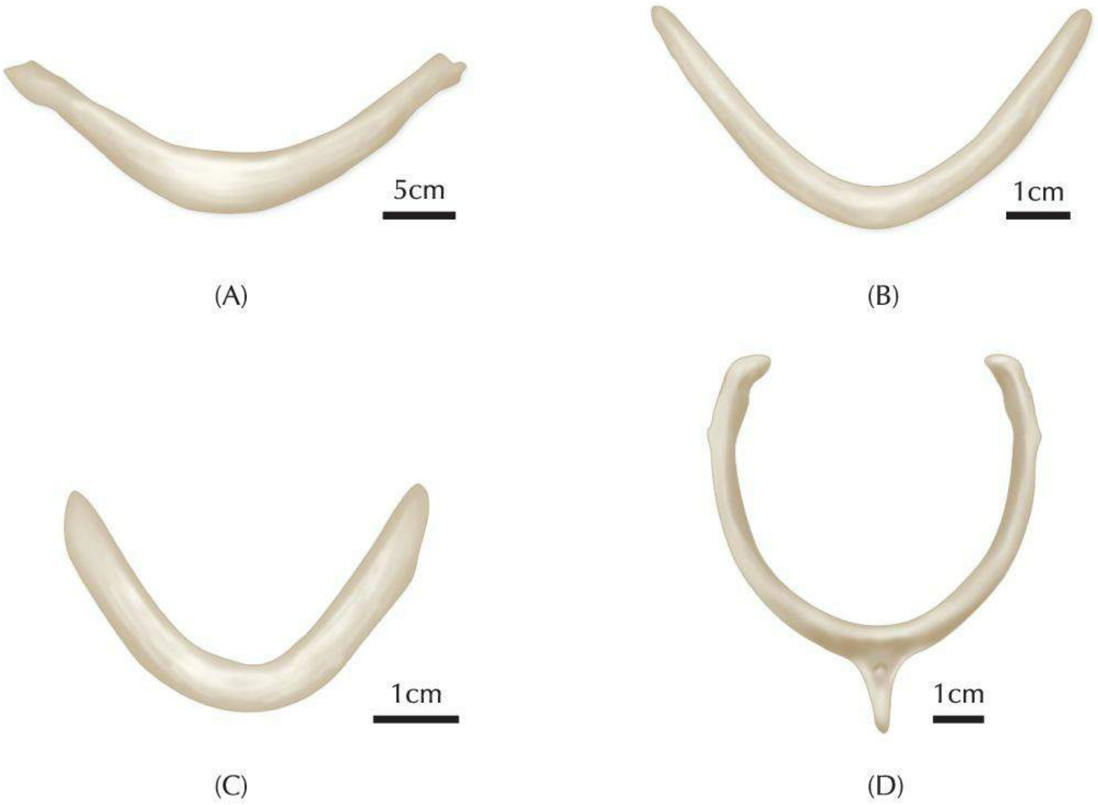
Figure 2–7 Pelvis evolution in the archosaurs. Comparison of the pelvic bones of *Coelophysis, Allosaurus, Tyrannosaurus, Ornithomimus, Deinonychus,* and *Archaeopteryx.*

The fused **clavicle** bones form the **furcula,** or wishbone, of birds. The furcula spans in front between the shoulder girdles. For nearly 150 years, the furcula was thought to be a unique, avian adaptation for flight. However, we now know that the furcula evolved early within theropod dinosaurs (Nesbitt et al. 2009). The theropod furcula was quite asymmetrical at first and later evolved to be symmetrical in Paraves (Figure 2–8).



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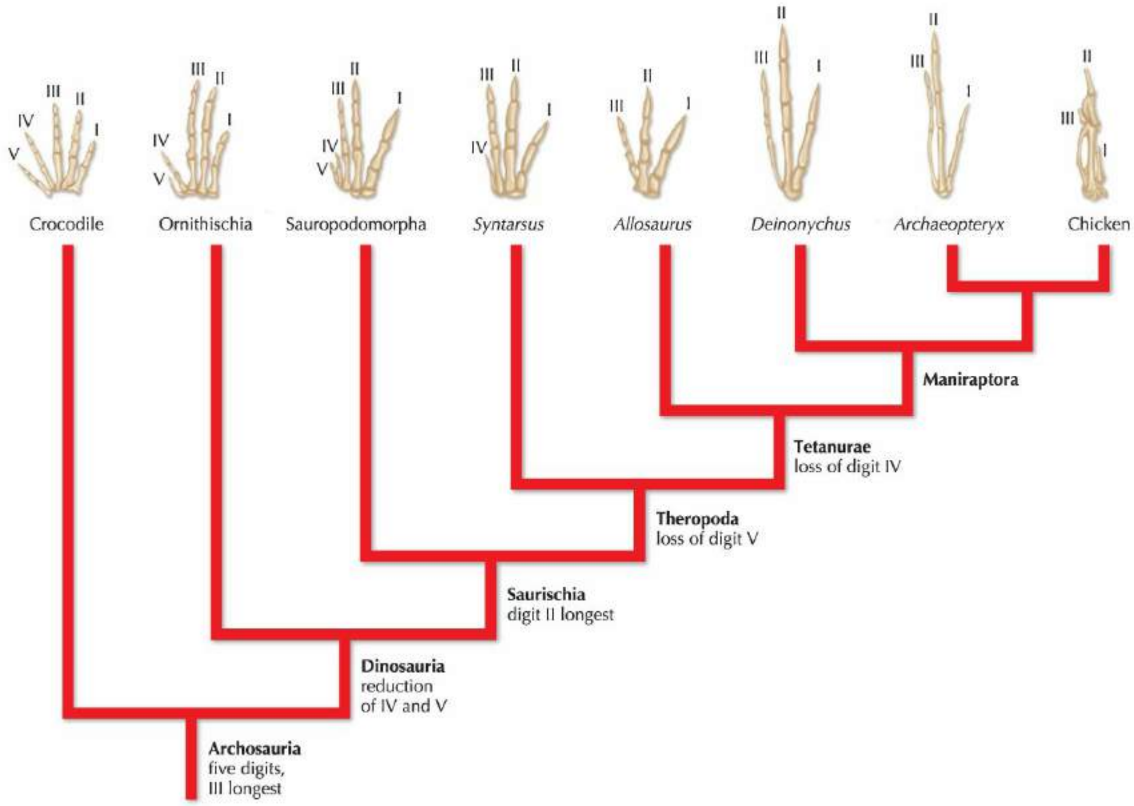
DATA FROM NESBITT ET AL. 2009

Figure 2–8 Furcula evolution in theropods. Comparison of the furculae of (A) *Tyrannosaurus*, (B) *Bambiraptor*, (C) *Archaeopteryx*, and (D) a Secretarybird.

The outer two digits of the hand were greatly reduced in the most recent common ancestor of the sauropods and the theropods (Figure 2–9). Hand digits IV and V were later lost completely in the most recent common ancestor of the allosaurids and the birds. The trend toward hand digit loss continued in multiple theropod dinosaurs, including the two-fingered *Tyrannosaurus rex;* the bizarre, one-fingered alvarezsaurid *Mononykus olecranus;* and the living, two-fingered, flightless Kiwis (*Apteryx*). The fingers of the raptor *Deinonychus* and *Archaeopteryx* show striking similarities in the relative lengths of the digits and phalanges (Wagner and Gauthier 1999; Figure 2–10).



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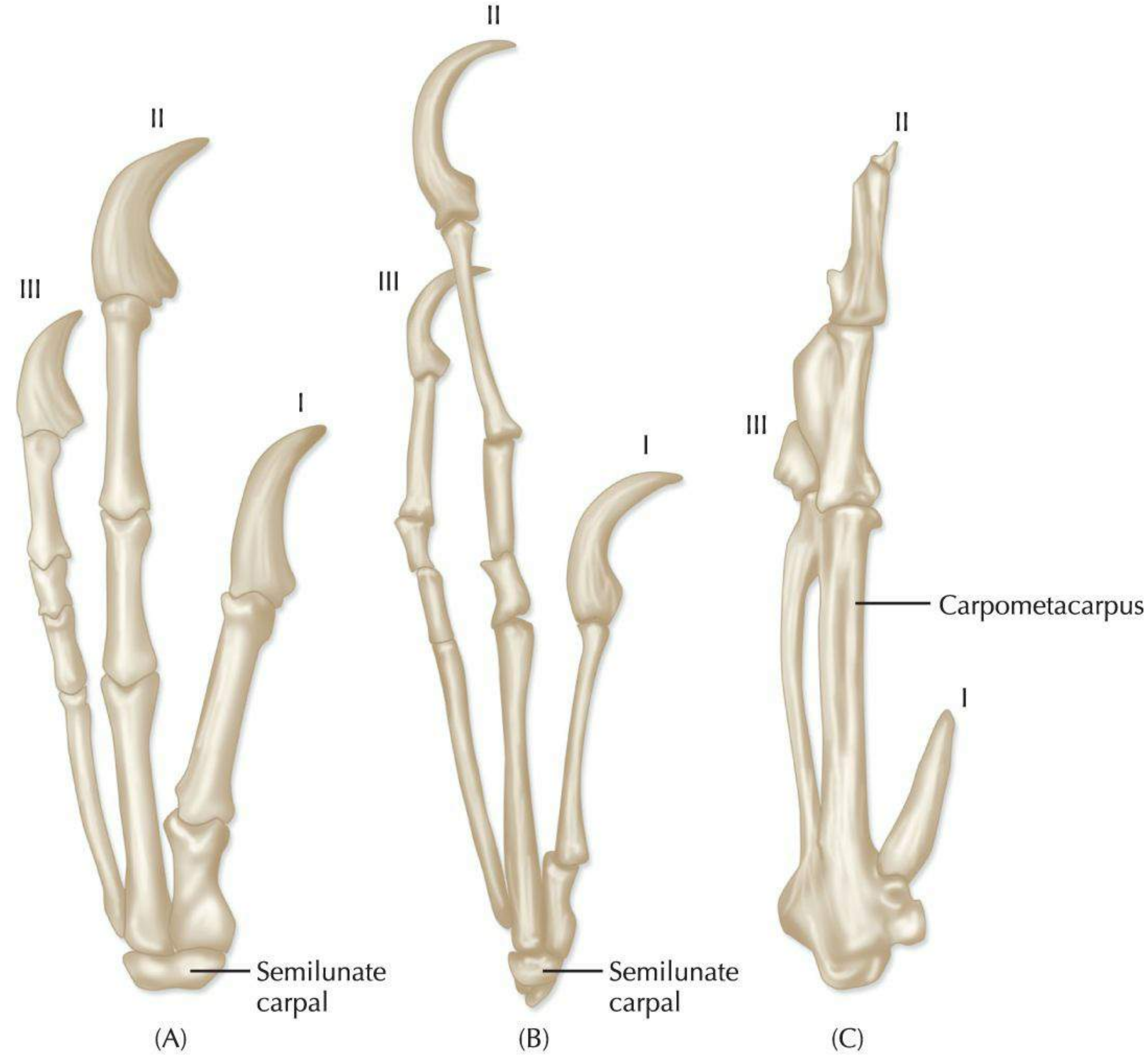
DATA FROM CURRIE AND PADIAN 1997

Figure 2–9 Finger evolution in archosaurs. Comparison of the hands of a crocodile, an Ornithischian dinosaur, a Sauropodomorph dinosaur, *Syntarsus, Allosaurus*, *Deinonychus*, *Archaeopteryx*, and a chicken.



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DATA FROM WAGNER AND GAUTHIER 1999

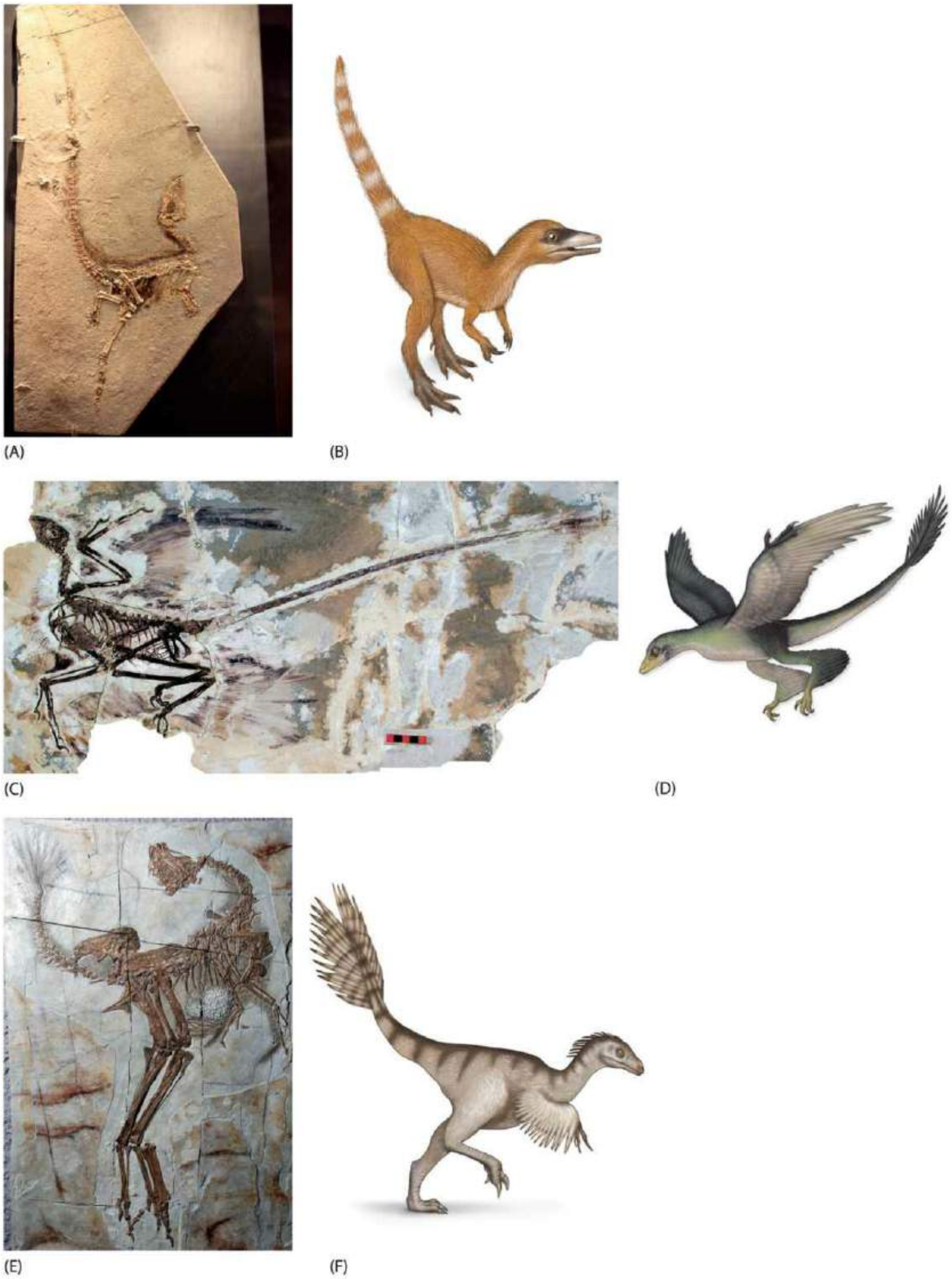
Figure 2–10 Finger evolution. Comparison of the hands and digits of (A) *Deinonychus*, (B) *Archaeopteryx,* and (C) a tinamou (*Nothura*). The bones of the third digits of *Deinonychus* and *Archaeopteryx* share an unusual pattern of relative lengths, starting from the base: long, short, short, long. *Deinonychus* and *Archaeopteryx* also share a moon-shaped wrist bone called the semilunate carpal. Many hand bones, including the semilunate carpal, were fused to form the carpometacarpus in the ancestor of enantiornithines and (C) living birds.

The ribs, vertebrae, and wing bones of living birds are penetrated by small branches of the membraneous, nonvascular air sacs that are a critical part of the unique, unidirectional lung respiratory system of birds (Chapter 6). These air-filled bones are referred to as **pneumatic bones.** Similar pneumatic vertebrae are found in a wide variety of theropod dinosaurs (O’Connor and Claessens 2005), implying that the anterior and posterior air sacs and the complex avian breathing mechanism are not unique to birds and likely evolved earlier in the theropod dinosaurs.

The wrists of dromaeosaurs, troodonitids, and *Archaeopteryx* all share a crescent-shaped bone formed by the fusion of wrist bones (or carpals) of digits I and II, which is called the **semilunate carpal** (see Figure 2–10). The semilunate carpal allows for both flexion and side-to-side movement. Within the Mesozoic birds, the semilunate carpal became fused into the **carpometacarpus** in the Pygostylia. The semilunate carpal allowed for the lateral hand movements that contribute to wing folding and the flight stroke of birds, but these anatomical precursors to the avian flight stroke evolved in the ancestor of Paraves.

Archaeopteryx and dromaeosaurs share a host of highly detailed similarities in the relative lengths and shapes of the phalanges, or finger bones, to maintain a grasping hand (see Figure 2–10). Intriguingly, in both dromaeosaurs and *Archaeopteryx*, the first and fourth phalanges of the third finger are longer than the second and third. Furthermore, the articulating surfaces of the phalanges of digit III are rotated, or twisted, by 50 degrees so that when the third finger was flexed, it curved inward to oppose the first finger (Wagner and Gauthier 1999; Gishlick 2001). Thus, dromaeosaurs and *Archaeopteryx* shared an unusual and derived grasping hand.

Perhaps the most powerful and unexpected support for the theropod ancestry of birds comes from the evidence of feathers on a broad diversity of coelurosaurs (Figure 2–11). Beginning with the discovery of vaned feathers on hands and tails of *Caudipteryx zoui* and *Protarchaeopteryx robusta* from the early Cretaceous Yixian Formation in Liaoning (Ji et al. 1998), China, a wide variety of feather structures have now been found (Prum and Brush 2002; Norell and Xu 2005). Vaned feathers that are structurally equivalent to modern birds are known from dromaeosaurs, troodontids, and oviraptorosaurs. Simpler branched structures, similar in structure to modern down feathers, and unbranched skin appendages of various shapes have also been found in alvarezsaurids, therizinosaurs, ornithomimids, compsognathids, and tyrannosaurs. Feather evolution will be discussed in greater detail in Chapter 4.



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(A) AKKHARAT JARUSILAWONG/SHUTTERSTOCK. (C) GETTY IMAGES. (E) ARDEA/DIOMEDIA.COM

Figure 2–11 Feathered nonavian theropod dinosaurs, such as (A, B) *Sinosauropteryx*, (C, D) *Microraptor*, and (E, F) *Caudipteryx*, provide further evidence that birds are theropod dinosaurs.

The secondary feathers of the bird wing form small bumps on the trailing edge of the forelimb bone, the **ulna** (Figure 2–12). These structures, called **quill knobs,** develop where wing feathers are attached to the ulna. Fossil quill knobs have now been found in various theropods for which fossil feathers are unknown, including *Velociraptor* (Turner et al. 2007) and even an allosaurid (Ortega et al. 2010).

(A) Richard O. Prum. (B, C) Mick Ellison

Figure 2–12 Quill knobs on the trailing edge of the ulna of (A) a Turkey Vulture and (B, C) *Velociraptor*.

Paleontological discoveries continue to document the enormous diversity of ecologies and body plans of theropods (Brusatte et al. 2014). The theropod dinosaurs include huge predators with vicious jaws and teeth and mysteriously tiny forelimbs, like *Tyrannosaurus* *rex;* lumbering therizinosaurs with tiny heads, long necks, and enormous hands; and the pigeon-sized *Microraptor gui* with long, asymmetrical feathers on both forelimbs and hindlimbs (see Figure 2–11C). In the context of the incredible diversity of theropods, birds can be understood as another evolutionarily successful variation in a broader adaptive radiation.

A host of shared, derived characters support the monophyly of the birds—the most exclusive monophyletic group including *Archaeopteryx* and the living birds. For example, birds share a completely reversed hallux (or hind toe), unserrate teeth, and 25 or fewer tail vertebrae. However, many of the features that were traditionally considered to be unique to birds—such as feathers, aerial locomotion, the furcula, air sacs with pneumatic bones, and so on—are now known to have originated earlier in theropod dinosaur evolution (see Box 2–2). By convention here, Avialae refers to the most exclusive monophyletic group that includes *Archaeopteryx* and living birds, and Aves refers to the monophyletic group of living birds. However, we will refer to all avialians, including *Archaeopteryx,* as birds.

Box 2–2

The Bird Origin Controversy Resolved

The hypothesis that birds evolved from small theropod dinosaurs goes back to the discovery of *Archaeopteryx.* Darwinian acolyte Thomas H. Huxley (1868) was particularly impressed by the similarities between *Archaeopteryx* and *Compsognathus,* a small theropod known from the same Jurassic limestone. However, Huxley was more interested in the question of the relationship of dinosaurs than the origin of birds.

Like Huxley, Gerhard Heilmann (1926) found numerous similarities in skeletal morphology between *Archaeopteryx*, other birds, and theropod dinosaurs. Despite these observations, however, Heilmann concluded that birds could not be related to theropods because theropods lacked **clavicles,** the chest bones that are fused to form the avian furcula, or wishbone. Heilmann was a strict adherent to the concept of "Dollo's Law," the idea that once a morphological structure has been evolutionarily lost, it cannot be regained.

We now know, however, that most theropods *had* clavicles that were already fused into a furcula and that the furculae of some dromoaeosaurs are extremely similar to *Archaeopteryx* (Nesbitt et al. 2009). If Heilmann were alive today, he would doubtless have embraced the theropod origin of birds.

Instead, Heilmann proposed that birds evolved from a poorly characterized group of more ancient archosaurs called "pseudosuchians," later referred to as "**thecodonts.**" We now know that the thecodonts are not a monophyletic group but rather a grab bag of poorly known, ancient archosaurs with unresolved phylogenetic relationships.

Heilmann's thecodont hypothesis became the mainstream view of the origin of birds for most of the twentieth century. However, John Ostrom (1969) described *Deinonychus antirrhopus*, the first well-preserved dromaeosaur fossil, from the Lower Cretaceous of Montana. Based on his observations of *Deinonychus*, Ostrom (1976) proposed that birds evolved from theropod dinosaurs and were most closely related to the dromaeosaurs. Ostrom focused particular attention on the detailed, shared similarities of the relative lengths of the digits and the phalanges in the hand and on the semilunate carpal in the wrist (see Figure 2–10).

Later, Jacques Gauthier (1986) provided the first phylogenetic analysis of the relationships of birds and dinosaurs. Many details have since been further resolved; the placement of the birds within the theropod tree has remained quite stable since that time.

The theropod origin of birds was met with substantial resistance, but some of the criticism was constructive. For example, problems with Ostrom's analysis of the homology of the semilunate carpal (Martin 1983b) was later resolved (Wagner and Gauthier 1999). However, by 1990, the debate over origin of birds became a full-fledged controversy. Although superficially focused on the validity of specific characters, the controversy was really over whether the origin of birds should be analyzed phylogenetically (Martin 1983a, 1983b, 1985; Feduccia and Martin 1998; Feduccia 1999, 2002).

A fundamental and enduring problem with critiques of the theropod origin of birds was that no testable alternative hypotheses were proposed (Prum 2002, 2003; Smith et al. 2015b). Eventually, Helen James and John Pourtless (2009) presented a phylogenetic analysis of a set of characters and a wider variety of nondinosaurian archosaurs. However, they did not establish significant support for a nontheropod origin of birds. This analysis has since been superseded by numerous studies of more comprehensive data sets that incorporate many newly discovered theropods that continue to support the closest relationship between birds, dromaeosaurs, and troodontids (Xu et al. 2011; Turner et al. 2012; Brusatte et al. 2014).

Numerous discoveries have also resolved specific problems raised by critics of the theropod origin of birds. For example, since 1998, the "temporal mismatch" between the late Jurassic *Archaeopteryx* and the late Cretaceous age of *Deinonychus* was resolved by the discovery of several additional fossils from the early Cretaceous and late Jurassic of China, including *Sinorithosaurus* and *Anchiornis huxleyi*. The “temporal gap” was an illusion of sampling.

Although birds and most theropods share three-fingered hands, critics of the theropod origin of birds disputed whether these were the same three digits. The phylogenetic pattern of the gradual reduction and loss of hand digits IV and V in theropod dinosaurs is very clear (see Figure 2–9), supporting the conclusion that theropods and birds have hand digits I–II–III. However, Burke and Feduccia (1997) observed that the digits of the avian hand develop in the positions of digits II–III–IV. They proposed that digit identity is determined by digit position and concluded that bird fingers cannot be homologous with those of theropods. However, subsequent studies have shown that digit identity is determined not by position within the hand or foot but by gradients of extracellular signaling molecules across the developing limb (Dahn and Fallon 2000). Experimental manipulations of signaling proteins in the developing chick foot can transform the identity of any digit independent of its position. Furthermore, analyses of the transcriptomes (i.e., all the genes being expressed) of the developing digits of the chicken hand and foot show closest similarities between the first digit of the hand and the hind toe, or hallux, of the foot. Thus, the overwhelming molecular developmental evidence supports the conclusion that the digits of the bird hand are I–II–III as predicted by the theropod origin of birds.

Critics of the theropod origin of birds also rejected the discoveries of many nonavian, feathered theropods as examples of fossil collagen—an abundant skin protein. However, recent analyses have shown that like many fossil feathers (Vinther et al. 2008; Li et al. 2010), the *Sinosauropteryx* skin filaments contain well-preserved melanin pigment granules, which collagen fibers would not have (Zhang et al. 2010). Critics of the theropod origin of birds ultimately had to accept that the dromaeosaurs and oviraptorosaurs, like *Caudipteryx*—which has such classical theropods features as a forward-facing pubis with a prominent pubic boot, like *T. rex*—were fully feathered (Feduccia 2002).

In conclusion, a tremendous volume of evidence from paleontology, phylogenetics, developmental biology, behavior, and even genomics supports theropod origin of birds (Prum 2002, 2003; Xu et al. 2014; Smith et al. 2015b). The relevance of the theropod origin of birds to the evolution and diversity of extant birds will be analyzed throughout this book.

2.5 Mesozoic Evolution of Birds

Tremendous progress has also been made in recent decades in understanding the evolutionary radiation of Mesozoic birds, between the origin of *Archaeopteryx* to the mass extinction of nonavian dinosaurs at the end of the Cretaceous.

After the evolution of *Archaeopteryx* in the late Jurassic period, birds gradually and incrementally evolved the definitive morphological features of modern birds. A wealth of new fossil birds, especially from the early Cretaceous of Liaoning, China, now bridges the once troublesome gap in the fossil record that separated *Archaeopteryx* from modern birds (Figure 2–13).

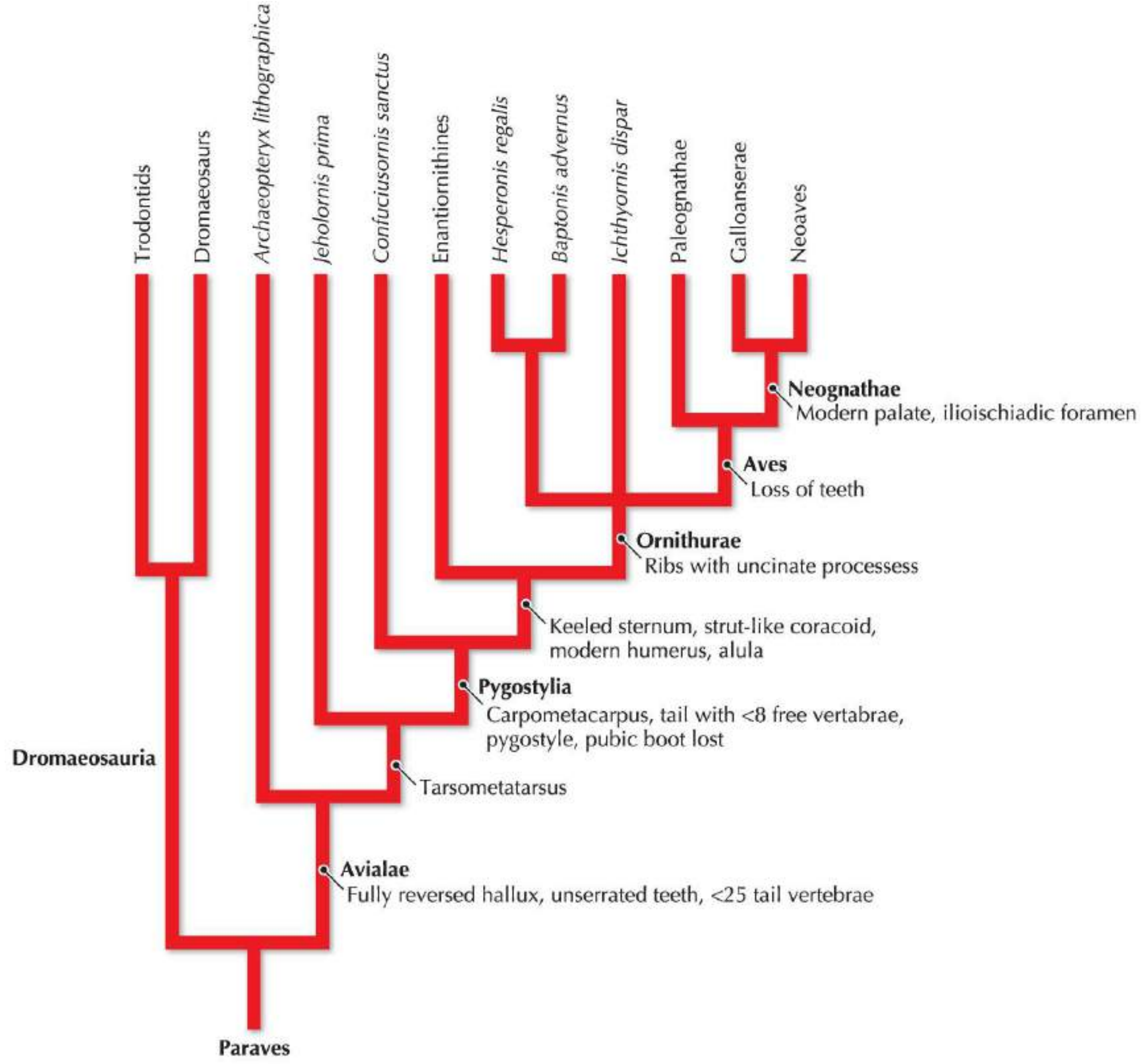

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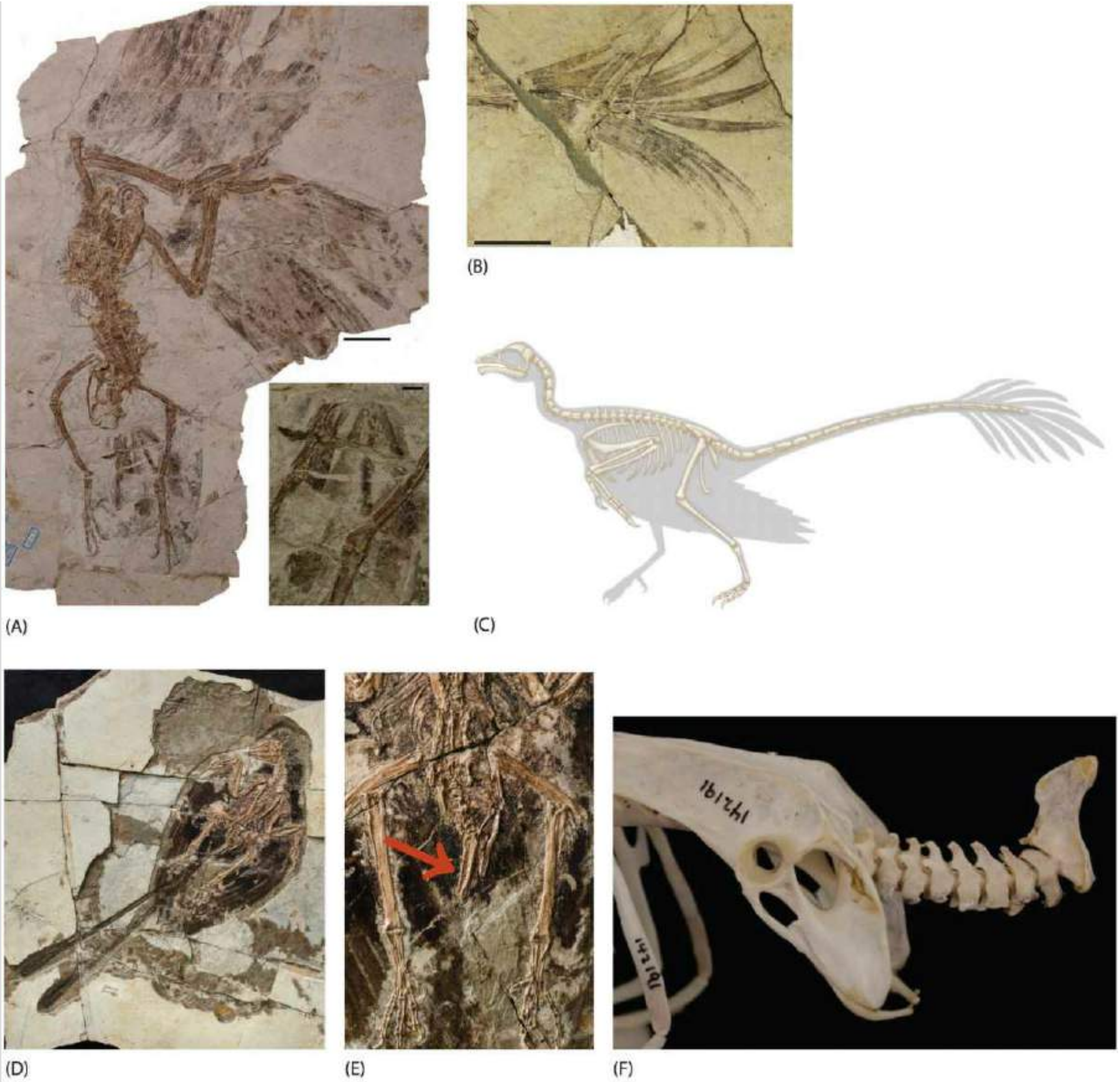
Figure 2–13 Phylogeny of Mesozoic birds with the names of major clades (bold) and the shared derived characters supporting each monophyletic group.

The phylogeny of Mesozoic birds documents that the flight morphology and flight capacity of modern birds evolved in a series of incremental steps. Furthermore, there was substantial ecological and behavioral diversity among birds from very early in avian evolution. Like *Archaeopteryx*, the early Cretaceous *Jeholornis* (120 million years old) had a long, bony tail, but *Jeholornis* shared with modern birds the completely fused lower leg bones, or **tarsometatarsus** (Figure 2–14). *Jeholornis* also had curious and highly distinctive, fan-shaped tufts of feathers at the tip and the base of its long tail (O’Connor et al. 2013).



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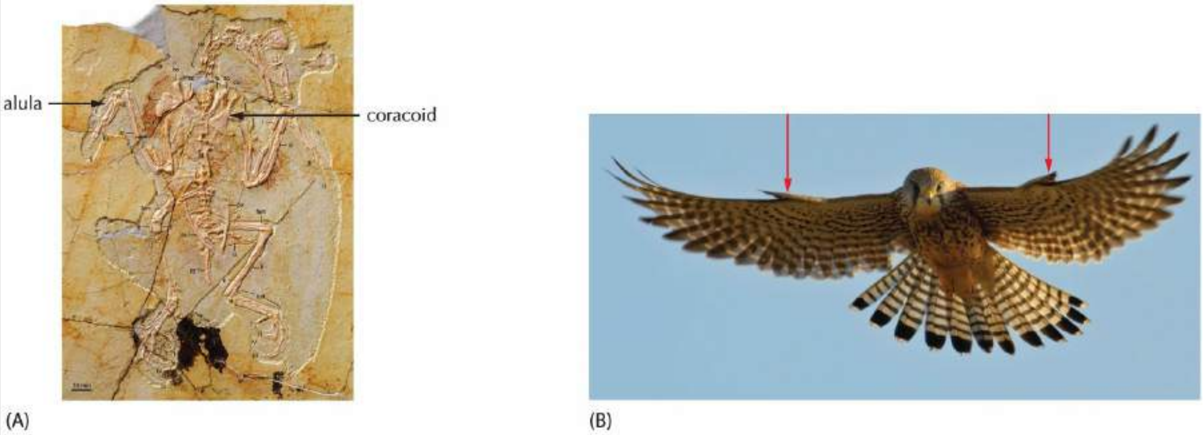
(A, B) O'Connor et al. (2013) Unique caudal plumage of Jeholornis and complex tail evolution in early birds. PNAS 110: 17404–17408. (D, E) Courtesy of L. Chiappe, Dinosaur Institute, Natural History Museum of Los Angeles County. (F) Richard O. Prum

Figure 2–14 Basal lineages of the Mesozoic bird evolution: *Jeholornis* and *Confuciusornis*. (A) *Jeholornis* skeleton, (B) tuft of feathers on the tip of the long tail, and (C) reconstruction of the living animal. A comparison of (D, E) the pygostyle of *Confuciusornis* (red arrow) and (F) modern Red-tailed Hawk.

The early Cretaceous *Confuciusornis* was among the first short-tailed birds. *Confuciusornis* shared numerous derived features with modern birds, including the carpometacarpus, a tail with fewer than eight free vertebrae, and a special bone created by the fusion of vertebrae at the tip of the tail, called the **pygostyle** (see Figure 2–14). The tail feathers insert on the pygostyle. Like modern birds, *Confuciusornis* also had a horny beak without teeth. However, beaks evolved convergently multiple times in early birds and in other dinosaurs, including *Oviraptor* and ceratopsians like *Triceratops*. Some *Confuciusornis* specimens have a pair of extremely long tail feathers with spatulate tips, which may be sexual display plumes found in only males or females (Chiappe et al. 1999).

The sister group to *Confuciusornis* and its relatives are two highly diverse radiations—the Enantiornithes and the Ornithurae. The Enantiornithes dominated the Mesozoic avian evolution (Chiappe 1995; Figure 2–15). Dozens of flight-capable species of diverse ecological forms ranged worldwide. They were as small as sparrows (e.g., *Sinornis;* Sereno and Chenggang 1992) and as large as vultures (e.g., *Avisaurus;* Varricchio and Chiappe 1995). Many were arboreal.



(A) Zhang Y, O’Connor J, Di L, Qingjin M, Sigurdsen T, Chiappe LM. (2014b) New information on the anatomy of the Chinese Early Cretaceous Bohaiornithidae (Aves: Enantiornithes) from a subadult specimen of Zhouornis hani. PeerJ 2:e407 https://doi.org/10.7717/peerj.407. (B) ryttersfoto/Getty Images

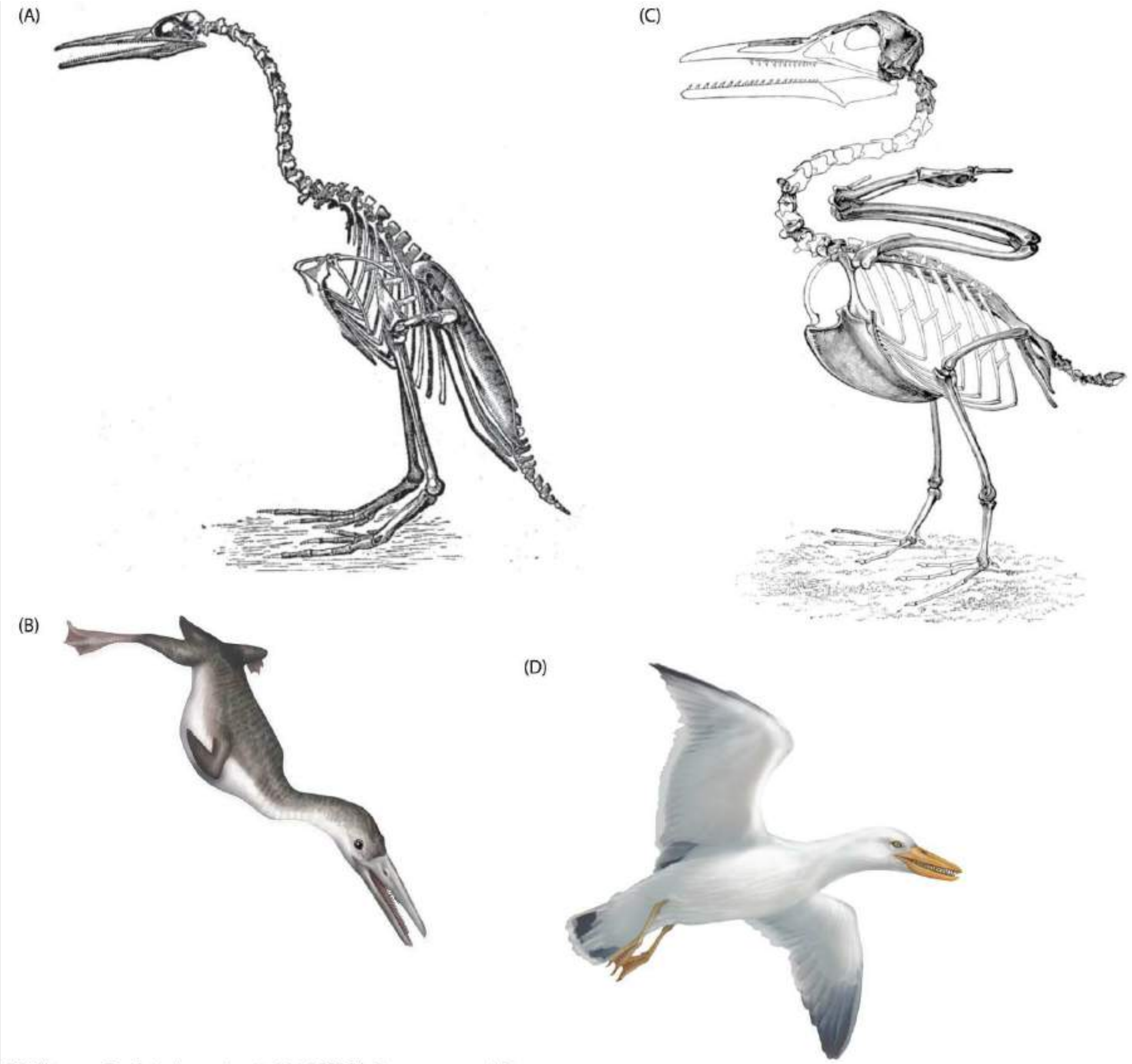
Figure 2–15 Enantiornithine birds evolved a modern wings and shoulder girdle. (A) *Zhouornis hani* with elongate coracoid and tiny feathered first digit called the alula. (B) American Kestrel deploys the alula (red arrows) at slow speed.

The enantiornithines shared with living birds numerous derived features of the modern avian flight morphology, including the keeled sternum (or breastbone) for the origin of flight muscles and the elongate, strutlike coracoid bone. The longer coracoid raised the shoulder joint, created the triosseal canal for the supracoracoideus tendon, and provided the capacity for the modern, flight upstroke (Chapter 5). The common ancestor of enantiornithines and modern birds also evolved the **alula,** or bastard wing, which is a tiny group of asymmetrical feathers on the tip of the first digit of the hand (see Figure 2–15). When extended, the alula creates a slot on the leading edge of the wing that helps to maintain laminar flow of air over the upper surface of the wing at slower speeds (Sanz et al. 1996).

None of the Enantiornithes survived into the Cenozoic. They disappeared along with the flightless dinosaurs in the mass extinction that marked the end of the Mesozoic era.

The sister group to the Enantiornithes, the Ornithurae, ultimately gave rise to modern birds. The ornithurine birds share the derived feature of **uncinate processes** on the ribs, which add stability to the upper rib cage and aid in flying and respiration (see Figure 1–3). Like the Enantiornithes, the toothed Ornithurae included small, finch-sized arboreal species in the early Cretaceous. By the late Cretaceous, ornithurine birds exhibited a wide range of sizes and lifestyles that mirrored those of modern wading birds, diving birds, perching birds, and even secondarily flightless (having evolved from “flighted” birds) terrestrial forms. Among the best-known early ornithurines are toothed seabirds—*Hesperornis, Baptornis,* and *Ichthyornis* (Figure 2–16).

They inhabited the Cretaceous seas that covered the central parts of North America and Eurasia. *Hesperornis* and *Baptornis* were powerful, foot-propelled diving birds that resembled modern loons but were entirely flightless. They ranged in size from that of a small chicken to the largest, *Hesperornis regalis*, which was from one to two meters in length. Flying above the same shallow seas were several species of toothed, ternlike birds in the genus *Ichthyornis* (see Figure 2–16).



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(A, C) OTHNIEL MARSH

Figure 2–16 Skeletal structures and reconstructions of the toothed-ornithurine birds. (A, B) *Hesperornis regalis* and (C, D) *Ichthyornis*.

Most of the Ornithurae disappeared along with dinosaurs in the mass extinction that marked the end of the Mesozoic era. Among the few survivors, however, were the ancestors of modern birds. The early radiation of living birds is discussed next in Chapter 3.

2.6 Evolution of Feathers

For most of the past century, the origin of birds, the origin of feathers, and the origin of avian flight have been treated as a set of interrelated questions. Traditionally, specific hypotheses about each of these questions were closely associated with specific positions on the others. Advocates of the thecodont origin of birds argued for an aerodynamic origin of feathers and an arboreal, or gliding, origin of flight. Beginning with John Ostrom, many advocates of the theropod origin of birds argued for a thermoregulatory origin of feathers and a cursorial, or running, origin of flight. However, more progress can be made on all of these questions by treating them independently and by documenting the evolutionary patterns before making strong conclusions about the evolutionary process or the mechanisms that have led to these innovations.

For more than a century, the modern feathers of *Archaeopteryx* separated it from all the small dinosaurs of similar form. It turns out, however, that feathers are not unique to birds but rather evolved earlier in theropod dinosaurs. This new awareness started with the discovery of the first “feathered dinosaur,” the turkey-sized *Caudipteryx* with a well-preserved fan of vaned feathers on its tail and forelimbs, and the slim, chicken-sized *Sinosauropteryx* with filamentous downlike feathers (see Figure 2–11). Fossil feathers have now been found on more than a dozen nonavian theropod dinosaurs (Prum and Brush 2002; Norell and Xu 2005).

Ancient theropod feathers included downlike filamentous structures, or “dino-fuzz,” and advanced, vaned, essentially modern feather structures. The relation of dino-fuzz to real feathers has been controversial; arguments range from their being unrelated structures to being precursors of feathers to being simplified feathers of flightless birds (Prum and Brush 2002; Lingham-Soliar 2003; Feduccia et al. 2005; see Box 2–2).

Less controversial are the well-preserved vaned feathers. Small *Microraptor gui* had front and hind wings that sported outer feathers with asymmetrical vanes, just as in the wings of modern flying birds (Xu et al. 2003; see Figure 2–11). Feathers clearly evolved in modern form in theropod dinosaurs and then diversified in form and function.

It was long presumed that feathers are so perfectly adapted for flight that they must have evolved through selection from elongate scales for this aerodynamic capacity. However, feathers evolved not as modified, mature scales but as a novel epidermal structure (Prum 1999; Prum and Brush 2002; see also Chapter 4). Contrary to most speculation during the twentieth century, feathers did not originate in concert with the evolution of flight. Rather, avian flight evolved after the origin of complex, vaned feathers. The asymmetric feather vane evolved into its fully modern form in the ancestor of enantiornithines and ornithurine birds (Feo et al. 2015). We will return to the evolutionary origin of feathers in Chapter 4.

2.7 Evolution of Flight

How did avian flight evolve, and just how well could *Archaeopteryx* fly? What caused the forelimbs of reptilian ancestors to evolve into protowings in the first place? Two basic theories have been proposed: an **arboreal,** or gliding, **theory** and a **cursorial,** or running, **theory.**

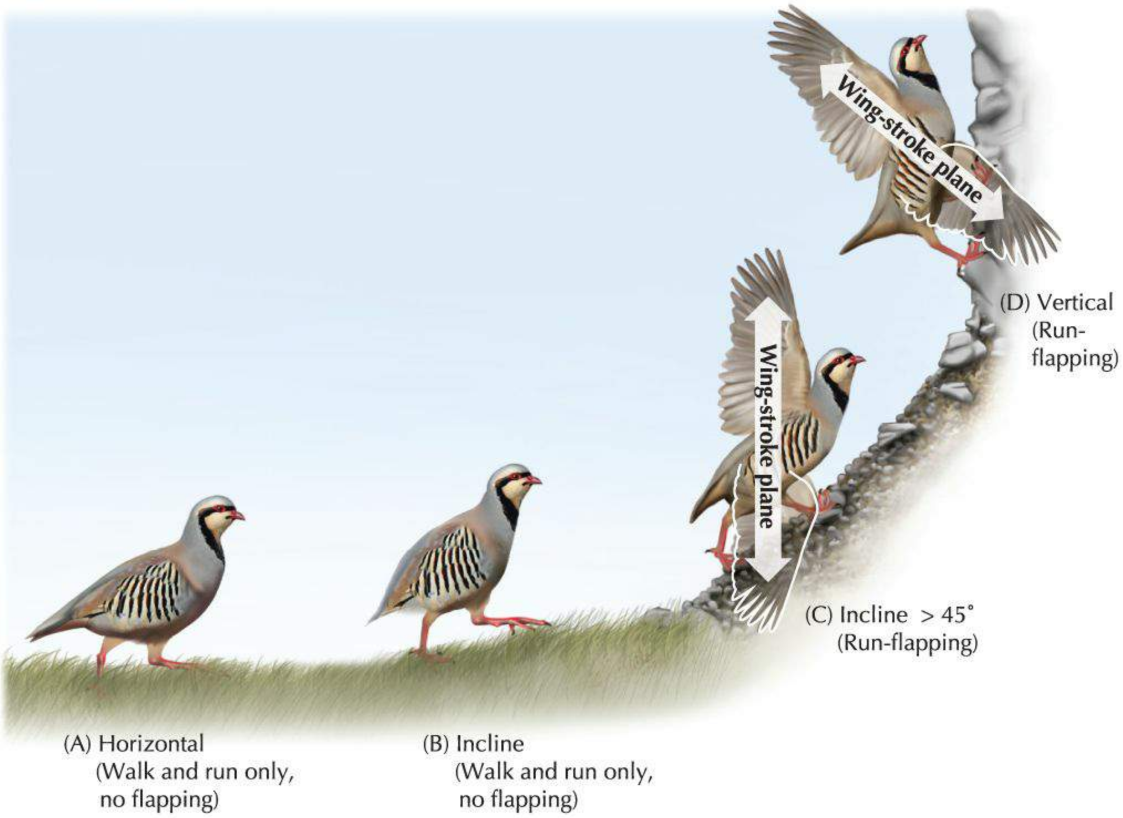
The arboreal theory proposes that the evolution of flight started with gliding and parachuting from elevated perches. This arboreal theory was favored for many years by opponents of the theropod origin of birds (Bock 1965; Feduccia 1980).

The cursorial theory proposes that elongated forelimbs enhanced leaping ability in a small, bipedal theropod dinosaur that ran and jumped to catch prey. The cursorial theory has been frequently advocated by proponents of the theropod origin of birds (Ostrom 1997; Padian and Chiappe 1998).

The arboreal versus cursorial theories are not clear alternatives. They pose a false dichotomy because the activities of the avian ancestors, including *Archaeopteryx* itself, may well have mixed these behaviors. The most important issue in the origin of flight is the evolution of the wing stroke that could produce the main components of powered flight: lift and thrust. A powered wing stroke required transformation of the wrist and shoulder from the skeletal wing precursors of theropod or other ancestors (Ostrom 1997). What were the behavioral steps that fostered this transformation?

From the phylogeny of theropods, it is clear that many of the anatomical and functional precursors of the avian flight stroke evolved for prey capture in entirely terrestrial theropods with a praying mantis–like forelimb movement and grasping hands (Padian and Chiappe 1998). This pattern provides strong evidence of the terrestrial context for many evolutionary events that together facilitated the evolution of avian flight. However, the biggest challenge to the cursorial theory is that the aerodynamic force of lift that makes flight possible is easier to produce at higher speeds (Chapter 5). It is easier to produce high airspeeds over the limbs by gliding down from a high perch than it is by running along the ground.

In an effort to expand the adaptive value of creating lift in a terrestrial context, Ken Dial (2003a) suggested that flapping their feathered forelimbs helped early terrestrial ancestors of birds climb steep inclines, such as tree trunks, to escape predators. Chickens and their relatives routinely improve foot traction and climbing ability through wing-assisted incline running (Figure 2–17). Incipient wings could have served avian ancestors in the same way, but the wing-assisted incline running of modern birds requires a modern shoulder that *Archaeopteryx* and other early birds did not have. Continued improvement of such aerodynamic assistance could have favored evolutionary changes in wrist and shoulder structure that led to the powered stroke of the avian wing. We will return to the evolutionary origin of flight in Chapter 5.



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DATA FROM DIAL 2003A

Figure 2–17 Overview of wing positions of a Chukar Partridge during wing-assisted incline running and the proposed transitions to powered flight. (A and B) Birds running over level substrates or shallow inclines do not use their wings to assist running. However, even partial wing development provides assistance to birds climbing inclines greater than 45 degrees. (C and D) A part of the wingbeat cycle (as much as 30 percent) directs aerodynamic forces toward the inclined surface, not skyward, which improves traction.

REVIEW KEY CONCEPTS

2.1 Birds Are Reptiles

Birds belong to a branch on the Tree of Life called reptiles, which also includes lizards, snakes, turtles, alligators, and crocodiles. Reptiles have many distinctive anatomical features, including a single occipital condyle, or ball-and-socket joint, between the skull and the neck. Among the reptiles, birds belong to the group Archosauria, which also includes alligators and crocodiles. Like birds, other archosaurs also build nests and provide parental care to their offspring.

Key Terms: *Archaeopteryx lithographica*, phylogeny, occipital condyle, stapes, tarsal bones, archosaurs, antorbital fenestra

2.2 *Archaeopteryx:* The Original Link Between Birds and Reptiles

Archaeopteryx lithographica was a fossil feathered reptile discovered in 1861 from the late Jurassic limestone in Bavaria. Now known from a dozen specimens, *Archaeopteryx* shared a full plumage of feathers, a pair of forelimb wings composed of feathers with asymmetrical vanes, and a hallux with modern birds, but it also shared teeth, a long bony tail, and gastralia, or belly ribs with reptiles. The discovery of *Archaeopteryx* provided powerful support for Darwin’s theory of evolution soon after the publication of *The Origin of Species*, and it became an iconic focus of more than a century of research into the origin of birds.

Key Terms: vanes

2.3 Putting Birds on the Tree of Life

The origin of birds is a question about where birds belong in the Tree of Life—the history of the evolution of living diversity, which we call phylogeny. Reconstructing phylogeny requires discovering clades, or monophyletic groups, which constitute the branches of the phylogenetic tree. We recognize clades by identifying shared derived character states, or new evolutionary features that are shared by the members of the clade. We also need to analyze the biological variation among species in order to identify which character states are derived and therefore informative to the phylogeny.

Key Terms: phylogenetic tree, clade, derived character state, primitive character state, homologs, in-group, out-group

2.4 Birds Are Dinosaurs

Birds are living dinosaurs. Understanding the evolutionary origin of birds requires exploring the phylogeny of dinosaurs. Birds belong to a clade of the bipedal and largely carnivorous dinosaurs called theropods. *Archaeopteryx* and other birds share many anatomical characters with various theropod groups, including a pubic boot, a furcula, the loss of the fifth toe, the loss of the fourth and fifth fingers, pneumatic bones, and vaned feathers. Birds—the clade that includes all the descendants of the most recent common ancestor of *Archaeopteryx* and all living birds—can be diagnosed by only a few shared derived features, including a completely reversed hallux, unserrated teeth, and fewer than 25 tail vertebrae. Some of these features—like the pubic boot and unserrated teeth—were subsequently lost before the evolution of the living birds.

Key Terms: ornithischians, sauropods, theropods, hallux, pubic boot, clavicle, furcula/furculae, pneumatic bones, semilunate carpal, carpometacarpus, ulna, quill knobs, thecodonts

2.5 Mesozoic Evolution of Birds

Mesozoic birds were ecologically diverse and ranged tremendously from sparrowlike to vulturelike in body size. The origin of modern, living birds involved the gradual and incremental evolution of modern bird morphology and flight capacity, including a greatly reduced tail, the loss of teeth, the fused tarsometarsus in the leg and carpometacarpus in the wing, the alula, modern asymmetrical flight feathers, and the modern shoulder, which made the advanced avian flight stroke possible.

Key Terms: tarsometatarsus, pygostyle, alula, uncinate processes

2.6 Evolution of Feathers

Feathers were long hypothesized to be an adaptation for avian flight. However, fossil discoveries now document that complex, vaned feathers evolved prior to the origin of birds and prior to the origin of flight in theropod dinosaurs. We will return to the evolution of feathers in Chapter 4.

2.7 Evolution of Flight

The two theories of the evolution of flight basic have been proposed: the arboreal (gliding) theory and the cursorial (running) theory. Many of the anatomical and functional precursors of the avian flight stroke evolved for prey capture in terrestrial theropods. These evolutionary events contributed greatly—but indirectly—to the evolution of avian flight. However, it is physically easier and physiologically less costly to produce the lift—the force necessary for powered flight—at speed by gliding than by running. We will return to the evolution of flight in Chapter 5.

Key Terms: arboreal theory, cursorial theory

APPLY YOUR KNOWLEDGE

1. How might have the extinctions occurring during the evolution of birds contributed to the success of the group?
2. Support the contention that birds are “merely glorified reptiles.” What features do birds and reptiles share in general, and what features specifically support theropods as the ancestors of modern birds?
3. Define derived character state and primitive character state. Which type of character states provides information about phylogenetic relationships?
4. How can the feather be both a derived character state and a primitive character state?
5. Without feather impressions, several fossils of *Archaeopteryx lithographica* were first classified as small dinosaurs. What other features did these fossils possess that could have been used to correctly place them among the birds?
6. Describe the Tree of Life and the nature of branches, nodes, and monophyletic groups.
7. How do ornithologists identify the polarity (“direction”) of

character evolution along the branches?

8. Darwin described the sudden appearance of flowering plants as an "abominable mystery" due to the lack of intermediate forms in the fossil record. For years, this also was true for birds. Is the same true today for the appearance of birds? Support the incremental evolution of birds from their reptilian ancestors using Figures 2–4, 2–6, 2–7, 2–9, and 2–13.

9. Describe the evolution of the reptilian forelimb as a "wing" before flight. For each new feature (derived character state), explain its advantage to a reptile that did not fly.

10. Compare and contrast the arboreal and cursorial theories proposed for the origin of flight. Apply each theory to *Archaeopteryx lithographica*, imagining it as an intermediate form and how it would have used its wings.

CHAPTER 3 *Phylogeny and Systematics*

ROBIN BUSH/GETTY IMAGES

The flightless, nocturnal kiwis (*Apteryx*) are endemic to New Zealand.

> [The] arrangement of the groups within each class . . . must be strictly genealogical in order

> to be natural. [Darwin 1859, p. 420]

The challenge of reconstructing the history of life belongs to the field of **systematics.** Systematists are scientists who investigate the evolutionary relationships among organisms through comparisons of fossils, preserved specimens, behavior, and the genetic code of life itself, DNA. Closely related species have immediate common ancestors that, in turn, had earlier common ancestors. Reconstruction of the tree of genealogical relationships among species—their **phylogeny**—provides a foundation for taxonomic classification and a framework for understanding the evolution of behavior, ecology, and morphology.

This chapter presents an overview of avian systematics. First is a summary of the relation between phylogeny and formal classification and the attributes of birds that provide clues to evolutionary history. Next is an introduction to molecular and morphological systematics. Then follows a brief introduction to the current state of the research on the phylogeny of birds. Finally, the chapter concludes with a preview of the nature of species.

3.1 Scientific Names

A logical system of scientific names is an essential prerequisite for the study of the biology of birds because nonscientific names of birds tend to vary with locale. The American Goldfinch, for example, has also locally been called the yellow-bird, thistle-bird, wild canary, and beet-bird (Figure 3–1). Each human culture employs its local bird names, fostering the need for standardized names that allow ornithologists throughout the world to communicate efficiently and exactly.

Gay Bumgarner/Alamy STOCKPHOTO

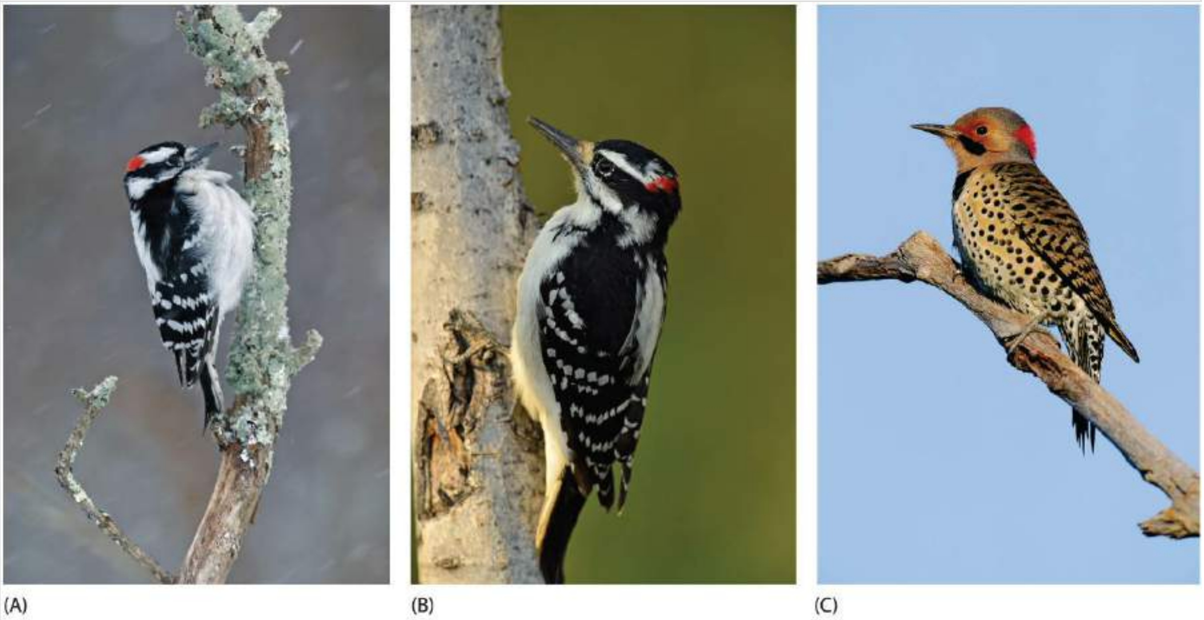
Figure 3–1 The American Goldfinch has many local names, such as wild canary, yellow-bird, thistle-bird, and beet-bird, but its scientific name is *Carduelis tristis*.

The science of naming and classifying organisms, including birds, according to standardized rules is called **taxonomy,** and the scientists who do this work are taxonomists. A **taxon** (pl. taxa) is any group of animals that is recognized in a classification. The Class Aves is a taxon that includes all species of living birds.

The rules of taxonomy are based on the system of nomenclature developed from 1735 to 1758 by Carolus Linnaeus, a Swedish botanist. Linnaeus assigned two latinized names to each species: the first denotes the genus—a group of similar, related species; the second denotes the species. The genus name is always capitalized, the species name is never capitalized, and both are italicized. Thus, the American Goldfinch is known formally as *Carduelis tristis,* which is a taxon that includes all individuals and populations of that species. This particular combination of names is unique; no other bird species—indeed, no other animal species—may have this same pair of names.

In addition to their scientific names, birds have English names as well as names in other languages. The American Ornithological Society establishes and regularly revises a list of valid names, both English and scientific, for all bird species in North America. The International Ornithologists' Union prepares lists of recommended standardized names in English, French, and Spanish (e.g., Gill and Donsker 2018).

Linnaeus perceived that all organisms could be classified in a **hierarchy,** or in nested sets of groups with increasingly closer relationships. Charles Darwin discovered that this hierarchy was the result of evolutionary history. For example, a cursory survey of North American birds will distinguish woodpeckers from owls. Less obvious are the differences between the Downy Woodpecker, the Red-bellied Woodpecker, and the Northern Flicker or the differences between the Great Horned Owl, the Barred Owl, and the Eastern Screech Owl. Recognition of the subtle differences between the Downy Woodpecker and the Hairy Woodpecker (Figure 3–2) or between the Eastern Screech Owl and the Whiskered Screech Owl requires even more expertise.



(A) James Zipp/Getty Images. (B) Don Johnston/Getty Images. (C) Zipp Jim/Getty Images

Figure 3–2 Three species of woodpeckers: (A) Downy Woodpecker; (B) Hairy Woodpecker; (C) Northern Flicker. The Downy Woodpecker (*Picoides pubescens*) and the Hairy Woodpecker (*Picoides villosus*) are more closely related to each other than either is to the Northern Flicker (*Colaptes auratus*).

Related taxa—those sharing a more recent common evolutionary history, as do the species of woodpeckers or owls or as do birds as a whole—constitute a **lineage.** As we discover more of the details of the phylogeny of birds, the classification of birds continues to change (see below). However, ornithologists now classify the diverse species of modern birds into 40 or more different major lineages, which are recognized as orders. Owls and woodpeckers are in different orders, Strigiformes and Piciformes, respectively. Note that the name of each order ends in “-formes.” In turn, each of the 40 or more orders comprises a hierarchical set of families and genera. All woodpeckers are classified in the same order and in the same family, the Picidae. Each bird family name ends in “-idae.” The very similar, closely related Downy Woodpecker and Hairy Woodpecker are classified in the genus *Picoides*, but the less closely related Northern Flicker is classified in the genus *Colaptes*, along with other species of flickers (Table 3–1).

Table 3–1 *Classification of Three Species of Woodpeckers*

Common Name	**Downy Woodpecker**	**Hairy Woodpecker**	**Northern Flicker**
Class	Aves	Aves	Aves
Order	Piciformes	Piciformes	Piciformes
Family	Picidae	Picidae	Picidae
Genus	*Picoides*	*Picoides*	*Colaptes*
Species	*pubescens*	*villosus*	*auratus*

Note: Full scientific names include the genus as well as the species, so the scientific name of the Downy Woodpecker, for example, is *Picoides pubescens*.

3.2 Phylogeny and Classification

The process of naming and classifying birds is an ancient and continuing one. *Ornithologiae*, by Francis Willoughby and John Ray, published in 1676, was the first formal classification of birds. This "cornerstone of modern systematic ornithology" (Zimmer 1926) arranged all birds then known into a logical, hierarchical classification. Nearly a century later, Linnaeus used this elementary classification as the model for subsequent classifications. These early efforts, however, classified birds according to superficial adaptations to aquatic versus terrestrial habitats, for example, rather than according to evolutionary relationship.

Charles Darwin's theory of evolution by natural selection transformed the philosophical basis of systematics into one based on common ancestries. In his classic work *On the Origin of Species by Means of Natural Selection* (1859), Darwin reflected on the hierarchy of similarity due to evolutionary relationships:

> I believe that the arrangement of the groups within each class, in due subordination and relation to each other, must be strictly genealogical in order to be natural; but that the amount of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or

> orders. [Darwin 1859, p. 420]

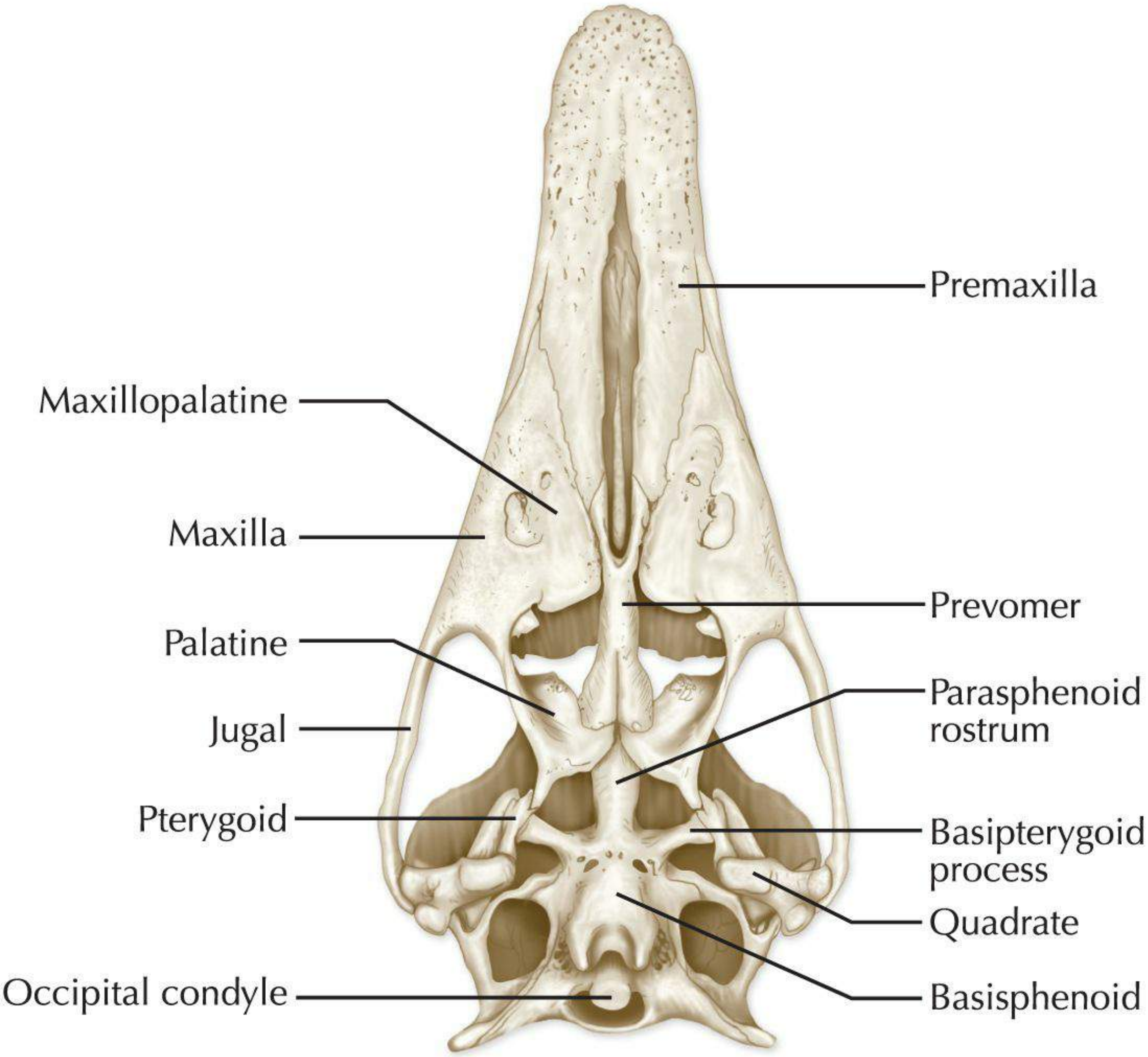
The goal of systematics is to discover the historic relationships of organisms, and prevailing classifications of birds attempt to portray these evolutionary relationships as proposed by Darwin. Theoretically, each taxon is **monophyletic;** that is, it includes all the descendants of a single common ancestor. A monophyletic group is also called a **clade.** A hierarchical organization of taxa indicates the relative closeness or distance of the evolutionary relationships among those taxa.

The Linnaean hierarchy was originally based on a limited number of traditional ranks, including class, order, family, genus, and species. As knowledge of biodiversity has expanded, new ranks have been introduced, such as subspecies and superfamily. However, it is clear that there can never been enough ranks to recognize all the branches in the Tree of Life as Linnaean taxa. Various efforts to replace or augment the Linnaean system with rankless clade names are being devised and debated in systematics.

3.3 Morphological Systematics

Reconstruction of the phylogeny of birds began with the analysis of morphological traits, or shared, derived anatomical characters that are the result of common ancestry. The evolutionary changes among birds in anatomy, structure, shape, and plumage provide evidence of their evolutionary history. Because different characters evolve at different rates, the challenge of morphological systematics is to find those characters that are informative to the phylogenetic branches one is trying to investigate. **Conservative characters**—those that do not easily change in the course of ecological adaptation—are of greater value for discovering older branches because they retain evidence of ancient ancestors. However, the possibility of convergence between unrelated species, which is prevalent in both external appearance and specific attributes (see section 1.4), poses a constant challenge to accurate reconstructions.

Darwin’s champion Thomas H. Huxley helped to lay the foundations of modern systematics in birds with his study of the arrangement of the bones of the avian bony palate, the skeletal partition between the nasal cavities and the mouth (Huxley 1867; Figure 3–3). Succeeding generations of ornithologists added new characters to the taxonomic tool kit. Some of the most important ones were the form of the nostrils, the structure of the leg muscles and tendons of the feet, the arrangement of toes, and the morphology of the vocal apparatus. Behavior, vocalizations, and proteins yielded clues to evolutionary relationships among some birds. So did plumage patterns of downy young (Figure 3–4).



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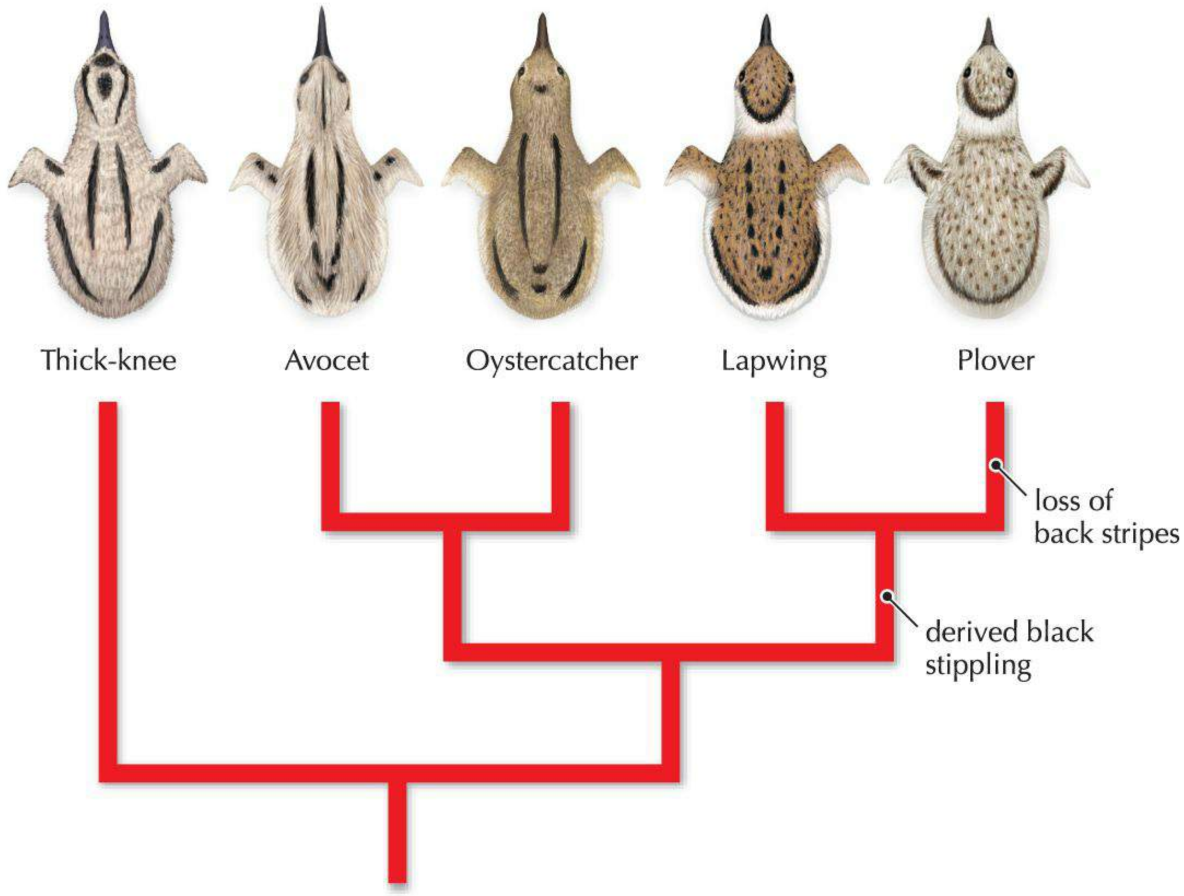
DATA FROM VAN TYNE AND BERGER 1976

Figure 3–3 Bony palate of the Greater Rhea, showing the complex arrangement of bones that represent the unique paleognathous palate of ratites and tinamous. All other birds have different arrangements of the elements of the bony palate.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
DATA FROM JEHL 1968, BAKER ET AL. 2007

Figure 3–4 The derived plumage color patterns of downy young shorebirds (Charadrii) provide evidence of the closer phylogenetic relationships of the lapwings and plovers (Charadriidae).

Unique characters define related groups of species—that is, those with a common ancestor. Perching birds, the members of the Order Passeriformes, for example, have several unique characters. They have unique sperm (Figure 12–7) and a preen gland with a unique nipple structure (Figure 4–25). They also have a specialized perching foot with a large hallux (rear-directed toe), uniquely arranged deep tendons, and simplified foot muscles that facilitate perching at the expense of more delicate toe movements (Raikow 1982). These features indicate that members of the Order Passeriformes evolved from a common ancestor; that is, they are monophyletic. Within perching birds, the explosively diverse songbirds, also called oscines, share a unique, complex, and derived syrinx, or vocal organ, with six pairs of intrinsic muscles (Figure 8–7). Thus, one cannot know in advance what sort of morphological features will provide evidence of the monophyly of a group of birds.

Morphological characters are often subject to convergent evolution among unrelated species. The details of foot structure reveal how unrelated birds evolved similar—but not identical—arrangements of the four toes (Bock and Miller 1959). Most perching birds have **anisodactyl** feet, with three forward toes and one rear toe (Figure 3–5), which is the primitive condition for all birds going back to *Archaeopteryx* and other theropod dinosaurs. However, at least eight groups—including almost all woodpeckers and their allies, most parrots, cuckoos, owls, the Osprey, turacos, and some swifts—have **zygodactyl** feet, with the first and fourth digits pointing backward and the second and third digits pointing forward. Different orientations of the working surfaces (condyles) of cuckoo toe bones versus woodpecker toe bones, for example, indicate that these unrelated birds have evolved the zygodactyl foot arrangement in different ways.

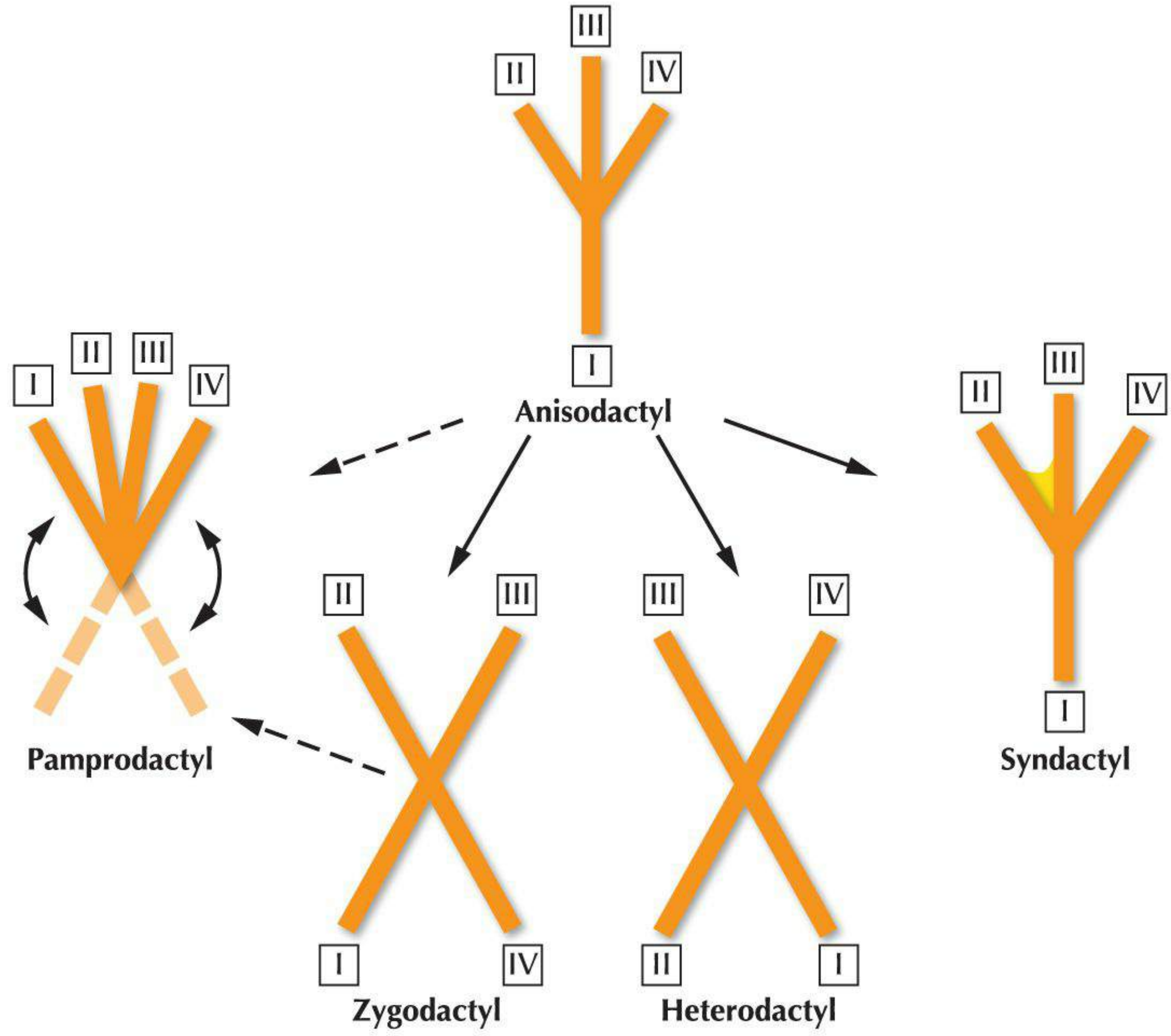


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Figure 3–5 The evolution of toe arrangements in birds (right feet shown). The common arrangement of toes II, III, and IV in front and the hallux (digit I) pointing to the rear is called anisodactyl, and it is the primitive condition in birds. Several different alternatives have evolved from the anisodactyl arrangement (arrows). The syndactyl foot, in which the bases of toes II and III are fused, characterizes the kingfishers, broadbills, and manakins. The zygodactyl arrangement, with toes II and III pointing forward and toes I and IV pointing backward, has evolved multiple times in the evolution of birds. In trogons, toes I and II, not toes I and IV, are rear directed (called heterodactyl). In the pamprodactyl foot of mousebirds and swifts, the positions of toes I and IV are not fixed; all four toes may point to the front. Dashed arrows indicate alternative origins of pamprodactyl toe arrangements.

Still other toe configurations are possible. Superficially, the trogons appear to have the zygodactyl toe arrangement, but the trogon’s first and second toes, not first and fourth, are directed backward, forming what is called the **heterodactyl** toe arrangement. The **syndactyl** foot, with two or three toes fused basally, characterizes the Order Coraciiformes and various families of perching birds, and the **pamprodactyl** foot, with all four toes directed forward, characterizes the mousebirds (Order Coliiformes) and some swifts (Order Apodiformes).

Morphological systematics of birds has been practiced for more than 200 years, and it was vitally important to the development of the phylogenetic systematics of birds. For example, the oscine passerines were first recognized as a taxonomic group on the basis of syringeal morphology in 1847 (Müller 1847). Morphological systematics remains essential to the analysis and classification of fossil birds (Mayr 2009). However, morphological data have proved to be less efficient at reconstructing the phylogeny of living birds than DNA sequence data. Although the characters used in morphological systematics are more reliable on average, character for character, than are DNA base pairs, the genomes of birds provide many millions of potential characters that evolve at a great variety of different rates.

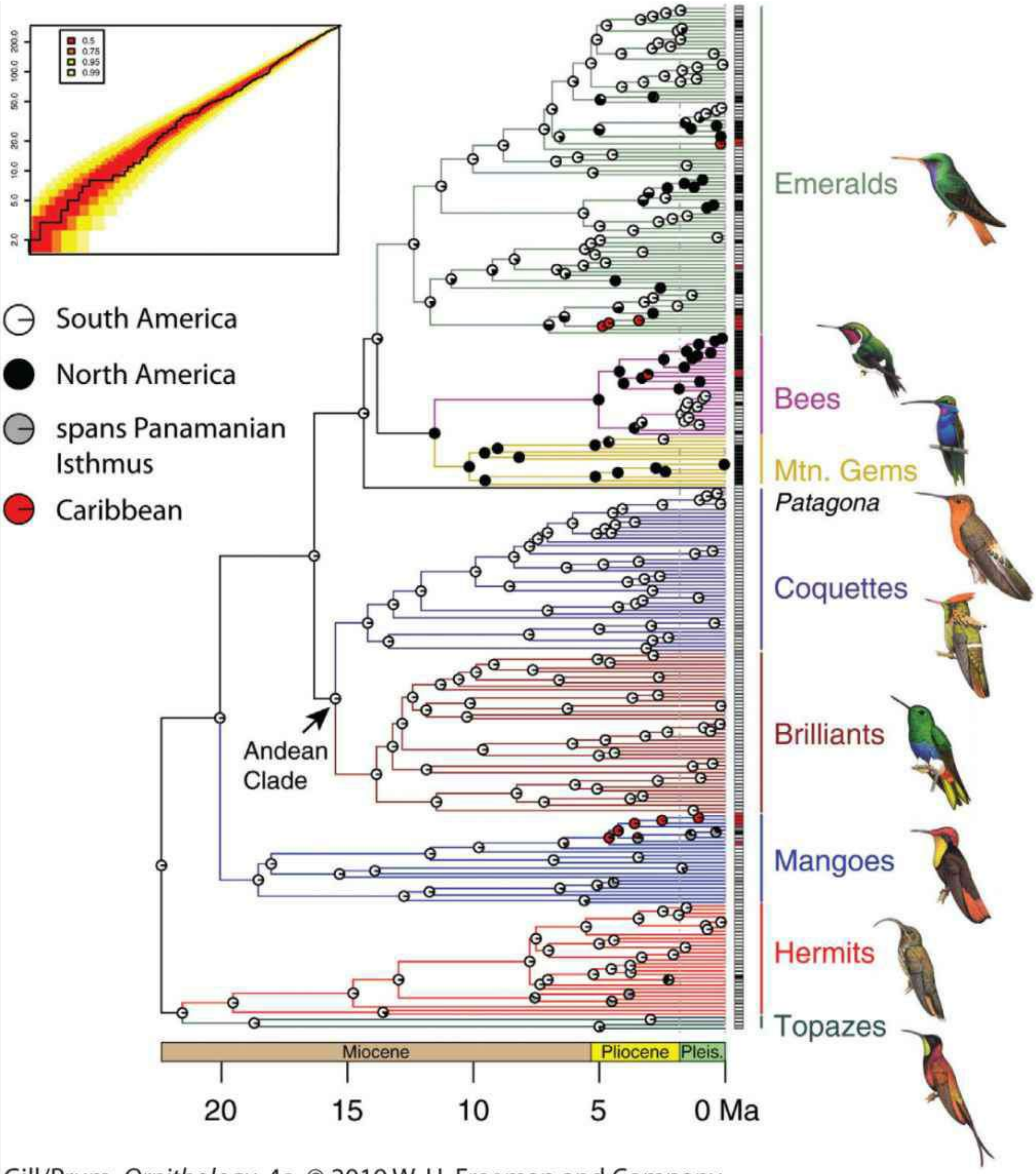
3.4 Molecular Systematics

The technology for sequencing DNA has revolutionized the investigation of the evolutionary relationships of birds. The logic of molecular phylogenetics is the same—shared, derived character states provide evidence of the recency of common ancestry. However, the character states are the identity of individual bases in the genome—adenine, thymine, cytosine, or guanine.

Rapidly increasing knowledge of DNA structure enables testing of earlier hypotheses based on morphological characters. Molecular studies often corroborate previous morphological evidence of relationships. However, molecular systematic analyses also challenge traditional views, reveal overlooked cases of convergence, and discover unsuspected relationships among taxa.

Automated gene sequencing and a growing selection of genes that evolve at different rates now allow the comprehensive construction of avian phylogenies. Faster-evolving genes, such as those encoded by mitochondrial DNA, help to resolve relationships among closely related species. Slower-evolving nuclear genes and intergenic DNA sequences help to resolve more ancient relationships. Phylogenetic studies at the family level often include data from multiple nuclear and mitochondrial genes.

For example, Jimmy McGuire and colleagues (2014) reconstructed the phylogeny of the hummingbirds using DNA sequences from four nuclear and two mitochondrial genes from 284 of the 338 species in the hummingbird family (Trochilidae). They identified nine major clades of hummingbirds that vary coherently in morphology, ecology, and geography (Figure 3–6). Among the results are the following:



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
REPUBLISHED WITH PERMISSION FROM ELSEVIER, J. A. MCGUIRE, C. C.WITT, ET AL., "MOLECULAR PHYLOGENETICS AND THE DIVERSIFICATION OF HUMMINGBIRDS," CURRENT BIOLOGY, 2014, 24(8), PP. 910–916, FIGURE 1. PERMISSION CONVEYED THROUGH COPYRIGHT CLEARANCE CENTER, INC.

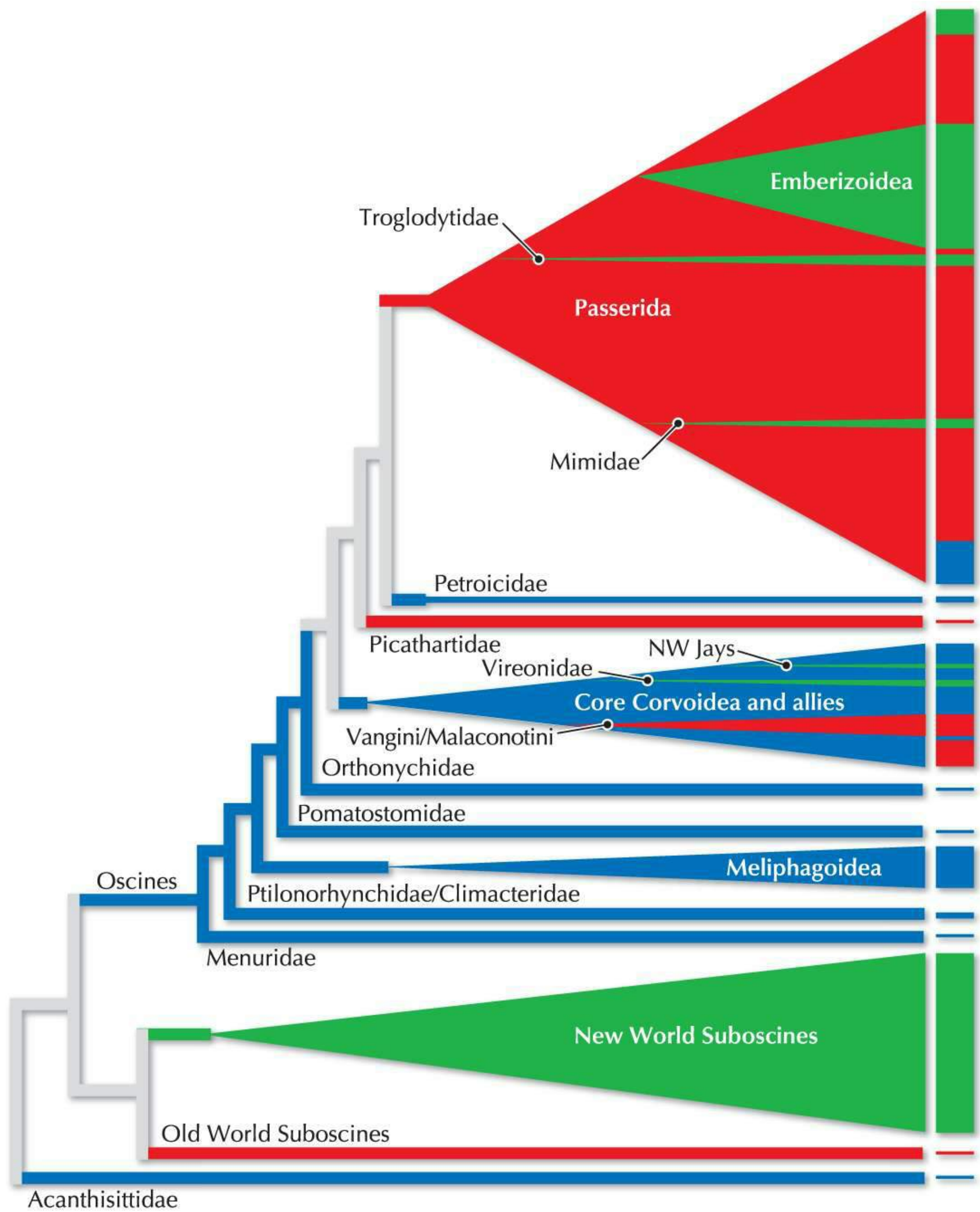
Figure 3–6 Time-calibrated phylogenetic tree of the major groups of hummingbirds. Note the explosive evolution and diversification of the Andean Brilliants and Coquettes (black arrow) during the Miocene.

- The hermits and topazes are the monophyletic sister group to the rest of the living hummingbirds.

- The coquettes and brilliants form a clade that has radiated explosively in the Andes of South America since the late Miocene.
- Most hummingbirds in the United States and Canada are relatively recent arrivals from the “bee” hummingbird clade of Central America.

As we will see in many chapters of this book, phylogenies provide essential tools for understanding the evolutionary history of avian biodiversity. For example, this hummingbird phylogeny documents the important impact of the Andean uplift in the diversification of the hummingbirds. Around 140 hummingbird species are found in the Andes, which constitutes a small fraction of the land area of South America. The phylogeny shows that Andean hummingbirds evolved from relatively few ancestors that colonized this new montane habitat and evolved to exploit new ecological niches created there.

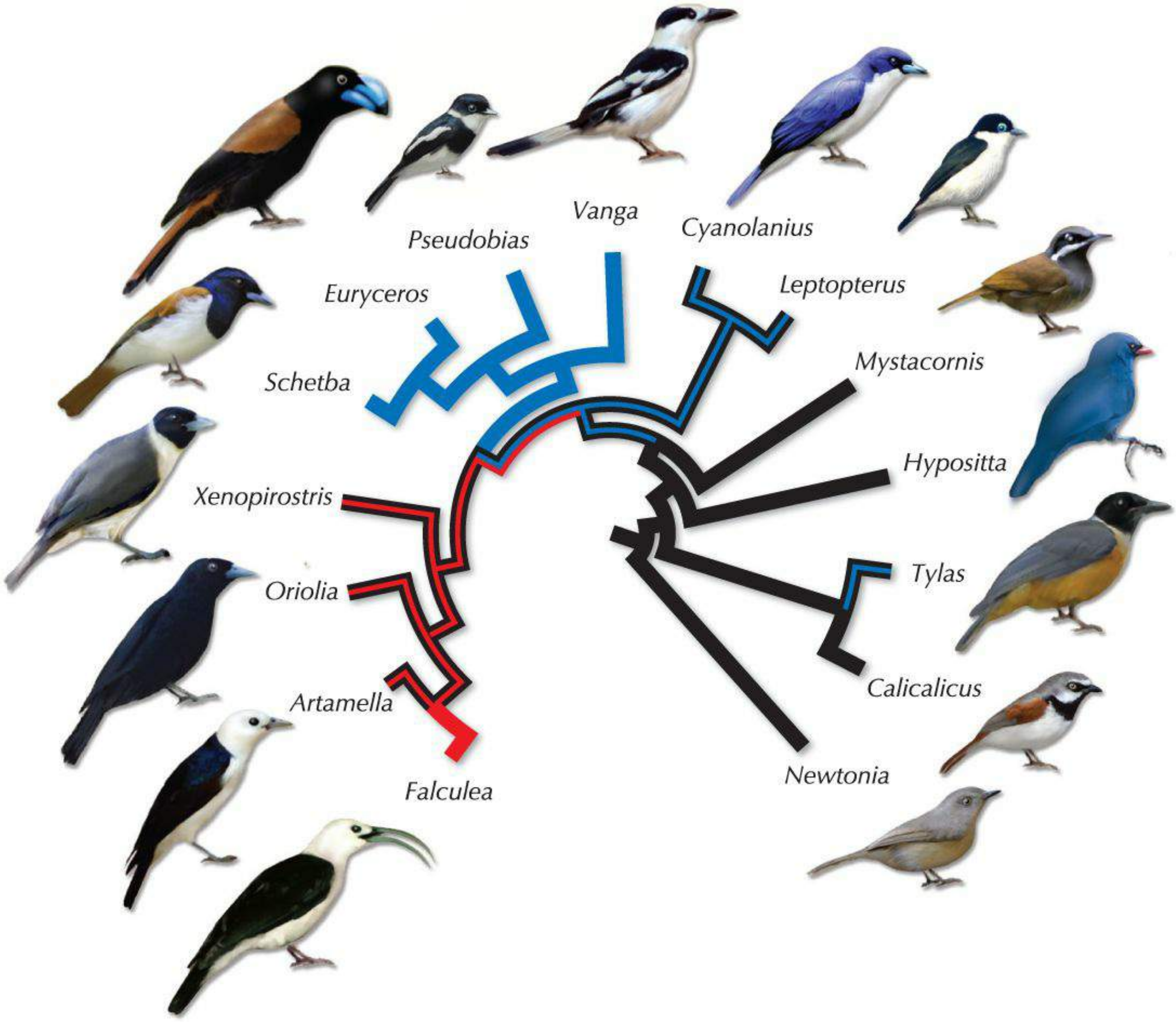
Multigene phylogenies have also revealed details about the evolution of perching birds (Passeriformes), including their biogeography (Figure 3–7). This single largest radiation of modern birds originated in ancient Australasia, followed by repeated worldwide expansions of successful groups (Barker et al. 2004). Two species of New Zealand wrens (Acanthisittidae), which represent the oldest perching bird lineage of all, still persist in New Zealand. The suboscine songbirds, which have simpler but more diverse syrinx than those of the oscine songbirds, split early into New World and Old World lineages. The New World suboscines—tyrant flycatchers, antbirds, and ovenbirds—became dominant members of the avifaunas of the New World tropics. The Old World suboscines—broadbills and pittas—did not. The oscine songbirds evolved and diversified originally in Australia, giving rise to a diverse radiation including lyrebirds (Menuridae), bowerbirds (Ptilonorhynchidae), honeyeaters (Meliphagidae), and others. Only a few lineages of oscine songbirds dispersed out of Australia and subsequently diversified into the two principal songbird clades—the Corvida and the Passerida—which became dominant components of most terrestrial bird communities around the world.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
Data from Barker et al. 2004

Figure 3–7 Phylogeny and diversification of songbirds (Passeriformes) based on two single-copy nuclear genes. The width of the bars on the right-hand edge of the tree are proportional to the number of species in each clade. The oscine songbirds evolved and diversified originally in Australia (blue). Only a few lineages of songbirds—the Corvida and the Passerida—subsequently expanded out of Australia into Eurasia and Africa (red) and North and South America (green) to diversify and become dominant components of terrestrial bird communities around the world.

Molecular phylogenies also provide insights into the evolution of avian morphology and ecology, particularly the process of **adaptive radiation,** in which a single ancestral lineage diversifies into an array of descendant species with an unusually high diversity of species or ecologies. For example, a phylogeny of the vangas (Vangidae) shows that a single common ancestor colonizing Madagascar radiated explosively into a diverse clade that encompasses an enormous range of diets and ecologies (Figure 3–8).



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DATA FROM REDDY ET AL. 2012

Figure 3–8 The 15 genera of Malagasy vangas include carnivores, frugivores, and insectivores, which forage by gleaning off of leafy vegetation (black lineages), catching insects in aerial sallies (blue lineages), and probing into hanging vegetation (red lineages).

3.5 Avian Phylogenomics

Advances in DNA sequencing technology have made it possible to investigate the phylogeny of birds with unprecedented genomic scale of data by incorporating dozens, hundreds, or thousands of genes from dozens or hundreds of species (Box 3–1). These phylogenomic studies have made tremendous progress in reconstructing the earliest branches in the phylogeny of birds and made it possible to understand the historical interrelationships of most orders of living birds (Hackett et al. 2008; Jarvis et al. 2014; Prum et al. 2015).

Box 3–1

A "Flock" of Avian Genomes

A **genome** is the complete set of genetic material of an organism. Just as the complete genome sequences have revolutionized many areas of biology and medicine, our expanding knowledge of avian genomes is contributing greatly to our understanding of avian genetics, evolution, and diversity.

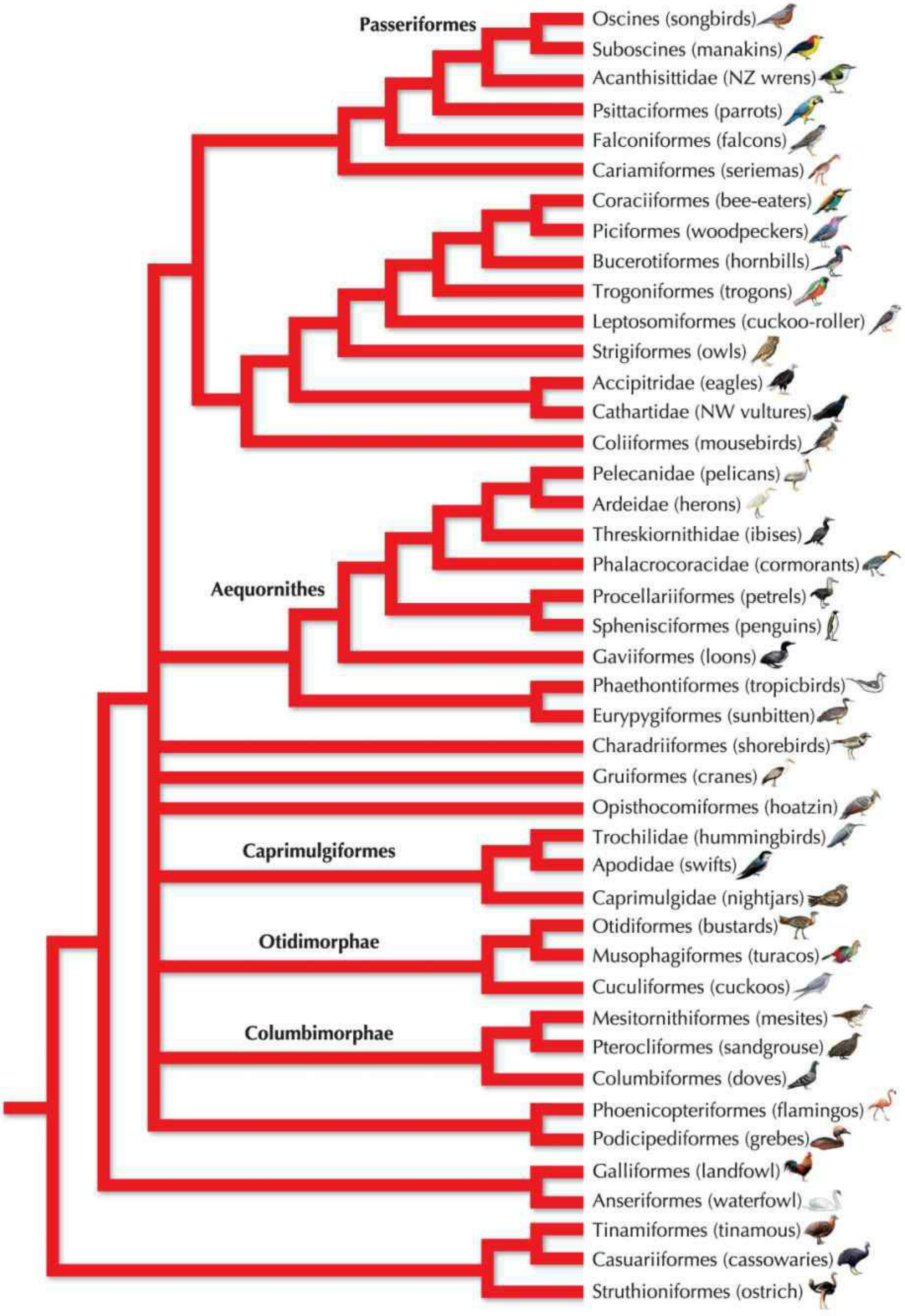
Because of the economic importance of the species, the chicken genome was the first avian genome to be published (Hillier et al. 2004). The chicken genome was followed soon by complete genomes for the Wild Turkey and Zebra Finch. Then, in 2015, a consortium of more than 100 researchers published a "flock of genomes," raising the total to 48 complete, annotated avian genomes from across all major lineages of birds from cuckoos to crows, hummingbirds to hoatzin, and ostriches to owls (Zhang et al. 2014a). Many more avian genomes are currently being sequenced, compiled, and annotated.

This unprecedented scale of genetic data allows us to make exciting new progress in ornithology. Avian genomes are smaller than the genomes of mammals and other reptiles, which range between 1.0 and 8 Gb (gigabases, or a billion nucleotides). The smallest known avian genome is 0.9 Gb in the Black-chinned Hummingbird, and the largest is 1.3 Gb in the ostrich. Because the size of the cell nucleus varies positively with genome size, paleontologists have used fossilized bone cells from 31 extinct dinosaurs to show that the reduced genome size of birds is the result of a long trend toward genome reduction in dinosaurs and other archosaurs (Organ et al. 2007). Reduction of avian genome size has involved the loss of more than 1,200 genes and the shortening of noncoding sequences within genes (called introns) and intergene regions. Birds are also unusual among vertebrates in that approximately two-thirds of their chromosomes consist of tiny microchromosomes. Large segments of the avian genome were lost when the ancestral, reptilian macrochromosomes broke apart to form these smaller microchromosomes.

Avian genomes provide critical insights into the evolution of novel avian gene families, including the feather beta-keratins (Chapter 4). Genomic analysis shows that the major diversity of feather keratins evolved before the origin of modern birds but that land birds have twice the number of feather keratin genes as waterbirds.

Through a combination of focused sequencing efforts and comparative genetic research, avian genomes will continue to revolutionize ornithology. In 2015, the Bird 10,000 Genome Project (B10K) announced the goal to sequence the genomes of all avian families, genera, and species in three phases over the next decade (Zhang et al. 2014a). Meanwhile, investigations using genomic tools to study the evolution of the wild bird morphology, physiology, and behavior will become a central tool in ornithology. It is likely that many genetic contributions to avian morphology, physiology, and behavior—from webbed toes to hibernation and migration—will be discovered and analyzed.

Despite the diversity of approaches, phylogenomic studies are uncovering many areas of strong agreement that provide confidence that we are reaching a clear understanding of the early phylogeny of birds (Figure 3–9). The details of these phylogenetic relationships could fill several chapters, but here is a sample of them:



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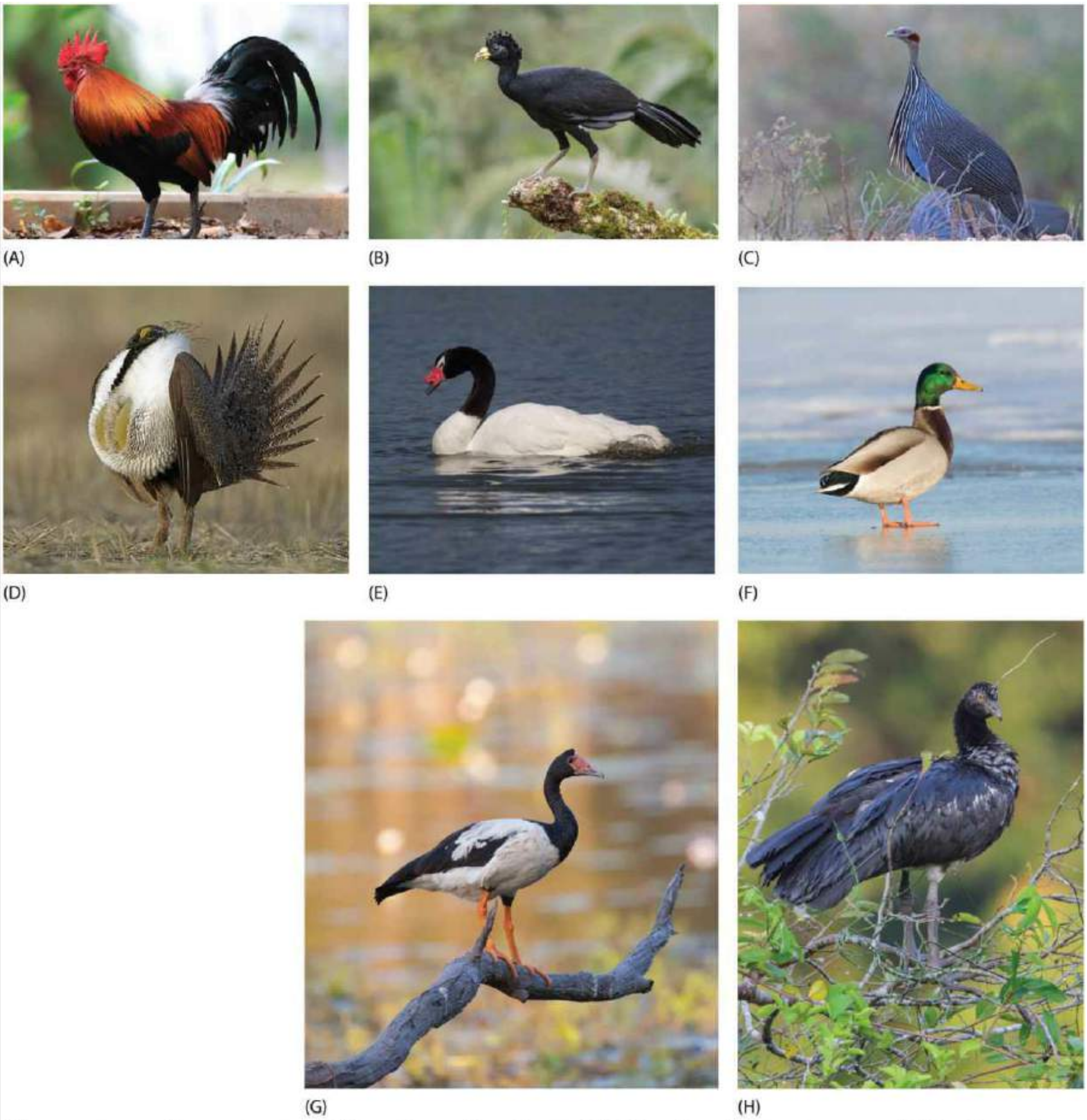
DATA FROM SUH 2016

Figure 3–9 The emerging consensus of phylogenomic studies of the avian Tree of Life. The major clade Neoaves consists of five to nine major lineages

- The Paleognathes—including the flying tinamous (Tinamidae) and the flightless ostriches, rheas, kiwi, emus, and cassowaries—are the sister group to the rest of living birds.
- The next branch includes the Galloanseres—the waterfowl and the pheasants and other game birds (Figure 3–10). It is the sister group to all the remaining birds—a clade called Neoaves.
- Within Neoaves, different studies generally agree on the existence of five to nine major clades.
- Some of the unexpected neoavian clades include the turacos, bustards, and cuckoos; the grebes and flamingos; and the doves, sandgrouse, and mesites (Figure 3–11).
- The diurnal swifts and hummingbirds have evolved from within the nocturnal nightjars and their relatives (Order Caprimulgiformes).
- There is a major land bird clade. Within the land birds, the closest relatives of the perching birds are the parrots, falcons, and South American seriemas, respectively.
- The ancestor of all land birds—that is, the most recent common ancestor of perching birds, parrots, woodpeckers, kingfishers, and so on—was a predator.



(A) featherCollector/Shutterstock.com. (B) Glenn Bartley/Getty Images. (C) © Geoff Jones/barraimaging.com.au. (D) Tom Reichner/Shutterstock. (E) © Geoff Jones/barraimaging.com.au. (F) Picture Press/S.-E. Arndt/Getty Images. (G) © Geoff Jones/barraimaging.com.au. (H) Glenn Bartley/Getty Images

Figure 3–10 The fowl-like birds (Galliformes) (A–D) and waterfowl (Anseriformes) (E–H) were among the earliest lineages of successful modern birds, the Galloanseres: (A) Red Junglefowl, (B) Great Currasow, (C) Vulturine Guineafowl, (D) Sage Grouse, (E) Black-necked Swan, (F) Mallard, (G) Magpie Goose, and (H) Horned Screamer.

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Figure 3–11 Representatives of major clades of Neoaves: (A) Spotted Nightjar, (B) Fiery-throated Hummingbird, (C) Great Bustard, (D) Yellow-bibbed Fruit Dove, (E) Red-legged Seriema, (F) Australian Hobby, (G) Great-billed Parrot, and (H) American Robin.

The age of the orders of modern birds has been contentious. However, the most recent calibrations of the radiation of living birds imply that only three living lineages of birds survived the Cretaceous-Paleogene mass extinction event: the ancestors of the Paleognathes, the Galloanseres, and the Neoaves (Prum et al. 2015). Very rapidly thereafter, at the beginning of the Paleogene, the neoavian birds differentiated explosively, giving rise to most major lineages in just a few million years. It is these short, rapid branching events that have made the reconstruction of Neoavian phylogeny so challenging. But our knowledge and confidence about higher avian phylogeny is advancing rapidly.

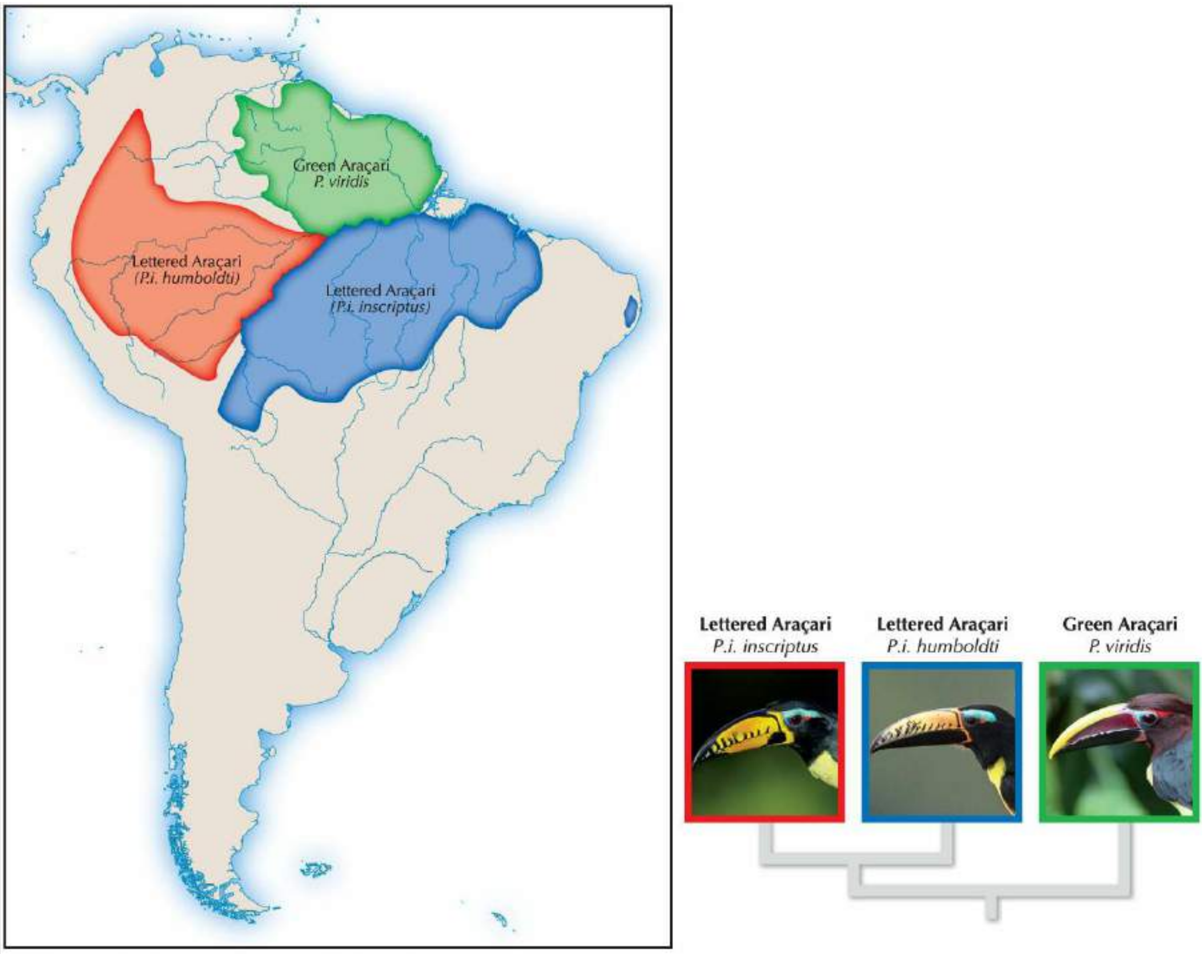
3.6 Species and Speciation

Species are fundamental units of biological classification. Bird species have characteristic sizes, shapes, songs, and colors as well as ecological niches and geographical ranges. Different species may interact ecologically, but they do not freely exchange genes or novel genetic-based adaptations. One prominent definition, the **Biological Species Concept (BSC),** states, “Species are groups of interbreeding natural populations that are reproductively isolated from other such groups” (Mayr 1970, p. 12). The criteria in the definition of biological species are the reproductive compatibility of individual organisms and the potential for the genetic exchange between two populations. Because the biological species concept may not provide the best units for investigating evolutionary history, ornithologists have been considering the alternative **Phylogenetic Species Concept (PSC)** and **Evolutionary Species Concept (ESC),** which are based on the phylogenetic history of lineages (Cracraft 1989; De Queiroz 2007; Sangster 2013). Chapter 19 considers both the process of speciation and the current debates about the species concept.

The process of **speciation** occurs through the division of one species into two or more descendant species as a result of the genetic divergence of isolated populations. Geographical separation of populations reduces the exchange of genes, thereby allowing independent divergence and enabling speciation. Most species of birds evolve as geographical isolates, although other kinds of reproductive isolation may sometimes play a role.

Bird populations become geographically isolated in two principal ways. First, pioneering individual birds may colonize an area, such as an oceanic island, and thus are separated from their main population. Classic examples of divergence and speciation come from remote islands such as the Galápagos and Hawaiian archipelagos. The birds on the Channel Islands off the coast of southern California also are distinct, as are the kingfishers on small satellite islands off the coast of New Guinea. On the mainland, islands of special habitats, such as desert oases or subalpine mountain forests, may set a similar stage for divergence and speciation of the populations that occupy them.

Fragmentation of habitats that were once continuous is the second way in which bird populations may become isolated. Some ornithologists think that the dry, cold climates of the Pleistocene epoch, for example, shrank the great Amazonian rain forests into much smaller fragments surrounded by grasslands (Haffer 1974). Recent molecular phylogenetic studies indicate that the differentiation of Amazonian forest birds predates the Pleistocene and that major rivers served as isolation barriers (Figure 3–12).



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DATA FROM CRACRAFT AND PRUM 1988, PATEL ET AL. 2011. IMAGES OF LETTERED ARAÇARI: GLENN BARTLEY/GETTY IMAGES; GREEN ARAÇARI: BLICKWINKEL/ALAMY

Figure 3–12 The ranges in Amazonia of three small toucans—the Green Araçari (*Pteroglossus viridis*) and two subspecies of the Lettered Araçari (*Pteroglossus inscriptus*)—reflect the history of past isolation of wet forest habitats.

Remnant populations are one of the consequences of historical changes. Ostriches, now restricted to Africa, once roamed throughout Asia. Hummingbirds, now restricted to North and South America, once hovered in what is now Europe. Tiny colorful relatives of kingfishers, called todies, are currently found only on the Greater Antilles of the West Indies, but they once also lived in Wyoming and France (Olson 1985). Widely separated areas may consequently share peculiar taxa. The very closely related species Azure-winged Magpie and Iberian

Magpie are found over 9,000 kilometers apart in eastern Asia and in Spain and Portugal, respectively (Kryukov et al. 2004).

Although the general patterns of geographical speciation in birds are well known, the details of the process of speciation are not. Slow adaptive divergence of populations and rapid genetic reorganization in small populations appear to be the primary modes of speciation. Still to be resolved are the roles of ecological and social adaptations as well as the timing and nature of the related genetic changes.

REVIEW KEY CONCEPTS

3.1 Scientific Names

Systematics is the study of the evolutionary relationships and diversity of organisms. Phylogeny is the explicit history of genealogical relationships among organisms, which is depicted as a tree. Taxonomy is the formal, hierarchical system of names attached to species and higher groups of organisms, including genus, family, order, and class. Related taxa constitute an evolving lineage that diversifies over time.

Key Terms: systematics, phylogeny, taxonomy, taxon/taxa, hierarchy, lineage

3.2 Phylogeny and Classification

As Darwin predicted, modern classifications recognize the phylogenetic history of organisms in terms of a hierarchical taxonomy. Each higher taxon recognized in a classification is hypothesized to be monophyletic—that is, it includes all the descendants of a single common ancestor.

Key Terms: monophyletic, clade

3.3 Morphological Systematics

Avian systematics uses shared, derived morphological traits characters to reconstruct shared ancestry. In general, conservative characters that do not change rapidly with ecology are the most informative. Phylogenetically informative morphological characters come from across the entire phenotype, including skeletal form, the leg and wing muscles, and the syrinx.

Key Terms: conservative characters, anisodactyl, zygodactyl, heterodactyl, syndactyl, pamprodactyl

3.4 Molecular Systematics

Molecular systematics involves identifying shared, derived characters in the sequence of the DNA of the organisms. Molecular phylogenies now provide stable, well-resolved hypotheses of relationship for the majority of birds of the world. For example, molecular phylogenetic data discovered that the early radiation of the oscine songbirds took place in Australia and that only a few lineages expanded out of Australia and radiated to become an important component of the avifauna of the rest of the world. Molecular phylogenies provide evidence to support adaptive radiation—disparate or rapid ecological diversification from a single common ancestor—as demonstrated by the vangas of Madagascar (Vangidae).

Key Term: adaptive radiation

3.5 Avian Phylogenomics

Recent advances in DNA sequencing make it possible to reconstruct entire avian genomes and to investigate avian phylogeny with large, genomic-scale data sets. “Next-generation” sequencing efforts have provided new insights and resolution to the higher-level phylogeny of birds—that is, the oldest branches in the avian family tree. For example, the diurnal swifts and hummingbirds have been shown to have evolved from within a radiation of nocturnal insectivores called Caprimuliformes. Likewise, the closest relatives of the perching birds are the parrots, falcons, and seriemas.

Key Term: genome

3.6 Species and Speciation

Species are fundamental units of biological classification. Species concepts can be defined in terms of current barriers to reproduction—as in the Biological Species Concept—or in terms of the phylogenetic history of lineages—as in the Phylogenetic and Evolutionary Species Concepts. Speciation is the process by which new species are formed. Most species of birds evolve through geographical isolation, although other mechanisms of reproductive isolation may sometimes play a role.

Key Terms: species, Biological Species Concept (BSC), Phylogenetic Species Concept (PSC), Evolutionary Species Concept (ESC), speciation

APPLY YOUR KNOWLEDGE

1. Why did the advent of DNA sequence analysis corroborate many of the taxa based on the older methods of grouping birds on morphological characters?
2. How is the organization of a drawer of silverware or a collection of minerals similar to the Linnaean organization of taxa and different from the modern organization of birds within taxa?
3. Compare and contrast the challenges and methods by which fossil birds from fossils and modern, living birds can be organized into a comprehensive phylogeny.
4. Reflect on the genetic diversity within a species and between

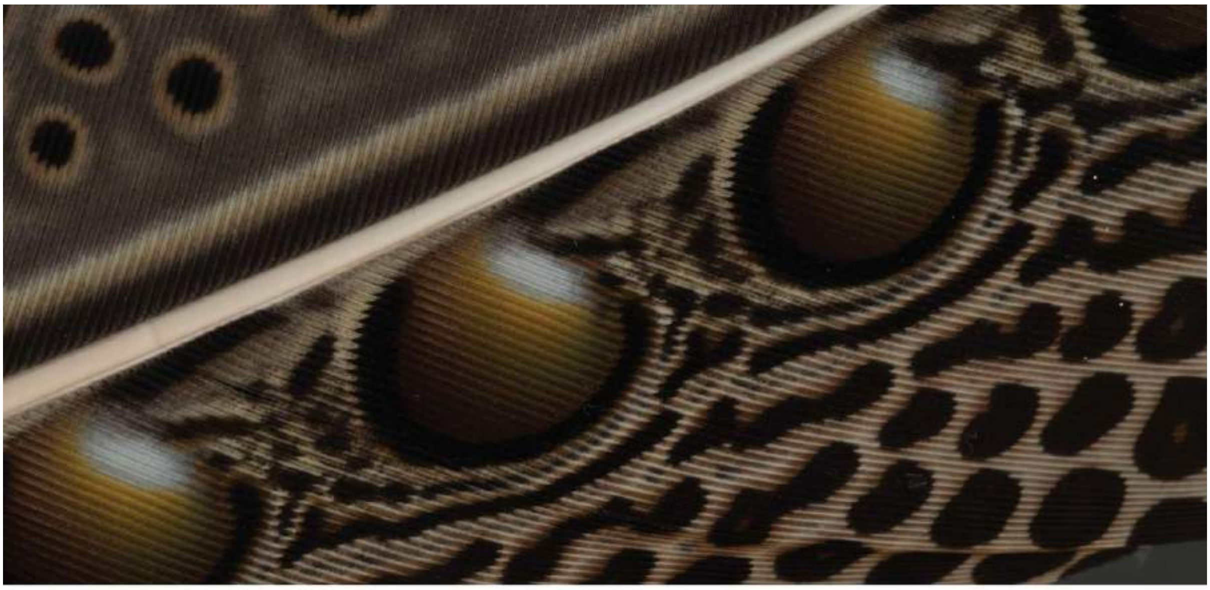
separate, closely related species that sometimes hybridize. What factors would you use to conclude that the two populations either were separate or the same species?

5. Define the terms *clade*, *taxon*, and *phylogeny*.
6. How are conservative characters and new, recently evolved, unique characters used to determine common ancestors and convergence?
7. What factors have contributed to the rapid diversification (speciation) of birds?

PART II *Form and Function*

Indian Peafowl [apiguide/Shutterstock.com]

CHAPTER 4 *Feathers*



MICHAEL DOOLITTLE

The complex feather pigmentation patterns of the secondary feathers of the male Great Argus create the impression of a series of three-dimensional golden spheres.

> Feathers are the most numerous, elaborate and diverse derivatives of the avian integument. [STETTENHEIM 2000, P. 461]

Feathers, the most distinctive feature of avian anatomy, are an extraordinary evolutionary innovation. Collectively referred to as the plumage, feathers are the most complex structures to grow out of the skin of any vertebrate, and they provide a rich diversity of functions in the lives of birds. They provide insulation for controlling body temperature, aerodynamic power for flight, and colors for communication and camouflage. Modified feathers also perform secondary roles—in swimming, sound production, hearing, protection, cleanliness, water repellency, water transport, tactile sensation, and support. The male Great Argus, an Asian pheasant, even uses its spectacular wing feathers to blow fallen leaves off of its display court (Davison 1982).

This chapter covers feather structures and functions. First, we consider basic feather structure and its variations, followed by a consideration of the major kinds of feathers in a bird’s plumage, their development, and their evolution. Highlighted next are the details of feather pigmentation and nanostructure that make birds so colorful. Feathers also host bacteria and ectoparasites. Their suppression requires regular preening, including application of oily secretions of the preen gland. Finally, seasonal molts replace worn feathers with new ones and sometimes replace cryptically colored feathers with colorful ones or vice versa. A consideration of the relations of molts and plumages follows a review of the functions of plumage color patterns.

4.1 Feather Structure

Feathers consist mainly of **beta-keratin,** a fibrous protein polymer that forms microscopic filaments that have strong mechanical properties. Beta-keratins are unique to birds and other reptiles. Beta-keratins have similar mechanical properties to the alpha-keratins found in the skin of all vertebrates, including humans and birds, but they are an entirely unrelated family of proteins with a very different molecular structure. Beta-keratins make up most of the hard structures of reptilian skin and the leg scales, claws, and beaks of birds. Feather keratins are a special class of beta-keratins that are characterized by a small deletion in their molecular sequence (Brush 1993).

Contour Feathers

The details of bird feathers have fascinated biologists for centuries (Figures 4–1 and 4–2). The complex, hierarchically branched structure of feathers creates the possibility for enormous structural and functional diversity. We begin by reviewing the structure of a typical body feather, called a **contour feather,** because together contour feathers constitute the outline, or contour, of the body.

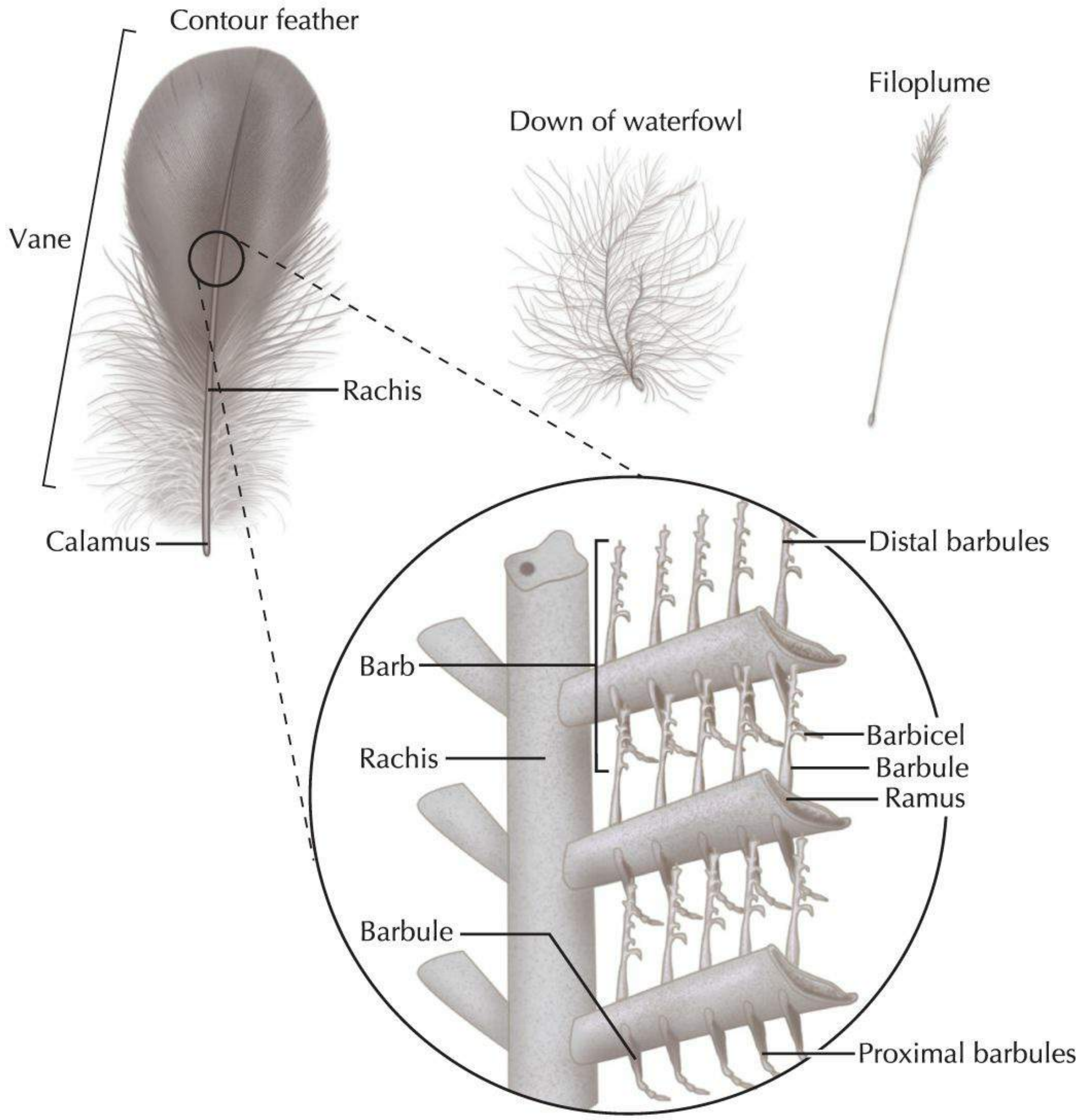


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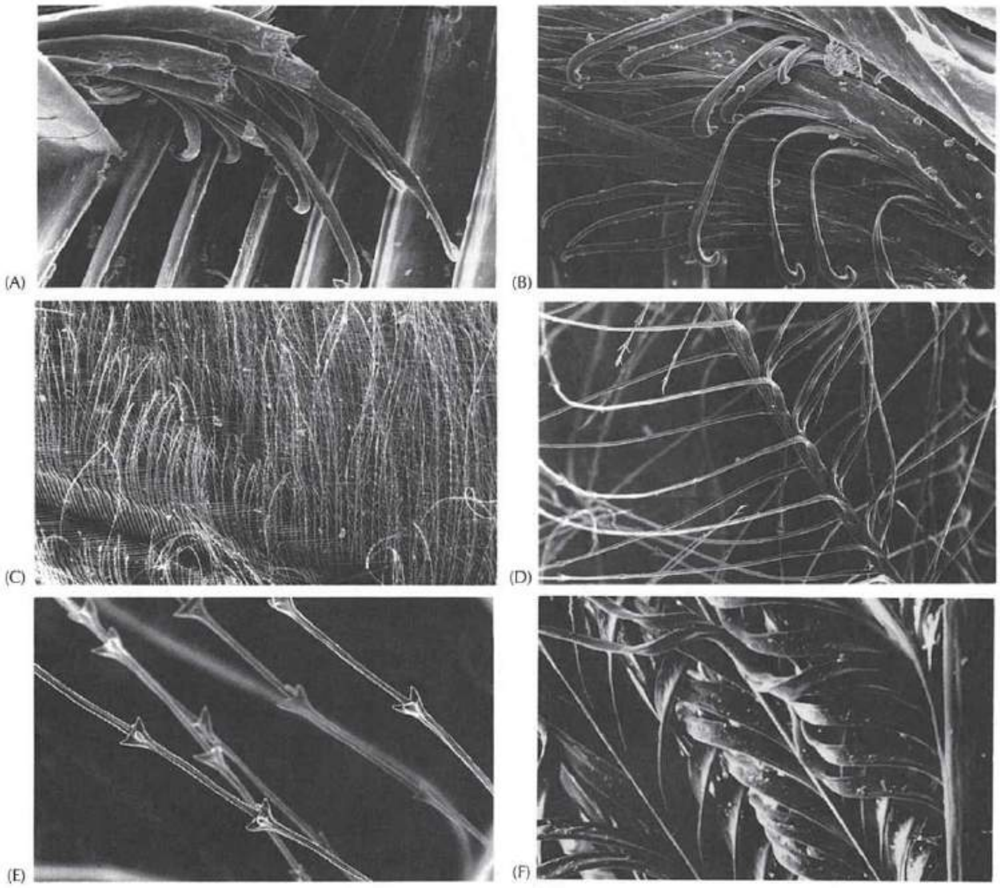
Figure 4–1 Structure of three kinds of feathers, with detailed structure of a typical contour feather.



COURTESY OF P. STETTENHEIM

Figure 4–2 Scanning electron micrographs of feather structures: (A) Wild Turkey, tail feather. Oblique view of distal barbules with hooklets interlocking with proximal barbules. 358×. (B) American Crow, wing feather. Distal barbules, displaced to show hooklets. Behind them are more distal barbules showing other, unhooked projections. 406×. (C) Barred Owl, upper wing covert. Dorsal oblique view. The vertical filaments are the tips of the distal barbules, which are unusually long. The elongate barbules create the velvety nap that quiets the airflow over the wings, producing the silent flight of most owls. 215×. (D) Domestic Goose, body down feather. Downy barb. The oblique thicker element is the ramus of the barb, and the thinner elements are the barbules. Although the down appears grossly to be a bunch of fluff, magnification shows that the barbules are arranged in a regular manner. 130×. (E) Domestic Goose, body down feather. Barbules on a downy barb, showing projections at each node, called nodal prongs. These prongs are homologous to the hooklets and other projections on pennaceous barbules. They are thought to serve in keeping the downy barbs from becoming entangled, thereby creating the fluffy texture, but how they do so is not known. 325×. (F) Namaqua Sandgrouse, abdominal feather. The vertical element on the right is the rachis, and the oblique elements are the rami of the barbs, bearing the coiled barbules that serve for holding water. 153×.

The fundamental features of a typical contour feather are a long central shaft and a broad, flat, planar **vane** on either side of this shaft. The tubular, hollow base of the shaft—the **calamus,** or quill—anchors the feather into the **follicle** in the surface of the skin. The rest of the shaft—the **rachis**—supports the feather vanes. Lateral branches off the rachis, called **barbs,** are the primary branches of the vane. Each barb consists of a tapered central axis, called the **ramus** (pl. **rami**), with rows of smaller branches, called **barbules,** projecting from both sides. The multicellular barb rami are composed of an outer layer of flattened **cortical cells** that are solid keratin around a spongy core of larger, box-shaped **medullary cells** that are empty and air-filled. The spongy medullary cells make barbs structurally strong and resistant to bending. Each barbule consists of a series of single cells fused end to end; the cells may be simple or may bear projections called **barbicels,** which may be elaborate and hooklike.

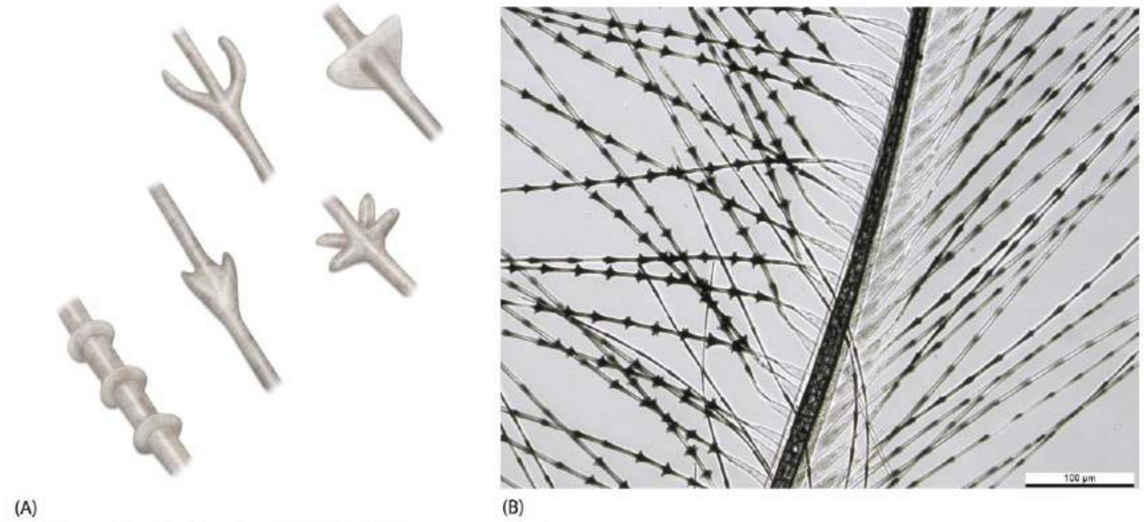
The barbs and barbules interlock to form the coherent but flexible surface of the pennaceous feather vane. This vane is created by the zippering interactions between the microscopic structures on the barbules on neighboring barbs. The **distal barbules** that extend toward the tip of the feather vane feature tiny hooklets. The **proximal barbules** that extend toward base of the feather have prominent grooves. The hooklets on the distal barbules reach over to connect with the grooves in the proximal barbules of the neighboring barb. Like Velcro, the mechanical interactions between these microscopic hooklets and grooved barbules create the planar vanes of pennaceous feathers.

Many contour feathers have a fluffy, downy, or **plumulaceous** portion of the vane, which is usually hidden, deep within the plumage. The downy barbules on the barbs at the base of the body feather are long, thin, and flexible and have small **nodal prongs** at the junctions of neighboring barbule cells. The downy bases of contour feathers provide insulation. The shape, distribution, and pigmentation of nodal prongs of down feathers provide critical evidence to the field of feather forensics (Box 4–1).

Box 4–1

Feather Forensics

Feather morphology can provide a unique source of forensic evidence in a diversity of investigations, including accidental bird–airplane impacts, industrial pollution, and wildlife smuggling (Dove and Koch 2011). The field of modern feather forensics was pioneered in the 1960s by Roxie Laybourne at the Smithsonian Institution and has been further developed in recent years by Carla Dove and others. Careful microscopic observations of feathers, especially downy barbules, has established highly distinctive and diagnostic features that can be used to identify many feather samples to order, family, or even species. The shape and pattern of pigmentation of nodal prongs, spines, and bases of plumulaceous barbules near the base of contour feathers are a particularly rich source of diagnostic characters. Because of the diversity and complexity of avian plumages and because some microscopic features are convergent among species with environment, feather forensics requires a vast knowledge of avian diversity and broad research experience with museum collections of birds of the world. Feather forensic researchers frequently testify in court about their findings. Dove’s forensic team at the Smithsonian has solved thousands of cases from around the world.



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Dove C. J.and S. L. Koch. 2011. Microscopy of feathers: A practical guide for forensic feather identification.
The Microscope 59: 51–77

(A) Variations in nodal prong morphology in downy feathers. (B) Photomicrograph of downy feather of the Ruby-throated Hummingbird, which shows an asymmetry in the width of the barbule bases that is characteristic of hummingbirds.

The contour feathers of some birds also include a secondary structure—an **afterfeather**—which is a mirror-image rachis and vane, attached to the same calamus (Figure 4–3). The barb and barbule structure of afterfeathers is typically plumulaceous. When the afterfeather is reduced to a simple rachis, it is called an **aftershaft.** The afterfeather’s primary function is to enhance insulation. Ptarmigans are grouse of high, cold alpine habitats. The afterfeathers of the winter plumage of a ptarmigan are three-fourths as long as the main feathers and provide essential insulation. The afterfeathers of its summer plumage are much shorter. In emus and cassowary, the main feather and the afterfeather are all identical in size (see Figure 4–3).

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Figure 4–3 Feathers with main vane and afterfeathers. (A) Contour feathers of a Wild Turkey have a pennaceous main vane, and a smaller, downy, afterfeather. (B) Contour feathers of Emu have a main vane and afterfeather of the same size.

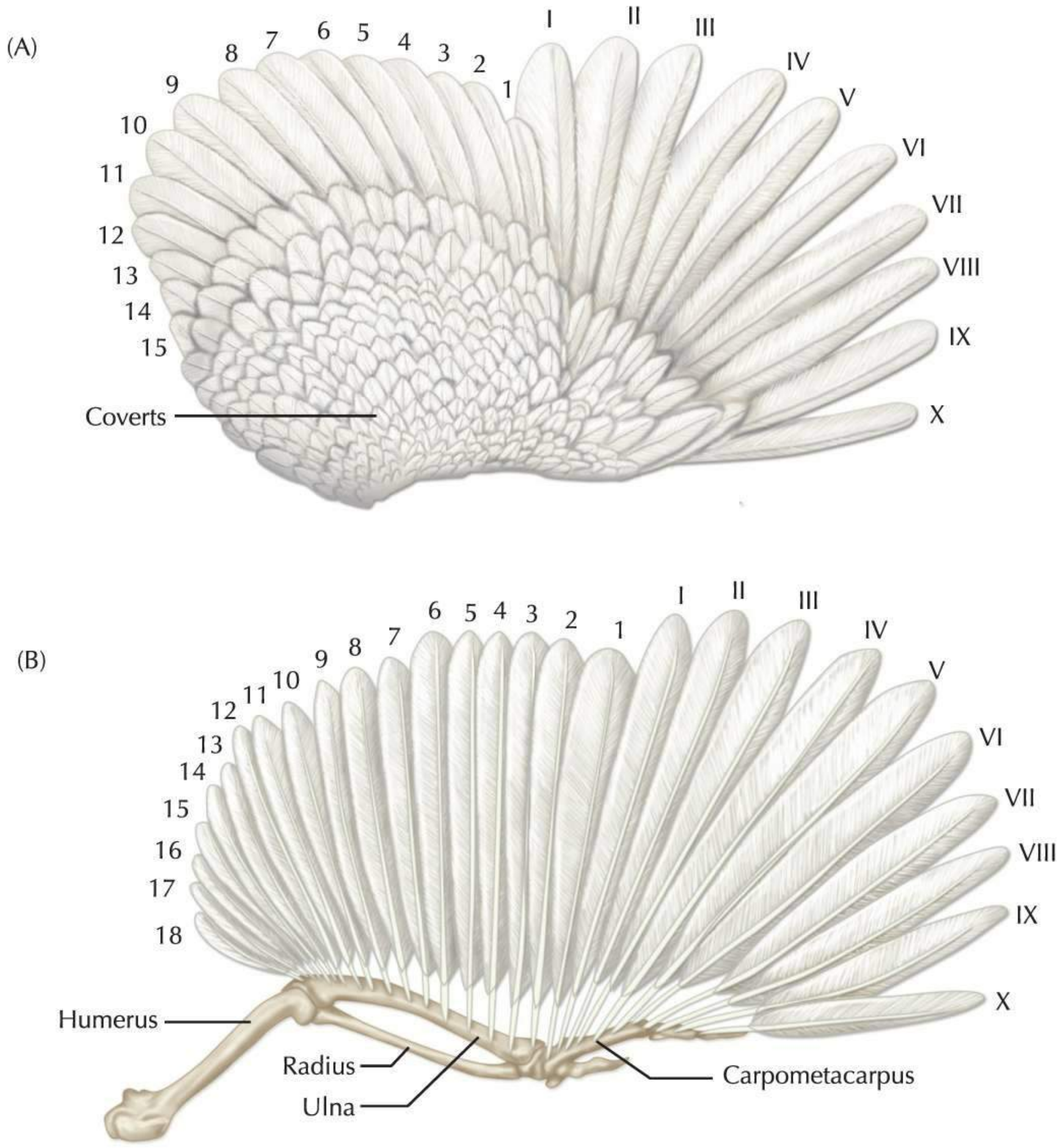
The smooth overlapping arrangement of vaned feathers in the plumage reduces air turbulence in flight. The tiny, flat contour feathers that cover a penguin’s body create a smooth, almost scaly surface that reduces friction during swimming.

Contour feathers are subject to striking modifications for different functions. Vane shapes range from long and pointed display feathers, like those on a rooster’s neck (called hackles), to short and round, like the head and facial feathers of small birds. The close spacing of large barbs with extra-long, curved barbicels produces water-repellent feathers in petrels, rails, and ducks. Conversely, the loss of these barbicels on contour feathers of cormorants and anhingas is an adaptation for diving. The loss of barbicels allows water to penetrate the plumage, soaking it and reducing buoyancy but requiring air drying of the feathers after a swim. Coiled barbules on the belly feathers of sandgrouse help them to transport water to their nestlings.

Flight Feathers

The flight feathers of a bird include the long, stiff, pennaceous, wing feathers, called **remiges** (sing. **remex**), and tail feathers, called **rectrices** (sing. **rectrix**). Because of their role in producing the aerodynamic forces necessary for flight, flight feathers have asymmetrical vanes in which the leading-edge vane of the feather is narrower than the trailing vane. Flight feathers have little importance in insulation, and all flight feathers lack an afterfeather.

The remiges create the aerodynamic forces that propel birds in flight (Figure 4–4). The outer (distal) remiges that attach to the bones of the hand and the second digit are called the **primaries.** The inner (proximal) flight feathers of the wing that attach to the trailing bone of the forearm, or ulna, are called the **secondaries** (see Figure 4–4). Most birds have 10 primaries; storks, flamingos, grebes, and rheas have 11; ostriches have 16; and some songbirds have nine. The flightless kiwis have only three or four primaries. The secondaries vary in number from six in hummingbirds to 19 in some owls and 40 in albatrosses.



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DATA FROM LUCAS AND STETTENHEIM 1972

Figure 4–4 Dorsal view (A) of the extended left wing of a White Leghorn Chicken and (B) of the skeletal attachments of the primaries and secondaries of the same wing. Primary remiges are numbered I to X; secondary remiges are numbered 1 to 15 in (A) or 1 to 18 in (B). Both primaries and secondary feathers are numbered starting at the wrist, and proceeding away from it.

Primaries are strongly asymmetrical in shape with the leading-edge vane narrower than the trailing vane. The outer primaries are often pointed at the tip. Secondaries also have asymmetrical vanes like primaries but blunter tips. In some species, secondary feathers have been modified for display purposes. For example, the broad, flaglike inner secondaries are essential for courtship in the Mandarin Duck. A quite different kind of modification for producing mechanical courtship sounds are the thickened, clublike feather shafts of the central secondaries of the Club-winged Manakin, a tiny denizen of montane cloud forests in northwestern South America (Box 4–2).

Box 4–2

The Bird That Calls Like a Cricket

Back in 1871, Darwin himself called attention to the thickened clublike shafts of the secondaries of the Club-winged Manakin as an example of how sexual selection could lead to the production of non-vocal, mechanical sounds in courtship. The mechanical sounds from the wings of this species substitute for the vocal sounds of other manakins (Bostwick and Prum 2003). Studies using high-speed video of the rapid-fire wing claps of this species revealed exactly how the shafts produce the courtship sound *tick-tick-ting* (Bostwick and Prum 2005). The mechanism is unique among birds and similar to the production of chirps by crickets (see the illustration). The fifth secondary acts as a “pick” that rubs back and forth across the ribbed surface of the adjacent sixth secondary as the secondaries oscillate back and forth over its back. The rubbing of the pick causes the hollow clublike shafts of the sixth and seventh secondaries to resonate and produce the *ting* as a sustained violin-like note.

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(A) TIM LAMAN/GETTY IMAGES

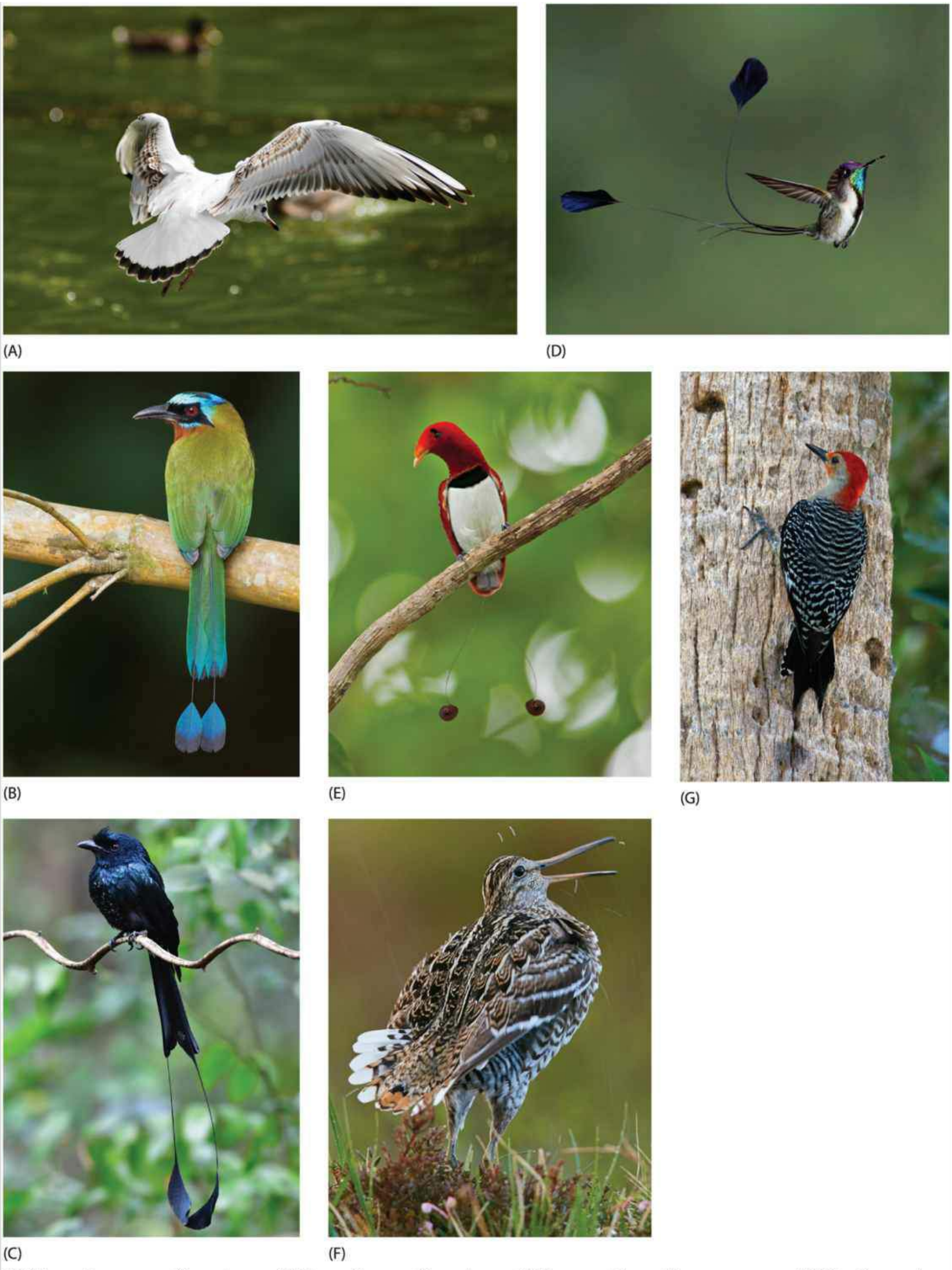
(A) Male Club-winged Manakin producing its mechanical wing sound. (B) Graphical illustration of how the tip of secondary 5 (the pick) moves across the surface of enlarged secondary 6 (the file) of the left and right wings. The mechanical impulses that result drive the resonance sounds of the shafts of secondary 6 and probably secondary 7. Relative motion of the pick and file is shown by the triangles and circles, respectively.

Silent flight, which enables an owl to surprise prey, results in part from two special structural features that muffle feather sounds (see Figure 4–2C). The distal barbs on the leading edge vanes of the owl's primaries have very long, filamentous tips, called **pennulae** (sing. **pennulum**) that create a fuzzy layer on the obverse surface of the vane that reduces air turbulence, especially at low speeds. Nightjars have a similar soft flight feather surface texture.

Because flight efficiency is directly linked to the structure of the primaries, major structural modifications of these feathers are uncommon. The narrow outer primaries of the male American

Woodcock, which produce trilling noises during courtship flights, are an exception. The modified primaries of flightless cassowaries consist only of 28-centimeter-long extensions of the hollow tubular calamus. These strong spinelike structures protect a cassowary’s flanks from abrasive vegetation. During the breeding season, long extensions of the second primaries of male Standard-winged Nightjars grow out and are used in courtship.

The flight feathers of the tail, or rectrices, attach to the fused caudal vertebrae, or pygostyle, at the end of the short avian bony tail. The usual 12 rectrices function primarily in control, steering, and braking during flight (Figure 4–5). The elaborate tails of birds-of-paradise and some hummingbirds serve primarily in display. Some motmots, kingfishers, hummingbirds, parrolets, and drongos have racquet-shaped rectrices with bare shafts and terminal vaned sections. The circular tail tips of a male King Bird-of-Paradise are tight whorls of rachises and inner vanes. Tail feathers are can also be modified for sound production—for example, in some snipes—or for bracing support in creepers, woodpeckers, woodcreepers, swifts, and penguins.



(A) iWorks Photography/Getty Images. (B) Danita Delimont/Getty Images. (C) Butterfly Hunter/Shutterstock.com. (D) Dubi Shapiro/NHPA/AGE Fotostock. (E) National Geographic Creative/Alamy stockphoto. (F) Markus Varesvuo/Nature picture library. (G) David Robinson/Snap2000 Images/Alamy

Figure 4–5 Tail feathers and their modifications: (A) unmodified tail of gull; racquet-shaped tail feathers of (B) a motmot, (C) a drongo, and (D) the

Marvelous Spatuletail (a hummingbird); (E) ornamental tail of a King Bird-of-Paradise; (F) sound-producing tail of a snipe; and (G) supporting tail of a woodpecker.

Downs, Bristles, and Other Kinds of Feathers

Unlike vaned feathers, **down** (or plumulaceous) feathers are soft and fluffy (see Figure 4–1). The down feathers vary from thick, continuous distribution in some chicks to restricted distribution among the other feathers in adult birds. Down feathers provide excellent lightweight thermal insulation and water repellency. Down feather of chicks, called **natal down,** typically lacks a rachis, but, as always, there are exceptions, including the natal down feathers of waterfowl. Natal down feathers grow from the same follicles that will later grow pennaceous contour feathers. Adult downs typically grow from specific follicles.

In most down feathers, the barbs and barbules are highly flexible and extend directly and loosely from the calamus or the rachis. Like the plumalaceous portions of contour feathers, the barbule cells of down feathers have tiny nodal prongs (see Figure 4–2E). Downy barbules entangle loosely, trapping air in an insulating layer next to the skin.

Semiplumes are intermediate in structure between down and contour feathers. A semiplume has a large rachis with loose plumulaceous but planar vanes. Some are close to down in structure, whereas others more closely resemble contour feathers. Semiplumes are usually hidden from view at the edges of the contour feather tracts (section 4.5). Semiplumes enhance insulation, fill out the aerodynamic contours of body plumage, and can serve as courtship ornaments.

Filoplumes are a very distinct class of hairlike feathers that function in sensing the movement and position of adjacent, vaned feathers (see Figure 4–1). A filoplume consists of a fine rachis with a terminal tuft of one to six short barbs with barbules at the tip. Disturbance of a filoplume's tufted tip is transmitted by the long, thin rachis to numerous sensory corpuscles within the follicle, which provides the bird with sensory information about its feathers (section 7.3). Distributed inconspicuously throughout the plumage, filoplumes are most numerous near mechanically active, or movable, feathers; each flight feather may have from eight to 12 filoplumes. Filoplumes associated with the flight feathers provide information that help the bird make aerodynamic adjustments; those in association with contour feathers also may help to monitor airspeed. Filoplumes are absent in (flightless) penguins and ostriches.

Bristles are specialized feathers with both sensory and protective functions (Figure 4–6). Bristles are simplified feathers that consist only of a stiff, tapered rachis with a few basal barbs. Semibristles are similar but have more side branches. Like filoplumes, many bristles have sensory corpuscles around their follicles. Except for those on the knees of the Bristle-thighed Curlew and on the toes of some owls, bristles are usually found on the heads of birds. The facial feathers of raptors tend to be simplified to bristles and semibristles, which are easier to keep clean than are fully vaned feathers. This condition reaches an extreme in the carrion-eating vultures, which have bare heads with scattered bristles. The eyelashes of such birds as ostriches, rheas, hornbills, and cuckoos consist of protective bristles, as do the nostril coverings of woodpeckers, jays, and crows (see Figure 4–6). The well-developed semibristles around the mouths of nightjars and owlet-nightjars act not only as insect nets but possibly also as sensors of tactile information in much the same way that a cat’s whiskers do.

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Figure 4–6 Bristles. (A) Whip-poor-will has well-developed bristles about the mouth. (B) Australian Owlet-Nightjar has elaborate bristles and semibristles around its bill and face. (C) Southern Ground Hornbills have luxurious eyelash bristles. (D) An exception to the usual head locations of bristles are those on the legs of the Bristle-thighed Curlew. (E) Structure of a typical bristle with a prominent rachis, and few or no barbs.

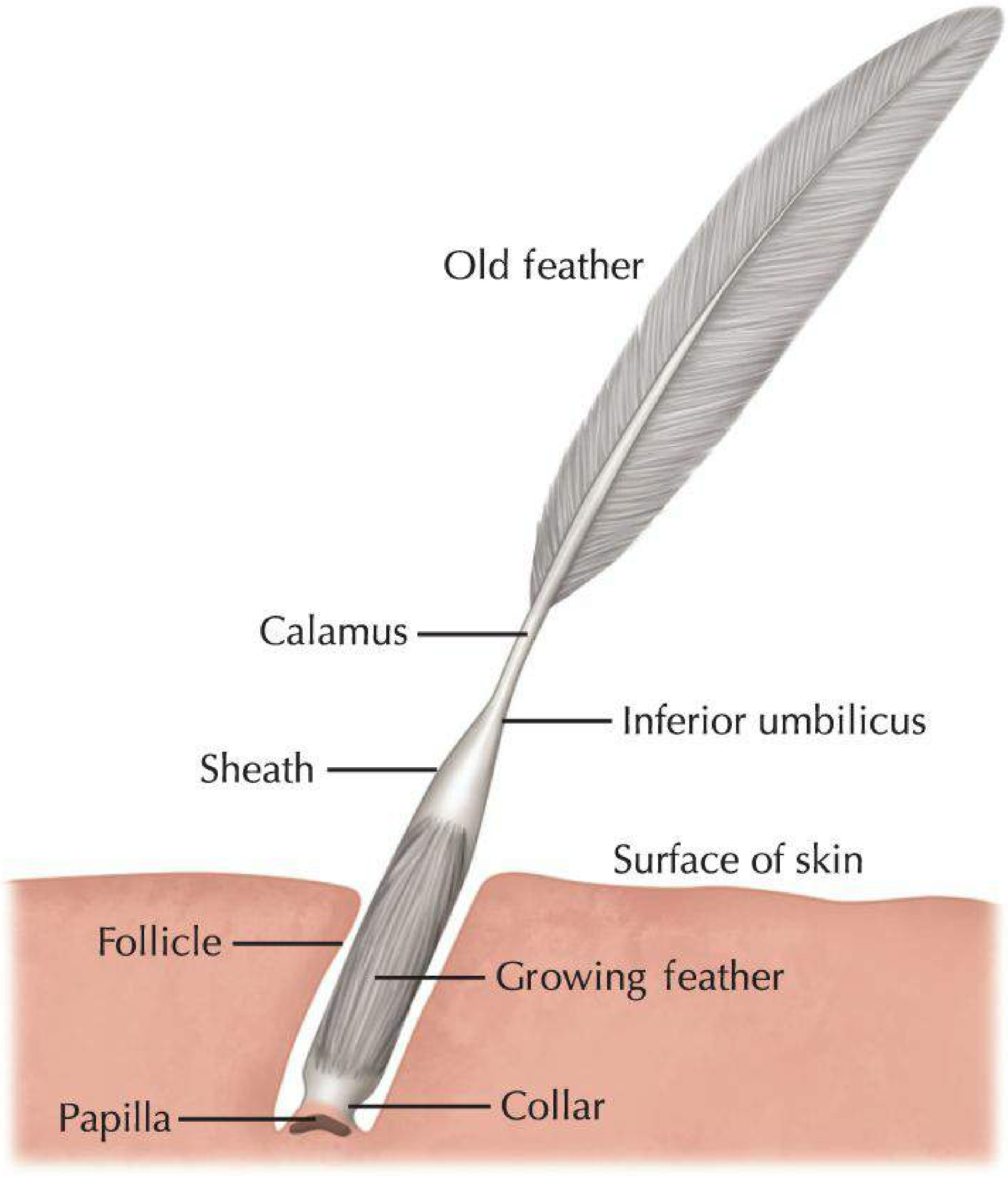
Special feathers called **powderdown** produce dustlike beta-keratin particles about one micrometer in diameter that resemble talcum powder. Powderdown feathers grow in dense, distinct patches, usually under the wings, in such birds as herons, doves, and the unique Cuckoo

Roller of Madagascar and Kagu of New Caledonia. As they preen their feathers, birds disperse this oily powder over the entire plumage. The still-disputed functions of powderdowns may include the waterproofing of feathers or defense against feather parasites (section 4.6).

4.2 Feather Development

Like hair, feathers are dead structures when mature. After they are fully grown, feathers cannot change color or form except through fading or abrasion. The first feathers of a bird develop on the embryo within the egg. Thereafter, feathers are replaced through regular, periodic **molt** throughout the life of the bird (section 4.8). Individual feathers may be replaced anytime if they are accidentally lost or damaged.

Feathers grow from specialized organs in the skin called follicles (Figure 4–7). The outer layer of the skin, or **epidermis,** is composed of cells that will keratinize and die when they mature. The inner layer of the skin, or **dermis,** provides nutrients and developmental signals to the epidermis. The follicle consists of a tubular in-pocketing, or invagination, of the epidermis. This unique configuration creates an outer, descending epidermal layer; an inner, ascending epidermal layer; and a central, dermal core (see Figure 4–7). All feathers are the tubular outgrowths of the inner, ascending, epidermal layer of the follicle. At the base of a follicle, where the epidermis turns, is the **follicle collar**—a persistent ring of feather stem cells that will divide to produce the cells of the feather from that follicle (Yue et al. 2005).



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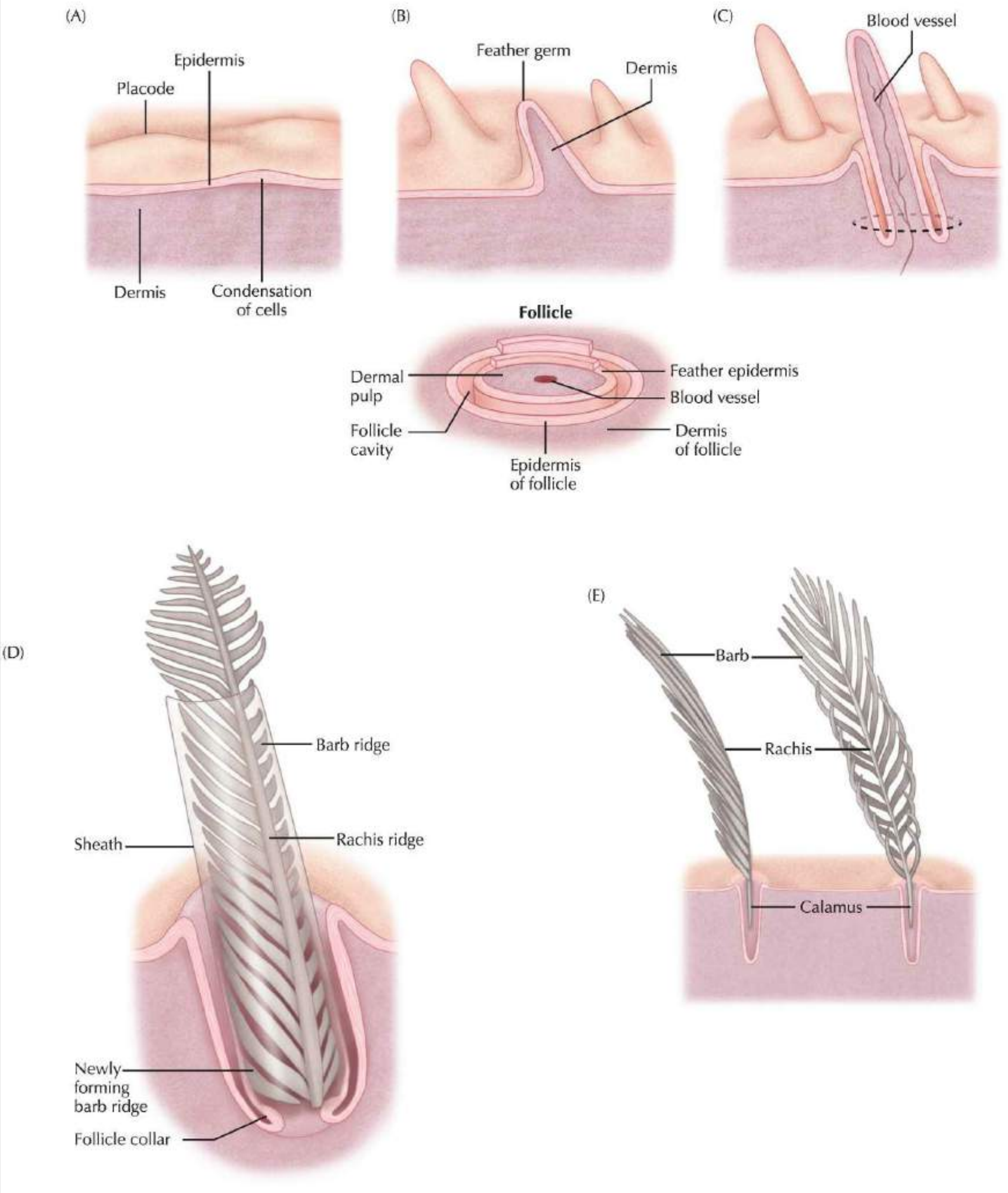
DATA FROM WATSON 1963

Figure 4–7 A new feather, growing from a papilla and collar in the follicle, pushes out the old feather.

In the life of a bird, a single follicle will produce a series of feathers that can be strikingly diverse in form. For example, in the Wild Turkey, the follicles on the head produce natal down feathers that lack a rachis in the embryo, then closed, pennaceous contour feathers in the young bird and simple bristles in the adult. In the male Ruff (Figure 13–11), the same follicles produce the elaborate, twisted, and highly variable display plumage used during the breeding season and the small, drab feathers of the nonbreeding plumage.

The development of the feathers begins in the embryo with the growth of feather **placodes,** which are tiny thickenings of the epidermis that determine the site where the follicle will develop (Figure 4–8). Next, the epidermal cells of the placode proliferate to create a tubular, short bud that is filled with dermis. Then a ring of epidermal cells around the base of the short bud grow down into the skin to create the feather follicle. The feather grows as the collar cells divide and proliferate, and these new cells push upward and out of the skin to form the mature feather. The different parts of the feather develop from different cells or cell layers of this tubular epidermal outgrowth.



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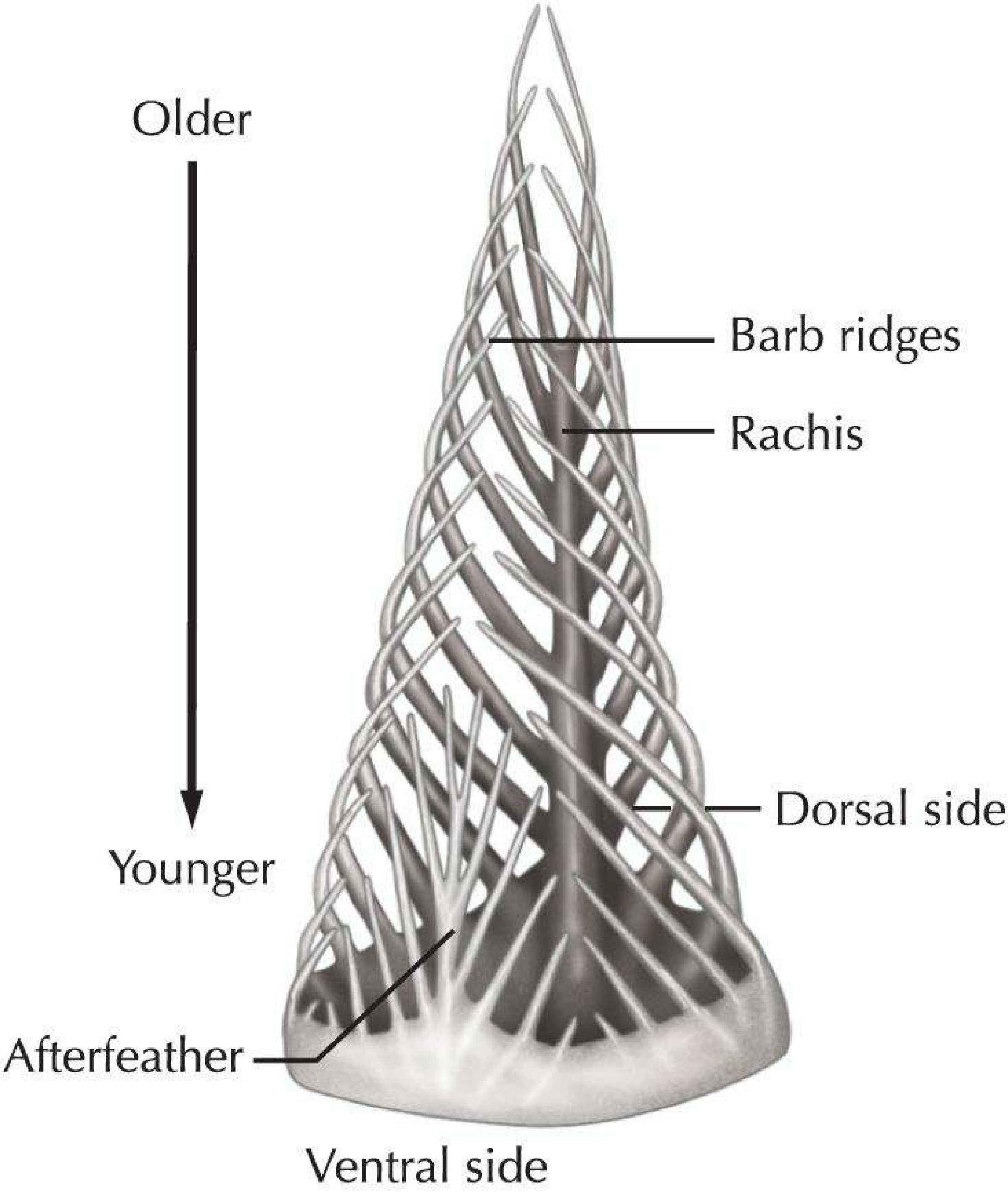
DATA FROM PRUM AND BRUSH 2003

Figure 4–8 Feather growth and development. (A) Feather growth begins with a thickening of the epidermis, the placode, over a condensation of cells in the dermis. (B) The placode elongates into the tubular feather germ. (C) Cells proliferate in a ring around the feather germ to create the follicle (detail of cross section at dotted ring below). Production of new keratinocyte cells in the follicle collar push older cells up and out to create the tubular feather. (D) The outermost layer becomes the sheath, whereas the inner layer divides into a series of barb ridges that develop into the barbs of the feather. (E) The feather emerges and unfurls from the sheath into its final shape. The follicle collar forms the calamus at the base of the feather.

The epidermal cells of the growing feather, or **feather germ,** use cell-cell signaling proteins to coordinate their differentiation into the various feather parts (Harris et al. 2002; see Figure 4–8). The outermost epidermal layer of cells becomes the **sheath,** which falls off when feather growth is complete. The intermediate cells become divided, or compartmentalized, into **barb ridges** that form the major branches of the feather vane. The barbules grow from horizontal rows of cells, called barbule plates, in the periphery of the barb ridges. The **barbule plates** on the sides of the barb ridge nearer to and farther from the rachis become the distal barbules and proximal barbules, respectively.

The developmental mechanism of the unique branched structure of feathers is likewise entirely unique. Feathers are branched like a tree, but they grow from their base like a hair. Like hair, the tip of the feather is older than its base, and each barb is older than its connection to the rachis. Thus, barbs do not grow *from* the rachis. Rather, barbs grow and then *fuse* to the rachis. In fact, the fusion of barb ridges on the dorsal side of the tube forms the **rachis ridge,** which becomes the rachis of the mature feather. To create the entire vane, new barb ridges form on the ventral side of the follicle and grow helically around the tube toward the dorsal side and ultimately fuse to the rachis (Figure 4–9).



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DATA FROM LUCAS AND STETTENHEIM 1972

Figure 4–9 The branching structure of the rachis and the barbs are created by helical growth of barbs ridges from the ventral to the dorsal side of the follicle, where the barb ridges fuse to first create the rachis and later fuse to the rachis. The afterfeather develops by the same mechanism with helical growth toward the ventral side of the follicle.

As the feather germ emerges from the skin, the epidermal cells begin to produce beta-keratin. Eventually, these cells fill entirely with insoluble beta-keratin, become completely cut off from nutrients, and die. The outer sheath then cracks open and falls off, and the tightly bound barbs uncoil and expand to create the feather vane. As feather growth ends, the epidermal tube becomes completely undifferentiated to produce the tubular calamus, which remains inserted in the follicle until the next feather grows in.

Throughout its growth, the core of living cells and blood vessels at the center of the growing feather, called the **dermal pulp,** is periodically resorbed by the dermis of the follicle. As the feather grows, the dermis produces a series of **pulp caps,** which resemble keratinized lids that keep the dermis from leaking out the tip of the feather germ. Pulp caps fall out when the feather unfurls from the sheath. But the pulp caps are retained within the calamus, and they can be easily observed in many large feathers, such as goose or raptor remiges. A small hole at the bottom of the calamus, known as the **inferior umbilicus,** is a vestige of the space filled by dermal pulp in the growing feather and provides further evidence of the essential tubularity of the feather.

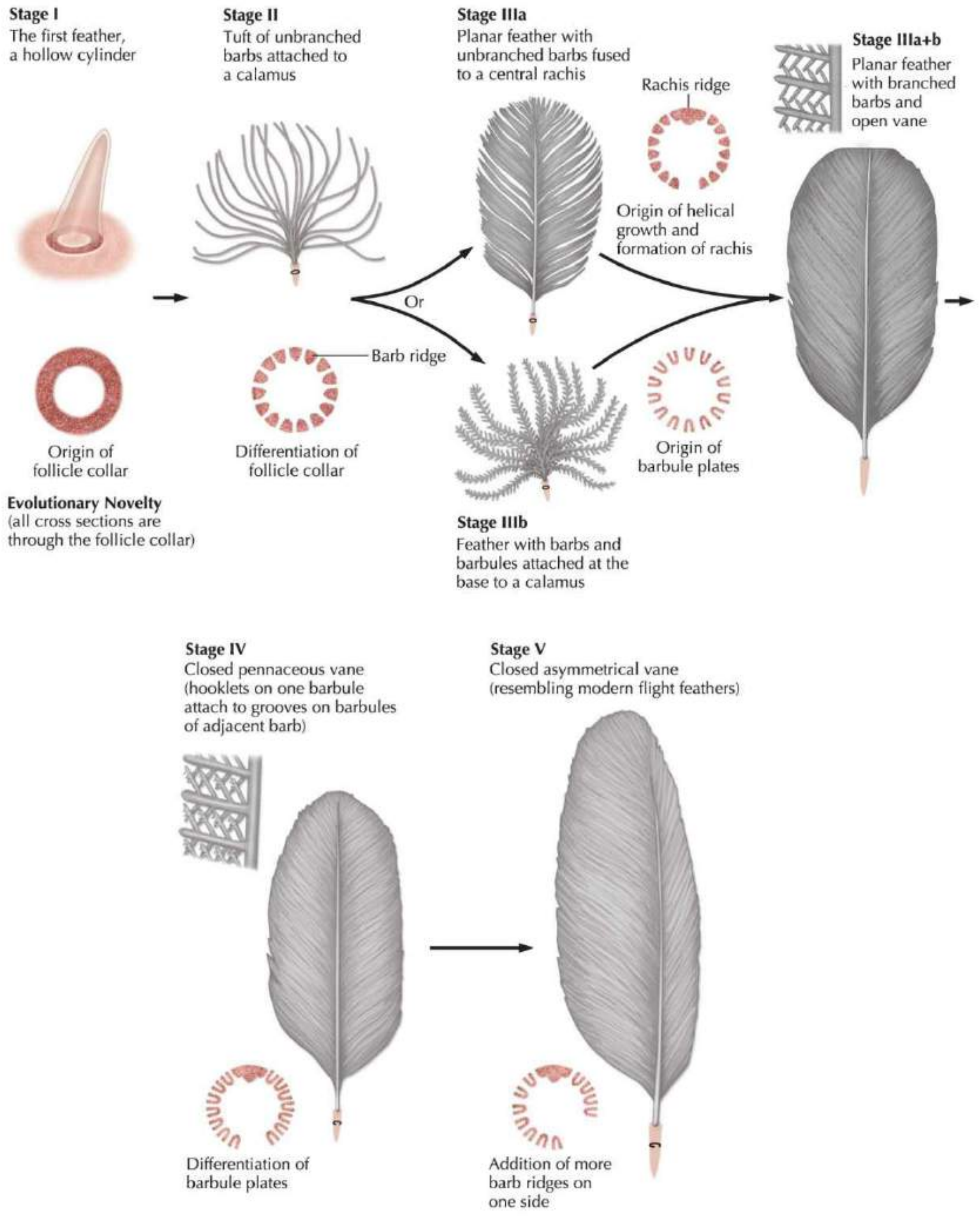
The follicle grips the feather by the calamus with a combination of muscular forces and friction. Substantial force—from 500 to 1,000 grams for a single body feather of the average chicken—is required to pull a feather from this grip. The tight grip of follicle muscles controlled by the autonomic nervous system may relax when a bird becomes mortally frightened. The resulting loss of feathers, known as **fright molt** (memorably, *shreckmauser* in German), is hypothesized to be an extreme antipredator adaptation. Nightjars, for example, easily drop their feathers when disturbed.

4.3 Evolution of Feathers

For most of the twentieth century, feathers were thought to have evolved from elongate scales through natural selection for aerodynamic function—starting with gliding and leading to powered flight (Parkes 1966). However, because the planar feather vane unfurls from a tube, we can see that the top and bottom surfaces of a feather vane are formed by the *outer* and *inner* surface of the feather germ, respectively. Thus, the surfaces of a pennaceous feather are not homologous with the surfaces of a scale. Therefore, the planar feather could not have evolved from an elongate scale.

Instead, the details of feather development inform a developmental theory of the evolution of feathers (Prum 1999). The complex process of the growth of a vaned feather implies that feathers must have evolved through a series of stages from simple to more complex. Each hypothesized stage was characterized by a new, evolutionarily novel mechanism of feather development, a highlight of the new scientific discipline “Evo Devo” (Carroll 2005). Given that some anatomical features are necessary for the development of others, the nature of feather development implies that some developmental novelties must have evolved prior to others. For example, the direct observation that the rachis is formed by the fusion of barb ridges implies that barbs evolved before the rachis.

The process of feather development predicts that feathers evolved through five distinct stages (Prum 1999). Each required a new mechanism of growth or a developmental novelty as feathers evolved their diversity and definitive form (Figure 4–10).



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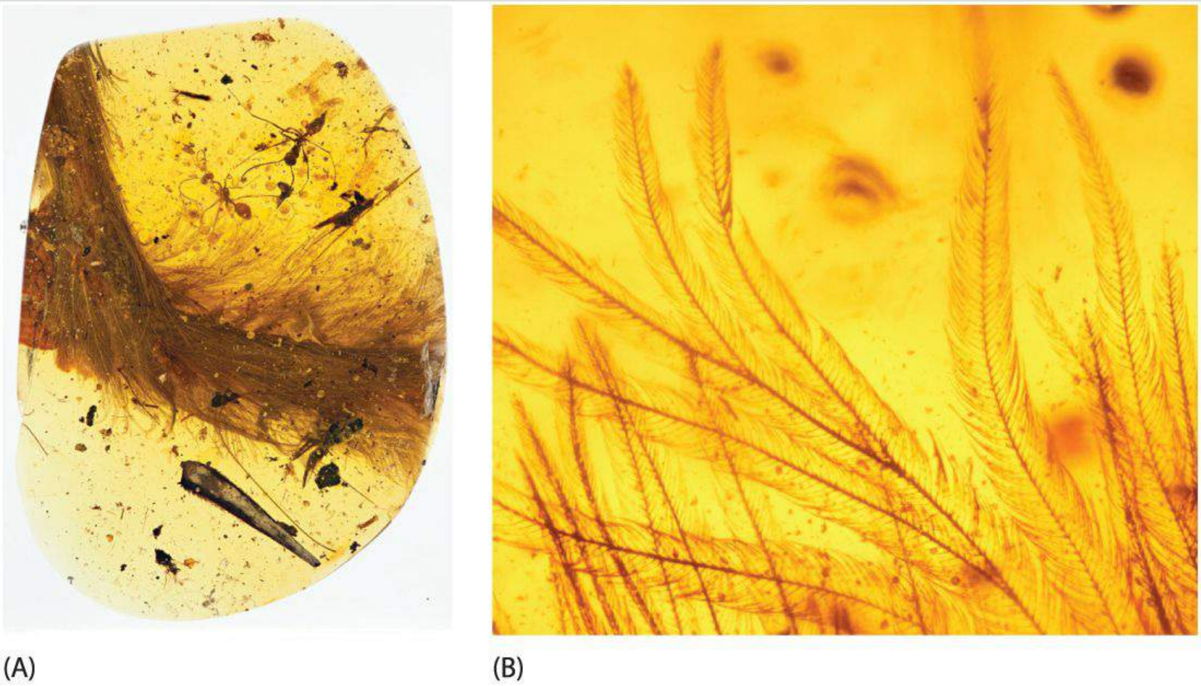
DATA FROM PRUM 1999

Figure 4–10 The developmental theory of the evolution of feathers proposes that feather complexity evolved through a series of innovations in the mechanisms of development. Each innovation gave rise to a more complex kind of feather. The first event was the origin of the ring-shaped follicle collar (stage I), which gave rise to a hollow, tubular feather. The next event was the subdivision of the collar into barb ridges (stage II), which produced a feather with a downy tuft of barbs. This was followed by either the origin of helical growth of barb ridges (stage IIIa) or the origin of barbule plates (stage IIIb). Both of these novelties were required for the evolution of a feather with a rachis, barbs, and barbules (stage IIIa+b). Next, the origin of differentiated barbule plates (stage IV) would have created the first feather with closed pennaceous vane. Finally came the evolution of the developmental mechanisms necessary to produce a flight feather with an asymmetrical vane (stage V).

Evidence in support of the developmental model of the evolution of feathers comes from the observation that feathers corresponding to each of the hypothesized stages are found in modern birds. For example, the calamus of every known feather corresponds precisely to stage I. Likewise, the unique cassowary wing feather is a simple tube that also conforms exactly to the predictions of stage I. Although these modern feathers are secondarily simplified, they demonstrate the capacity of feather follicles to produce all of these hypothesized morphologies.

Additional evidence in support of the developmental model comes from the molecular mechanisms of feather development. The same systems of signaling genes have been repeatedly co-opted, or reutilized, in the development of novel feather morphologies (Harris et al. 2002).

As discussed in Chapter 2, paleontological evidence documents that feathers were present in many theropod dinosaurs. The diversity of the feathers of nonavian theropod dinosaurs also supports the predicted early stages of the developmental theory of feather evolution (Prum and Brush 2002; Xu et al. 2014). Recently discovered feathers from a basal coelurosaur preserved in mid-Cretaceous amber have barbs, a rachis, and simple undifferentiated barbules, corresponding perfectly to stage IIIa+b (Xing et al. 2016; Figure 4–11). Only later, in the exclusive common ancestor oviraptorids and living birds, is there evidence for feathers with a coherent planar vane (stage IV). The dramatic discovery of a variety of both primitive and completely modern feathers from numerous lineages of theropod dinosaurs, including the basal relatives of *Tyrannosaurus rex*, demonstrates that feathers first evolved in bipedal, terrestrial, meat-eating theropod dinosaurs before the origin of birds and before the origin of avian flight (see sections 2.6 and 2.7). However, it is still difficult to be confident about the adaptive functions of earlier stages of feather complexity. The possible functions of early stage feathers include thermoregulation, water repellency, camouflage, social and sexual communication, or a combination of these.

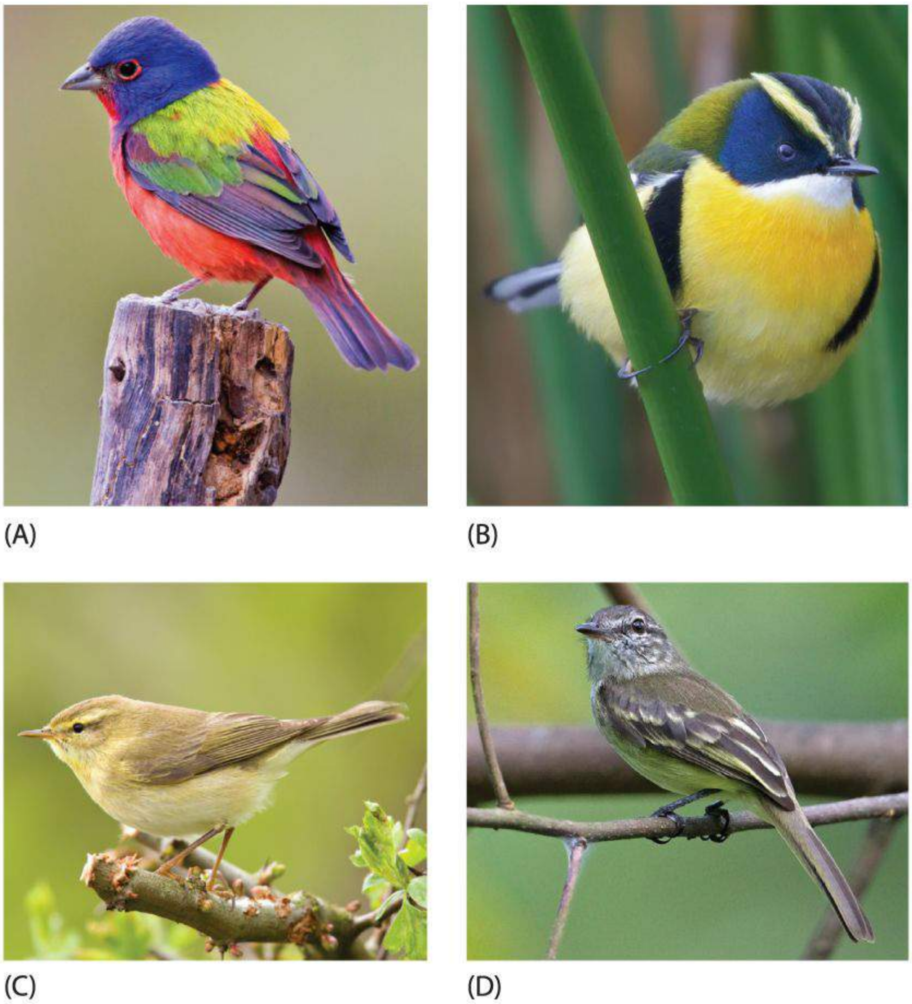


Courtesy of Dr. Ryan McKellar, Royal Saskatchewan Museum

Figure 4–11 The discovery of open pennaceous fossil feathers in mid-Cretaceous Burmese amber from (A) the tail of a coelurosaurian theropod dinosaur documents the evolution of (B) doubly branched feathers with both barbs and barbules (stage IIIa+b) deep in the theropod phylogeny.

4.4 Feather Colors

The stunningly colored plumages of birds are an important reason that birds have captured the human imagination for so long. Male Painted Buntings from the southeastern United States sport patches of brilliant reds, greens, and blues (Figure 4–12). The tiny Many-colored Rush Tyrant of South America features red, orange, blue, green, yellow, black, and white; locally, it is called *Siete Colores*, meaning "seven colors." At the other extreme are drab gray olive birds, including many flycatchers of North and South America (Tyrannidae) and the leaf warblers (*Phylloscopus*) of Europe and Asia (see Figure 4–12).



(A) Danita Delimont/Getty Images. (B) Glenn Bartley/All Canada Photos/Getty Images. (C) Andrew_Howe/E+/Getty Images. (D) robin chittenden/Alamy stockphoto

Figure 4–12 Plumage coloration varies among species of birds: (A) male Painted Bunting, (B) Many-colored Rush-Tyrant, (C) *Phylloscopus* warbler, and (D) Forest Elaenia.

Light is a range of electromagnetic radiation between 300 and 750 nanometers (nm) in wavelength. Different wavelengths are perceived as different colors, and all wavelengths together appear as white. Feather colors come in many shades, hues, and tints because of organic pigments deposited in the feather cells and nanometer-scale structures of feather cells. Avian **pigments** are organic chemical compounds that absorb the energy of certain wavelengths of light and reemit the energy of other wavelengths to produce the observed colors. Pigments contribute to visible colors by absorbing the wavelengths of light complementary to the color perceived. For example, pigments that produce a red color absorb light wavelengths smaller than 620 nm. Pigments that produce blue hues absorb wavelengths greater than 450 nm. **Structural colors** result from the physical, optical interactions between incident light and feather nanostructures. Pigmentary and structural mechanisms often function together to produce new colors that are not achievable by either mechanism alone.

Pigments

The four major classes of feather pigments are melanins, carotenoids, psittacofulvins, and porphyrins (Figure 4–13). A fifth class of pigments—pterins—is suspected to occur in penguins but has yet to be chemically confirmed.

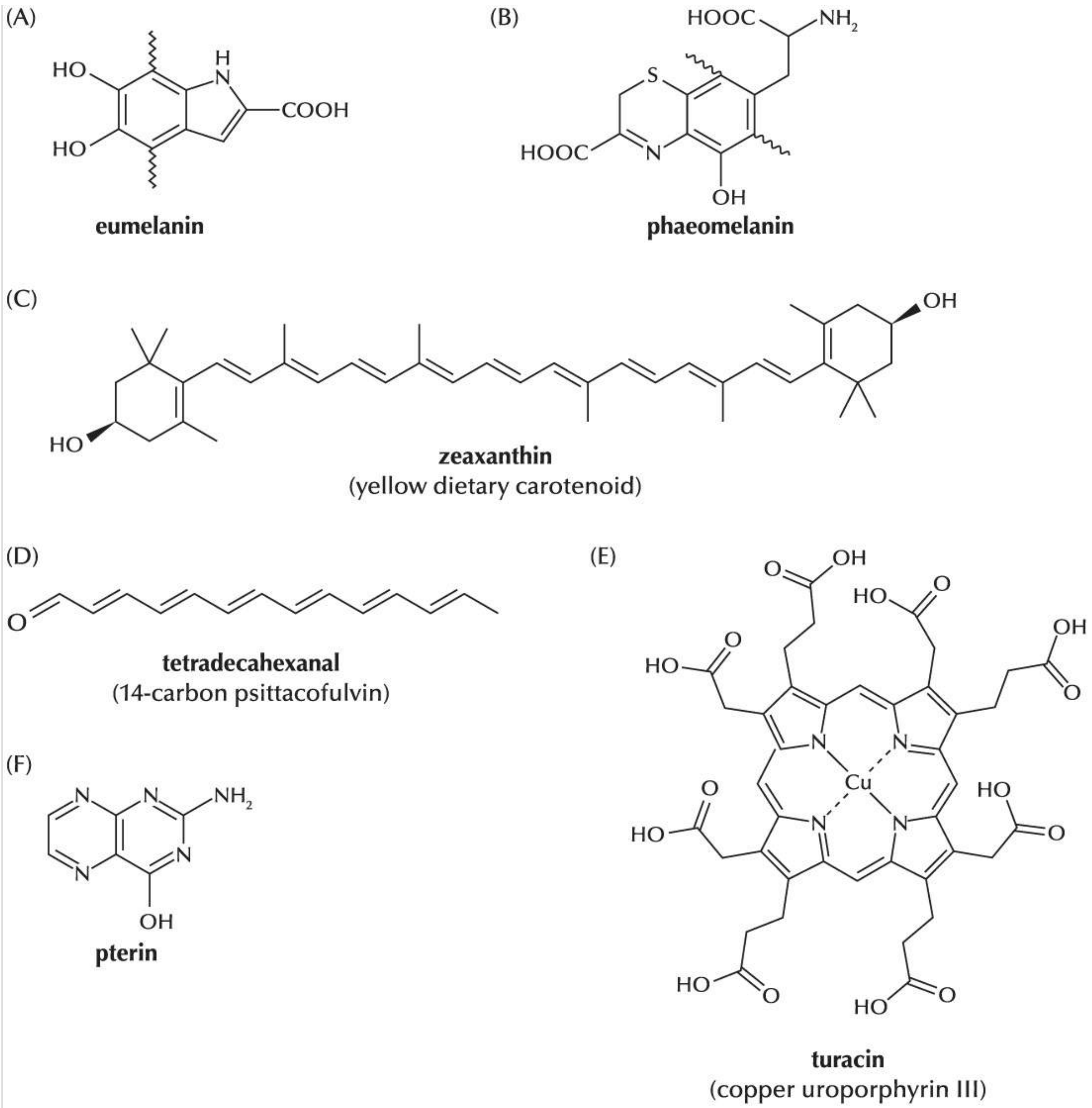


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Figure 4–13 The molecular diversity of avian feather pigments. (A, B) Black eumelanins and brown pheomelanins. (C) Carotenoids. (D) Psittacofulvins. (E) Porphyrins. (F) Pterins. All these pigment molecules have chains or rings of carbons with alternating double and single bonds. Because this molecular structure allows neighboring carbons to share electrons, the length of this chain “tunes” the pigment molecule or polymer to absorb specific wavelengths of light.

Melanins produce earth tones—grays and blacks, browns, and buff colors. **Carotenoids** produce bright yellows, oranges, reds, and purples. **Psittacofulvins** produce the yellow, orange, and red feather colors in parrots only. **Porphyrins** are responsible for unique, bright, olive green and magenta plumage colors in turacos and a few other birds.

With the exception of albinos and a few all-white species, almost all birds have some melanin pigment in their feathers. Melanin pigment is synthesized from the amino acid tyrosine by mobile pigment cells called **melanocytes,** which creep about in the dermal layer of the skin. After receiving signals from the pituitary hormone melanocortin, melanocytes manufacture pigment organelles, called **melanosomes,** that contain long chains of polymerized melanin molecules. Melanosomes are transferred into some feather cells and then incorporated into its beta-keratin as that cell matures. Within-feather, melanin pigmentation patterns—like spots, dots, stripes, and scales—are produced by complex temporal and spatial patterns in melanosome transfer (Prum and Williamson 2002; Figure 4–14).

COURTESY OF RICHARD O. PRUM

Figure 4–14 The diversity of within feather pigmentation patterns—the spots, stripes, and patches within a feather vane—develop through the controlled transfer of melanosomes to specific young feather cells during feather development.

Like other vertebrates, birds produce two kinds of melanin. **Eumelanin** produces black and gray colors, and **pheomelanin** produces red brown, rufous, and buff tan colors. The same two pigments are responsible for black and red hair in humans. Color patterns within feathers or over the body are produced by the distribution of eumelanins and phaeomelanins. For example, bold plumages of Gray Catbird and Hooded Pitohui and the finely vermiculated rufous and black feather patterns of the Whip-poor-will are produced by a controlled distribution of eumelanin and pheomelanin among and within feathers (Figure 4–15).

(A) Johann Schumacher/Photolibrary/Getty Images. (B) Daniel Heuclin/Biosphoto. (C) Nature Photographers Ltd/Alamy stockphoto

Figure 4–15 The plumage colors of the (A) Gray Catbird, (B) Hooded Pitohui, and (C) Whip-poor-will are produced by black and gray eumelanins and brown pheomelanin.

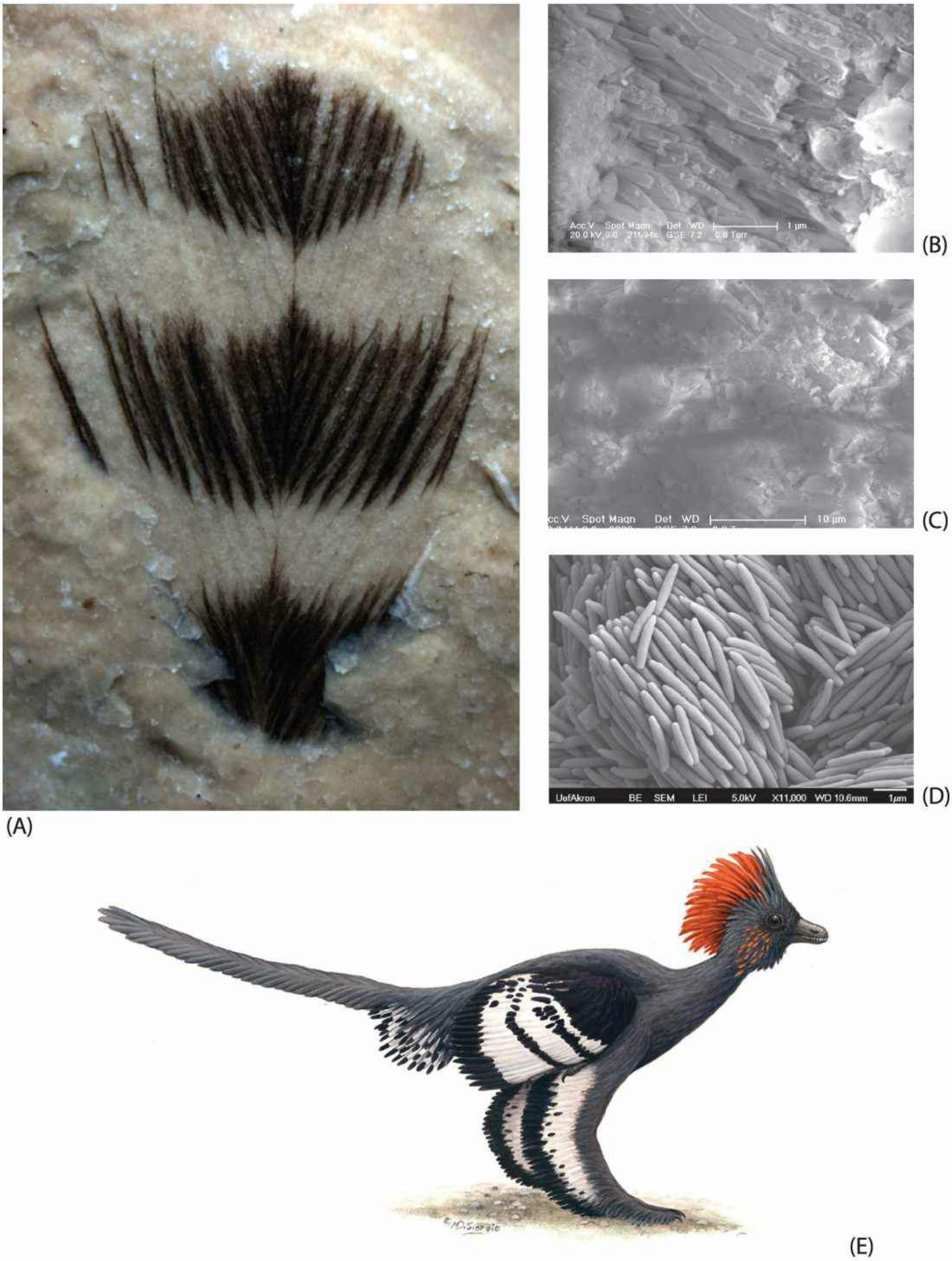
Like gravel in concrete, melanosomes also make feather keratin more resistant to mechanical stress and wear (Burtt 1979). Dense melanin concentrations in the black wing tips of high-speed aerial species, such as gulls and gannets, reduce the fraying of those feathers. Melanosomes also help protect the feathers of desert species from sand abrasion.

Recent discoveries demonstrate that melanosomes and even melanin molecules can be preserved in fossils. This discovery has led to an entirely new field investigating the plumage colors of fossil birds and dinosaurs (Box 4–3).

Box 4–3

Melanin Coloration of Fossil Feathers

Since the early 1980s, paleontologists have interpreted the oblong microscopic structures they observed in fossil feathers as the remains of bacteria that consumed the feather proteins during fossilization. However, an analysis by Jacob Vinther and colleagues (2008) of a Cretaceous fossil feather with a naturally striped, black-and-white color pattern demonstrated that these structures were not bacteria but fossilized melanosomes preserved from the original feather. This discovery led to an entirely new field of fossil melanin coloration. Subsequent discoveries have documented fossil feathers with starling-like, metallic, iridescent structural colors (Vinther et al. 2010). Analyses comparing the size and shape of fossil melanosomes to the eumelanin and pheomelanin melanosomes of extant birds have led to the reconstruction of the plumage coloration patterns of the nonavian theropods *Sinosauropteryx prima* (Zhang et al. 2010) and *Anchiornis huxleyi* (Li et al. 2010). These results establish that plumage coloration pattern complexity and complex social or sexual communication evolved in theropod dinosaurs before the origin of birds.



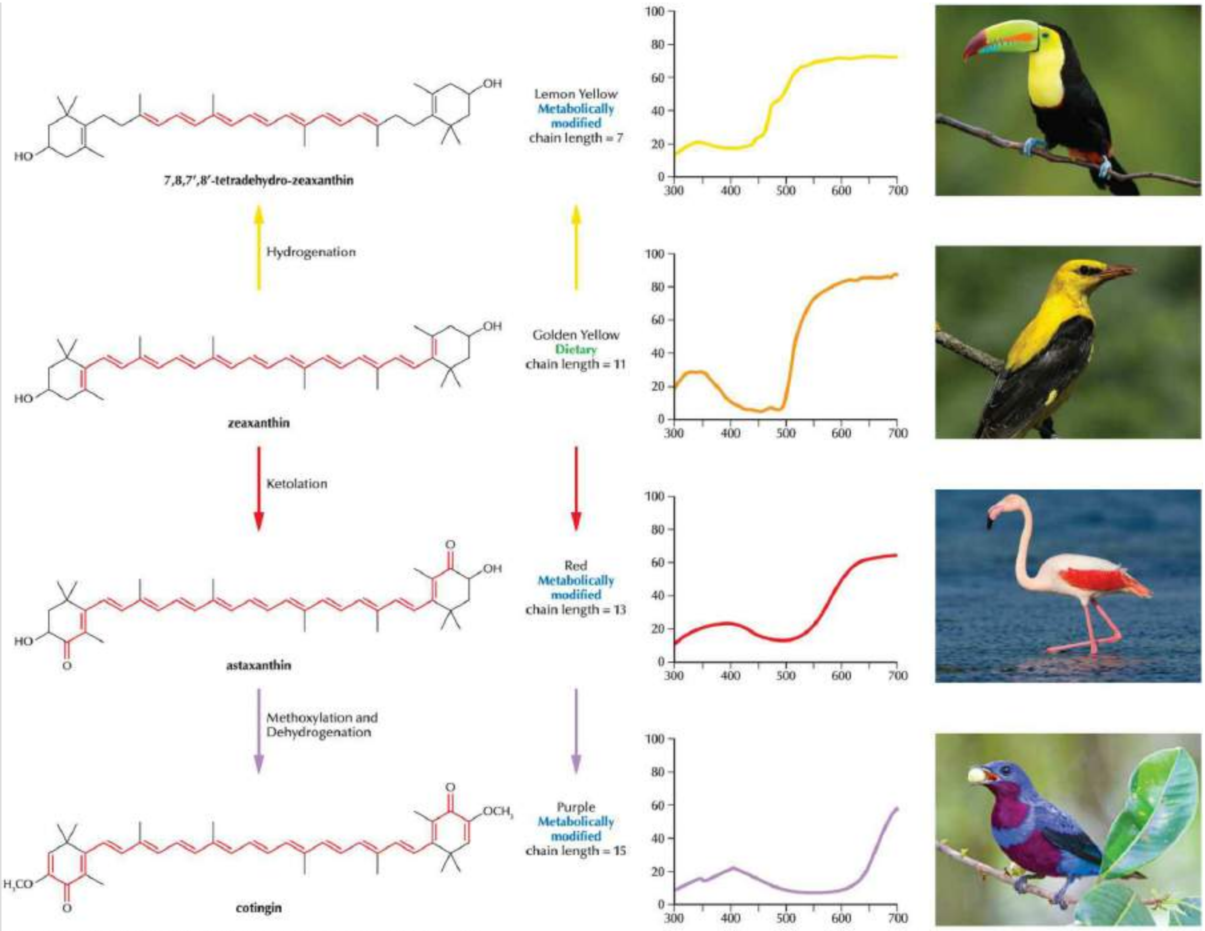
(A-C) COURTESY OF RICHARD O. PRUM. (D) COURTESY OF MATTHEW SHAWKEY, BIOLOGY DEPARTMENT, UNIVERSITY OF GHENT (E) MICHAEL DIGIORGIO, COURTESY OF RICHARD O. PRUM

Melanin pigmentation in fossil bird feathers. (A) A fossil feather from the Crato Formation, early Cretaceous, Brazil, showing black and light bands. (B) Electron micrograph of the dark bands reveal preserved melanosomes. (C) Light areas reveal only the rock matrix. (D) Eumelanin melanosomes from the feather of a modern Red-winged

Blackbird are nearly identical in form to those preserved in the fossil. Scale bars: (a) 3 mm, insert 1 mm; (b) 1 µm; (c) 10 µm; (d) 1 µm. (E) Reconstruction of the eumelanin and pheomelanin plumage patterns of the late Jurassic, maniraptoran dinosaur *Anchiornis huxleyi*.

Melanins also increase a feather's resistance to degradation by beta-keratin–eating bacteria (Goldstein et al. 2004). The ubiquitous soil bacterium *Bacillus licheniformis* secretes an enzyme that erodes the beta-keratin matrix of the feather. Black feathers with melanin suffer less erosion than do white feathers, which lack melanin. This finding helps to explain why birds of wet climates tend to be dark colored (Burtt and Ichida 2004; Shawkey and Hill 2004). Better camouflage in darker, wetter habitats is the traditional explanation. But birds in wetter climates also bear higher densities of bacteria in their plumage, which would favor higher levels of feather melanin to increase resistance to destructive bacterial enzymes.

Carotenoid pigments are responsible for most bright red, orange, and yellow and many purple colors of bird plumage (Figure 4–16). Most avian carotenoids are characterized by two six-carbon rings with a chain of 18 carbons separating them.



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Photos: From top to bottom: Eduardo Rivero/ Shutterstock.com; Bildagentur Zoonar GmbH/Shutterstock.com; Saverio Gatto/ Alamy stockphoto; Ciro Albano, http://www.nebrazilbirding.com

Figure 4–16 Different carotenoid plumage colors (right column) are produced by different pigment molecules (left column), which vary in the length of the central chain of alternating carbon double bonds (red highlights). The longer the chain, the longer wavelength the color (center column). Birds absorb yellow carotenoids, like zeaxanthin (second row, left), from the diet and metabolically modify dietary molecules to produce new pigments with longer (red and purple arrows) or shorter (yellow arrow) chains of double bonds. Top row, lemon yellow throat of the Keel-billed Toucan; second row, rich golden yellow body plumage of Eurasian Golden Oriole; third row, pink and red body plumage of Greater Flamingo; bottom row, purple throat and belly of Banded Cotinga.

Carotenoid molecules are originally produced by plants and are absorbed by birds from their diets as vitamins. Most common dietary carotenoids are yellow pigments, like β-carotene, lutein, and zeaxanthin. Birds physiologically modify these yellow, dietary carotenoids to produce distinct molecules with novel colors. To date, 39 different carotenoid molecules have been described from bird plumages (LaFountain et al. 2015). Lengthening the chain of alternating carbon double bonds in the molecule produces orange, red, and purple pigments (see Figure 4–16). Shortening the chain of carbon double bonds produces pigments with lighter, lemony yellow colors. Just as harp strings of different lengths resonate sympathetically with different frequencies of sound, the length of the conjugated carbon chain affects the wavelength of light that will be absorbed by a carotenoid molecule.

The color of the carotenoid pigmented plumage is also influenced by the way in which the pigment molecules are bound within the feather. For example, the brilliant red plumages of the Scarlet Ibis and male Summer Tanager are colored by the same, single carotenoid—canthaxanthin—as the brilliantly purple axillary plumes of the White-browed Purpletuft (Mendes-Pinto et al. 2012; Figure 4–17).

(A) Christian Hütter/Getty Images. (B) © Juan Carlos Vindas/Getty Images. (C) Nick Athanas

Figure 4–17 The red plumages of (A) Scarlet Ibis and (B) Summer Tanager and the purple plumage of the (C) White-browed Purpletuft are all produced by the same carotenoid pigment: canthaxanthin. The colors vary in how the carotenoid molecules are bound within the feather.

Because carotenoid molecules come from the diet, carotenoid plumage coloration has been hypothesized to be an honest signal of individual health, condition, or genetic quality (Box 4–4).

Box 4–4

Is Carotenoid Plumage Brightness an Indicator

of Mate Quality?

The male House Finch varies in plumage color from bright to pale red or even yellow orange. With a series of elegant experiments, Geoffrey Hill (2002) demonstrated not only that the plumage color of the male House Finch is related to diet but also that females prefer brightly colored males to dull-colored males. Hill hypothesized that high-quality males have intrinsically superior foraging ability and better access to carotenoid-rich foods that brighten their colored badges. This **"honest signaling"** mechanism has since been invoked to explain the evolution of many avian carotenoid ornaments.

The huge unanswered question is, by what mechanism is carotenoid feather coloration associated with male quality, if at all? The original hypothesis rested on assumption that the supply of carotenoids is limited in the diets of wild birds, but very few data support this assumption. More recently, Hill and Johnson (2013) have proposed that red ketocarotenoids' plumage coloration indicates individual genetic quality because these metabolic transformations require coevolved compatibility between the mitochondrial and nuclear genomes that encode the enzymes and structures in this pathway. Future research will need to establish whether there is appropriate nuclear and mitochondrial genetic variation within avian populations for this mitonuclear compatibility mechanism to drive ketocarotenoid plumage evolution. Alternatively, carotenoid plumages may evolve because they are attractive, not because they provide any additional information about mate condition or quality (Prum 2010; LaFountain et al. 2015).

Andrew McLachlan/AGE Fotostock

A male House Finch with carotenoid pigmentation.

In summary, carotenoid plumage colors are determined by which dietary carotenoids are concentrated from the diet, which feather keratinocytes they are deposited into and at what concentrations, what metabolic transformations are performed on them, and how are these molecules bound within the feather.

The bright yellow, orange, and red feathers of parrots are not colored by carotenoid pigments (see Figure 3–11G). Rather, parrots produce their rainbow of long-wavelength colors from a special set of lipochrome pigments called psittacofulvins, which they manufacture in the growing feather (McGraw and Nogare 2005). Psittacofulvins are simple hydrocarbon chains of 14 to 20 carbons with seven to 10 double-bonded carbons that are very similar in structure to the central chain of a carotenoid. Unlike carotenoids, which are generally dispersed within feather cells, psittacofulvins appear to be quite localized within the feather.

The fourth class of feather pigments, porphyrins, are ring-shaped molecules that are chemically related to iron-containing red hemoglobin and to the manganese-containing green chlorophyll pigments of plants. The magenta red pigment in the wing feathers of many turacos is produced by a copper-contained porphyrin called **turacin,** or uroporphyrin III (Figure 4–18A). A related porphyrin pigment, called **turacoverdin,** is responsible for the bright olive green colors of many turacos and is also found in the wings of the Wattled Jacana, the green feathers of Blood Pheasants, and Crested Partridges (Dyck 1992; Figure 4–18B).

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Figure 4–18 Unusual plumage pigments. The red of the (A) Knysna Turaco is produced by the pigment turacin. The green of the turaco and the greenish yellow of the (B) Wattled Jacana wings are produced by the related pigment turacoverdin. The yellow plumage patches of the (C) King Penguin are produced by an unidentified pigment that may be a pterin.

Porphyrins are also present in the reddish brown or brown feathers of at least 13 orders of birds, notably owls and bustards, but their role in plumage coloration in these species is poorly understood. In these birds, porphyrin pigments are chemically unstable and easily destroyed by sunlight. Because porphyrins show intense red fluorescence under ultraviolet (UV) illumination, the presence of red fluorescence can be used to identify new feathers and to document patterns of molt (section 4.8).

Another distinct class of pigments have been identified in the golden yellow crest and facial feathers of penguins (McGraw et al. 2007; Figure 4–18C). These pigments have been provisionally called “spheniscens.” Based on their spectral properties, fluorescence, and the conditions required to extract them from the feathers, they are thought to be pterins—bicyclic compounds containing both carbons and nitrogens in the rings.

Extreme feather pigmentation is associated with many unusual modifications to the feather vane. Fusion of the developing barbs produces feathers that look like strips of plastic, as, for example, do the crown feathers of the Curl-crested Araçari, a small Brazilian toucan, and the central tail feathers of the Red Bird-of-Paradise. The “plastic” feathers of the bird-of-paradise function in courtship display, but why the araçari has such feathers is not known. The familiar Cedar Waxwing of North America is named for its waxlike wing-feather tips with fused, bright red terminal barbs.

Structural Colors

Many of the brightest feather colors—rich parrot greens, shimmering bluebird blues, and explosive hummingbird iridescences—are structural colors that result from the physical, optical interactions between incident light and **nanostructures** in the feather. Bright skin and eye colors can also be structural (Box 4–5). In general, white is a structural "color" produced by the backscattering of all light wavelengths. In contrast, the scattering of a specific subset of visible wavelengths produces structural colors of specific hues (e.g., blue, green, or red). This process, called **constructive interference,** or coherent scattering, occurs when light waves bounce off the interfaces of nanometer-scale structures in the feather. The nanostructures create predictable differences in the distance traveled by the light waves scattered by different objects in the feather. Most of the scattered wavelengths will be out of phase—that is, the peaks and troughs of the scattered waves do not align—and the waves cancel one another (that is destructive interference). Waves that are in phase after scattering will constructively interfere to produce a brighter light of a specific wavelength. Larger-scale nanostructures produce longer-wavelength, redder colors; smaller-scale nanostructures produce shorter-wavelength, bluer or ultraviolet colors. Color-producing nanostructures must be precisely sized to within 10 nanometers—that is, ten one-billionths of a meter—or the color produced will be observably different to another bird.

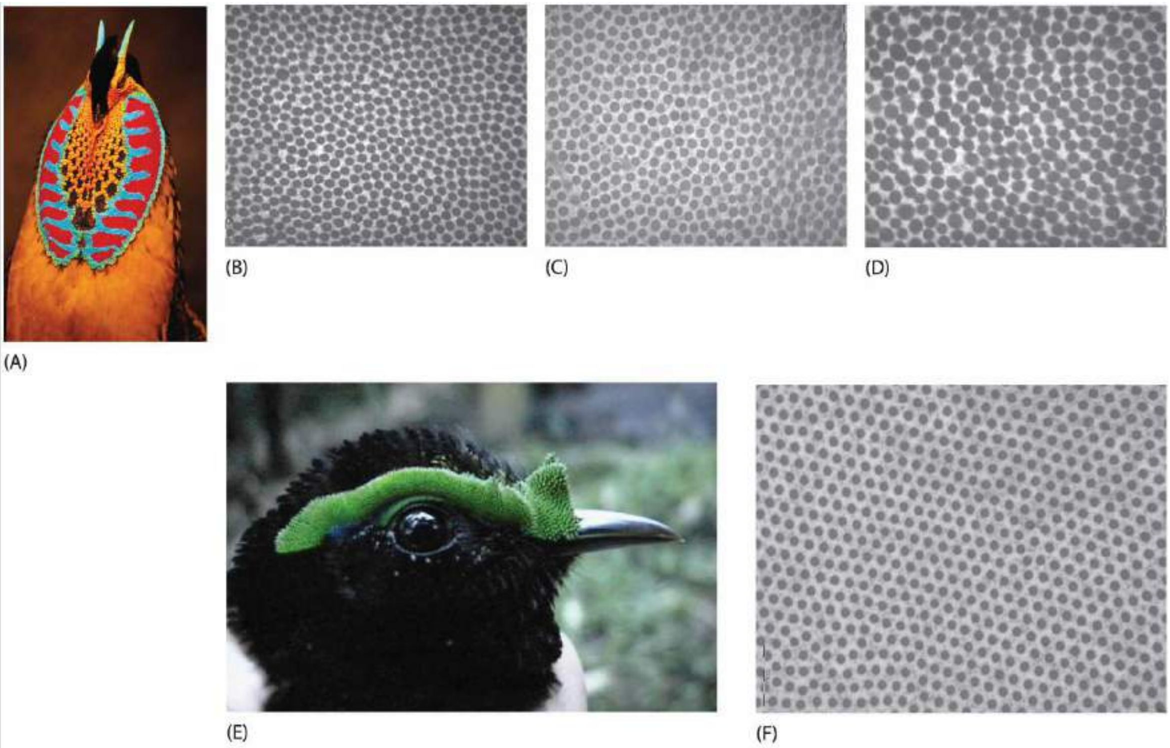
Box 4–5

Structural Colors of Bird Skin and Eyes

Structural colors are prominent not just in the feathers of birds but also in the skin and eyes of many birds. Structurally colored blue or green skin is known in at least 50 families of birds (Prum and Torres 2003). The structural colors of bird skin are produced by constructive interference of light waves from arrays of parallel collagen fibers in the skin. The size and spacing of the fibers produce colors of various hues ranging from deep ultraviolet and blues to greens, yellows, and orange.

Almost all color producing collagen arrays are quasi-ordered, but the fleshy green and blue facial caruncles of the Velvet Asity, a species found only on Madagascar, are arranged in a nearly perfect hexagonal pattern (Prum et al. 1999). Ultraviolet structural colors are now known from the skin of the tragopans, Bulwer’s Pheasant, Blue Coua, Toco Toucan, and others.

The colors of the irises of bird eyes are produced by a very complex mixture of carotenoid and pterin pigments and structural colors produced by iridophores (Oliphant 1987). Iridophores are living pigment cells that include arrays of pigment crystals, and they are responsible for the structural colors of amphibian and reptile skin. In birds, they remain only in the iris and may have been lost elsewhere with the evolution of feathers.

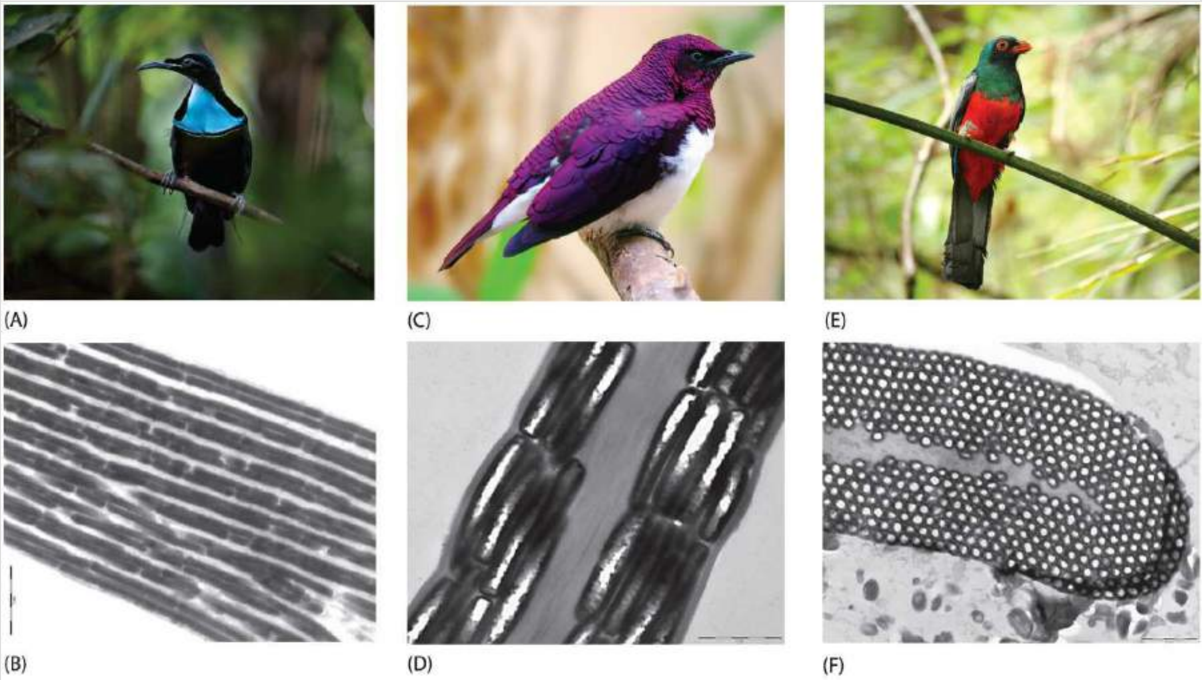


(A) Gary Vestal/Getty Images. (B–F) Courtesy of Richard O. Prum

Structural color of avian skin: (A) Display of Cabot’s Tragopan; transmission electron micrographs (TEMs) of color-poducing collagen arrays in the (B) ultraviolet, (C) light blue, and (D) orange areas of the facial wattles. The brilliant red areas are colored by blood in capillary vessels. (E) Velvet Asity. (F) TEM of the green portions of its facial caruncles.

Three different general classes of structural features produce the structural colors of feathers (Prum 2006). First is the “incoherent,” or random, reflectance of all visible wavelengths from unpigmented feathers producing white when light scatters off cellular air bubbles. The Rock Ptarmigan has evolved large, irregularly sized air bubbles in the barbules that increase the magnitude of light scattering to match the brilliant white snow (Dyck 1979).

A second class of feather structural colors is produced by constructive interference from arrays of melanosomes in the beta-keratin of feather barbules (Figure 4–19). Color-producing melanin granules in feather barbules are arranged in regular layers or in square or hexagonal crystals. These periodic spatial organizations result in **iridescence,** or change in hue with angle of observation or illumination. Iridescence happens because the difference in the distance traveled between light waves scattered by different objects changes with the angle of illumination and observation.



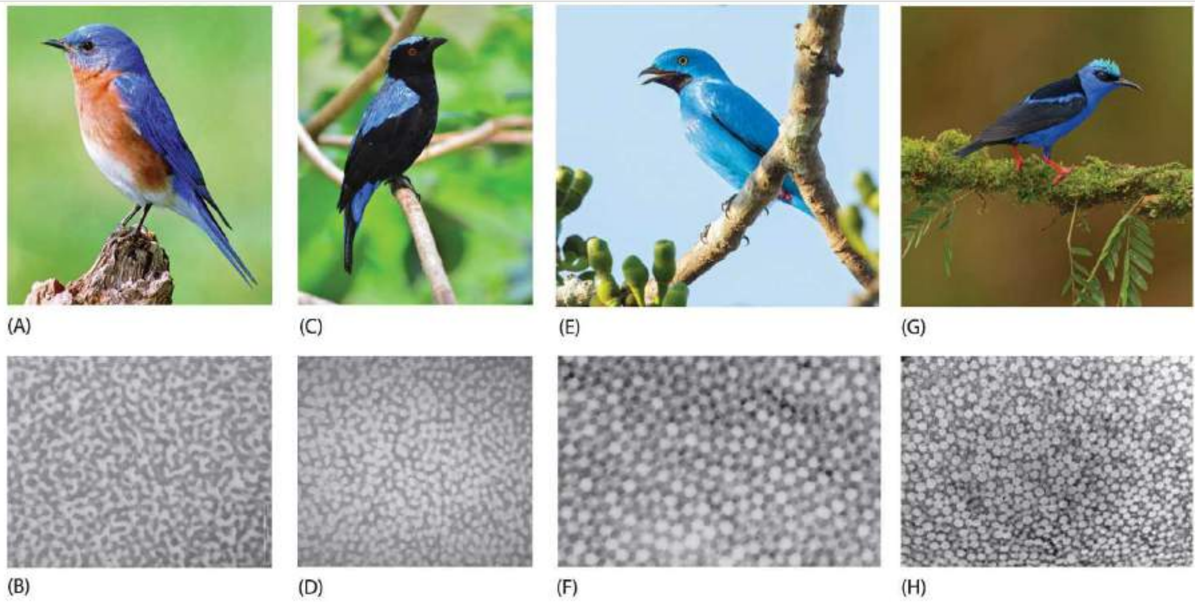
(A) Nick Garbutt/Naturepl.com. (C) MarkusMayer/Shutterstock. (E) Miroslav Hlavko/Shutterstock. (B, D, F) Courtesy of Richard O. Prum.

Figure 4–19 Iridescent plumage colors are produced by constructive interference from arrays of melanin granules in the feather barbules: (A, B) Magnificent Bird-of-Paradise; (D, E) Violet-backed Starling; (E, F) Slaty-tailed Trogon. Melansomes can be arranged in (B, D) laminar layers or (F) hexagonal crystals. Melanosomes in (B) are solid, whereas (D, F) are air-filled.

The color produced will be determined by the size of the melanosomes and the distances between them. Some birds have evolved unique air-filled melanosomes that produce even brighter colors more efficiently than solid melanin granules do (see Figure 4–19). For example, from seven to 15 layers of hollow, air-filled, pancake-shaped melanin granules produce the brilliant colors of hummingbirds. The intense metallic green colors of trogons and quetzals are made by arrays of air-filled, capsule-shaped melanin structures. In contrast, the oily metallic sheens of Common Grackles and European Starlings are produced by interference between light waves scattered by the surface of the feather and by a single, thick layer of melanosomes within the barbule beta-keratin below.

Although melanosomes used by birds to create iridescent barbule colors are composed of the molecular pigment eumelanin, these are still structural, not pigmentary, colors. The colors produced are a result not of the differential light absorption by melanin molecules but rather of the light-scattering properties and the size and spatial organization of the melanosomes.

The third class of structurally colored feathers is the noniridescent colors produced by spongy nanostructures made of air bubbles and beta-keratin inside of the medullary cells of feather barb rami. Examples of these structural colors are found in the Eastern Bluebird, the Asian Fairy-Bluebird, the Plum-throated Cotinga, and the Red-legged Honeycreeper (Figure 4–20). These colors are produced by constructive interference, but they lack iridescence because the air bubbles are not organized in any laminar or crystalline order like the melanin arrays of iridescent barbules. Instead, the air bubbles are all similar in size and distance apart from one another, but they are randomly packed together and do not form a periodic crystal. Again, arrays of smaller bubbles produce bluer colors, and larger bubbles make greener colors.



(A) Millard H Sharp/Getty Images. (C) Butterfly Hunter/Shutterstock. (E) Glenn Bartley/Getty Images. (G) Time Zurowski/Getty Images. (B, D, F, H) Courtesy of Richard O. Prum.

Figure 4–20 Noniridescent structural colors are produced by constructive interference from arrays of air bubbles in the beta-keratin in the medullary cells of feather barb rami. (A, B) Eastern Bluebird and (C, D) Asian Fairy-Bluebird have channel-shaped nanostructures. (E, F) Plum-throated Cotinga and (G, H) Red-legged Honeycreeper have spherical nanostructures. Electron micrographs are shown at different scales.

Spongy medullary structural colors come in two distinct spatial varieties: channels and spheres (Saranathan et al. 2012; see Figure 4–20). Each type has evolved multiple times within birds, but each family of birds with structural color has evolved either one type or the other. In other words, all structurally colored kingfishers, fairy wrens, thrushes, parrots, and pittas have channel nanostructures, and all toucans, cotingas, manakins, tanagers, and estrild finches have spherical nanostructures.

Combinations of Structural and Pigmentary Color

Structural and pigmentary coloration mechanisms frequently interact. For example, many color-producing nanostructures lie on top of a thick layer of melanin, which absorbs any white light that would be scattered randomly by the unorganized tissue below. Likewise, because pigment can only absorb light, all pigmentary colors rely on the scattering of light by air-filled medullary cells or other feather surfaces in order to produce pigmentary colors.

However, pigments and structural colors can be used in combination to produce additional colors that cannot be made with either mechanism alone. For example, many spongy barb nanostructures produce a turquoise color with two reflectance peaks—one in the green and one in the ultraviolet or blue (Figure 4–21). Bright green plumage colors are produced by a combination of spongy medullary structural color with a yellow carotenoid or (in parrots) psittacofulvin pigment. These green colors are not produced by color mixing—a simple combination of blue and yellow. Rather, the function of the yellow carotenoid pigment is to absorb the shorter, bluer peak and produce a pure green color (see Figure 4–21). Some unusual feather colors, however, are produced by color mixing. For example, the purple color of the nape of the Blossom-headed Parakeet is produced by a combination of structural blue color from the medullary barb rami and red psittacofulvins in the barbules.

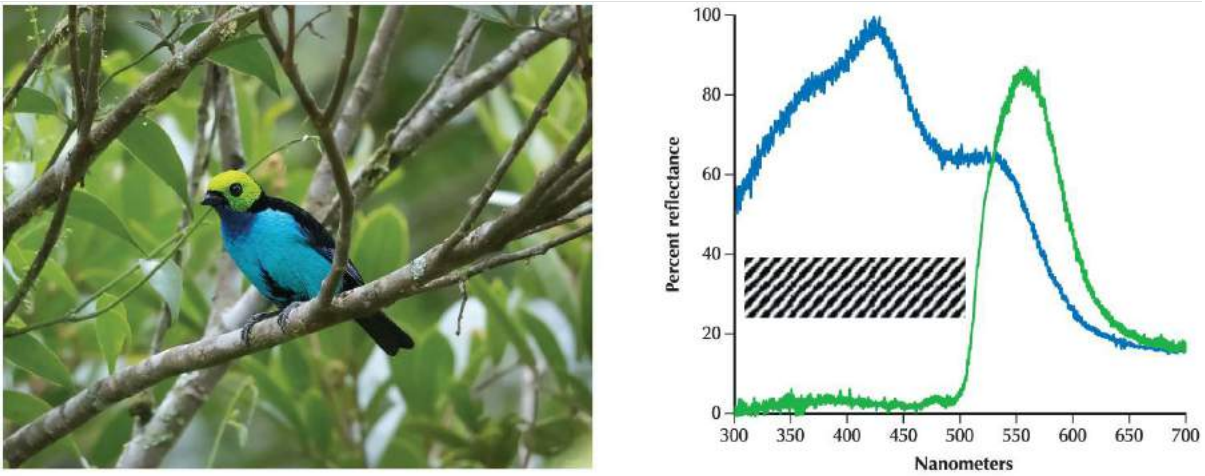


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Figure 4–21 The turquoise belly (blue line) and vibrant green crown feathers (green line) of the Paradise Tanager have identical feather nanostructures, but the green crown has additional yellow carotenoid pigments: zeaxanthin and lutein. The yellow pigments in the green feathers absorb the blue and ultraviolet wavelengths (hatching) to produce a brilliant, saturated green color.

Ultraviolet Colors

The feather colors of birds, especially blues and violets, are rich in UV reflectance, between 320 and 400 nm in wavelength. For example, the Blue Whistling Thrush from Southeast Asia has brilliant, structurally colored UV spots on its breast that have a reflectance peak at 340 nm and are completely invisible to humans. The powerful blue color of the male Eastern Bluebird and Western Bluebird (*Sialia*) includes strong UV components. The difference between the bright color of male bluebirds and the more subdued color of females corresponds to the thickness of the spongy nanostructure (Shawkey et al. 2003).

Most UV colors are structural, but some carotenoid pigments exhibit significant UV reflectance. For example, the brilliant carotenoid color of the Scarlet Ibis looks red to humans, but it also has a substantial UV reflectance that is visible to birds (see Figure 4–17). The purple carotenoids of the Pompadour Cotinga are even more extreme and result in visible red and blue reflectance that produces a purple color.

UV reflectance, as well as differences between sexes, appears to be a general and ancestral feature of bird-feather coloration, not an occasional oddity. Almost all of the 312 species surveyed, belonging to 142 bird families, have significant amounts of UV in their color spectra (Eaton and Lanyon 2003).

The importance of UV reflectance to bird biology and behavior was overlooked until the late 1990s, largely because humans can't see UV wavelengths. But birds can; they have a fourth, UV-sensitive cone in their retinas that humans lack (Chapter 7).

Genetic Control of Feather Color

Because the causes of plumage coloration are both anatomically diverse and mechanistically complex, the genetic control of feather coloration and coloration patterns is an enormous question. Except for the melanin patterns, little is known about the genetic control and inheritance of feather colors (Buckley 1987). The presence, absence, and pattern of deposition of particular pigments is often controlled by genes that segregate and recombine in predictable combinations, just as the genes that control blue eyes versus brown eyes in humans do.

Genes that regulate the production of melanosomes can contribute to overall plumage darkness (Roulin and Ducrest 2013). For example, the melanocortin-1 receptor (*MC1R*) gene is expressed on the cell membrane of melanocytes. When the hormone melanocortin binds to this receptor, the melanocyte is stimulated to produce melanosomes. *MC1R* gene mutations that function like a permanently switched on receptor can greatly increase melanosome production and, thus, melanistic plumage. For example, the Bananaquit is a nectar-feeding, black, yellow, and white Neotropical tanager. Individuals from the entirely black populations of Bananaquit on the Caribbean islands of St. Lucia and Grenada have a single DNA point mutation in *MC1R* that leads to an amino acid substitution in the receptor protein and produces a completely melanistic plumage (Theron et al. 2001; Figure 4–22). Similarly, melanistic individuals within populations of jaegers, Snow Goose, and Barn Owl are homozygous for various *MC1R* mutations (Mundy et al. 2004).

(A) Paul Wittet/Shutterstock. (B) Paulson Des Brisay. (C) ZUMA Press, Inc./Alamy. (D) Robert Shantz/Alamy. (E) A. Morris/VIREO

Figure 4–22 Variation in the intensity of melanin pigmentation within species can be influenced by mutation in the melanocortin-1 receptor gene: (A) Normal and (B) melanistic individuals of Bananaquit. (C) Color phases of Barn Owl. (D) White and (E) blue color phases of Snow Goose.

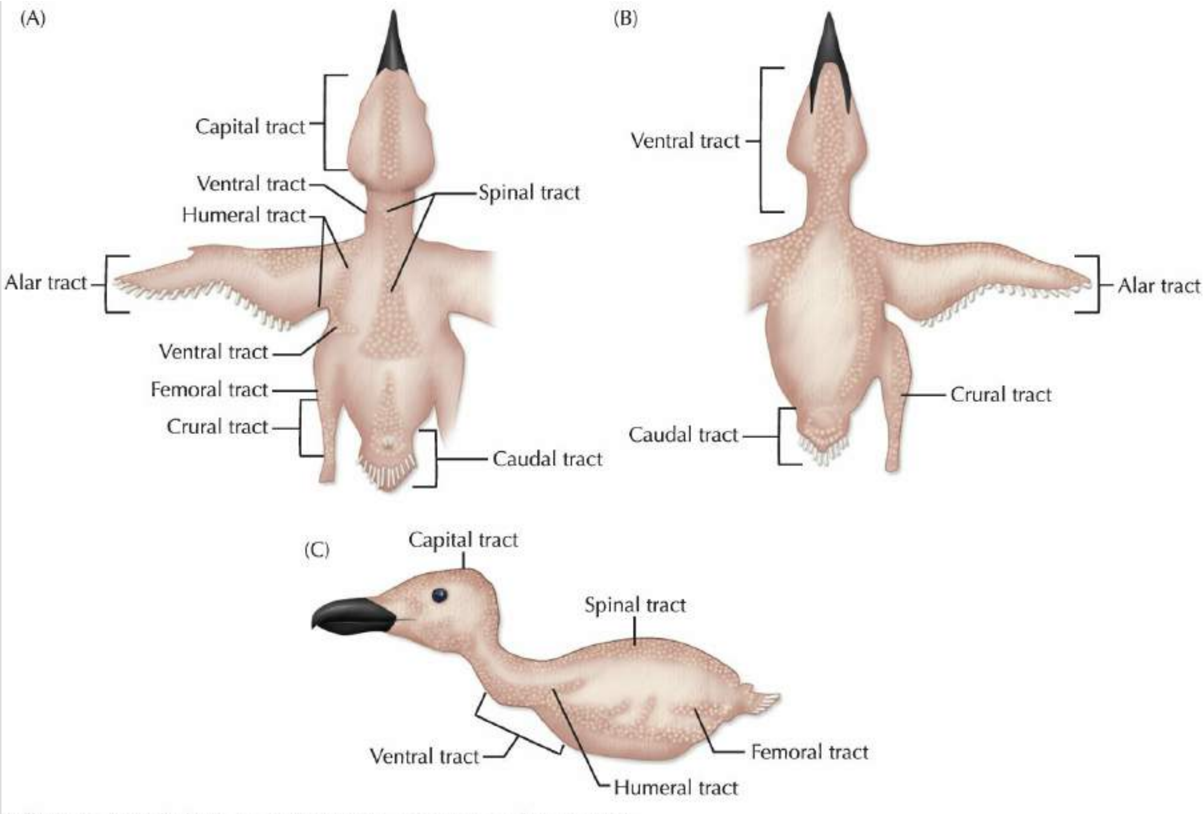
Analogous to human eye colors are alternative plumage colorations, called color phases, in birds. The Gouldian Finch, a brightly colored Australian species commonly kept as a cage bird, comes in red-faced, black-faced, and yellow-faced color phases. Genetic color morphs are widespread among bird species. They include dark-colored versus white phases of herons, seabirds, and geese; rusty versus gray phases of owls and nightjars; black versus pied phases of oystercatchers and passerine songbirds; and buffy versus grayish downy chick colors of swans, geese, and terns.

4.5 The Plumage

The entire plumage of birds consists of thousands of feathers. A Tundra Swan has roughly 25,000 feathers, of which 20,000 (80 percent) are on its head and neck (Wetmore 1936). Songbirds typically have from 2,000 to 4,000 feathers, of which 30 to 40 percent are on the head and neck.

The lightness of a single feather belies the total weight of a bird’s feather coat. The plumage of a Bald Eagle weighs about 700 grams, more than twice as much as its skeleton (272 grams), and between 17 and 20 percent of its total adult body mass (Brodkorb 1955).

Although feathers cover the entire body of a bird, they are not distributed over the skin uniformly in most birds. Rather, feather attachments are densely grouped in particular areas called feather tracts, or **pterylae,** that are separated by regions of skin with few or no contour feathers, called **apteria.** Like the comb-over hairstyle of a bald man, the apteria are not evident without close examination because the feathers spread out to cover the entire body. The nine major feather tracts (Figure 4–23) can be subdivided into as many as 100 separate regions that vary extensively among avian taxa. The study of these arrangements is called **pterylosis.**



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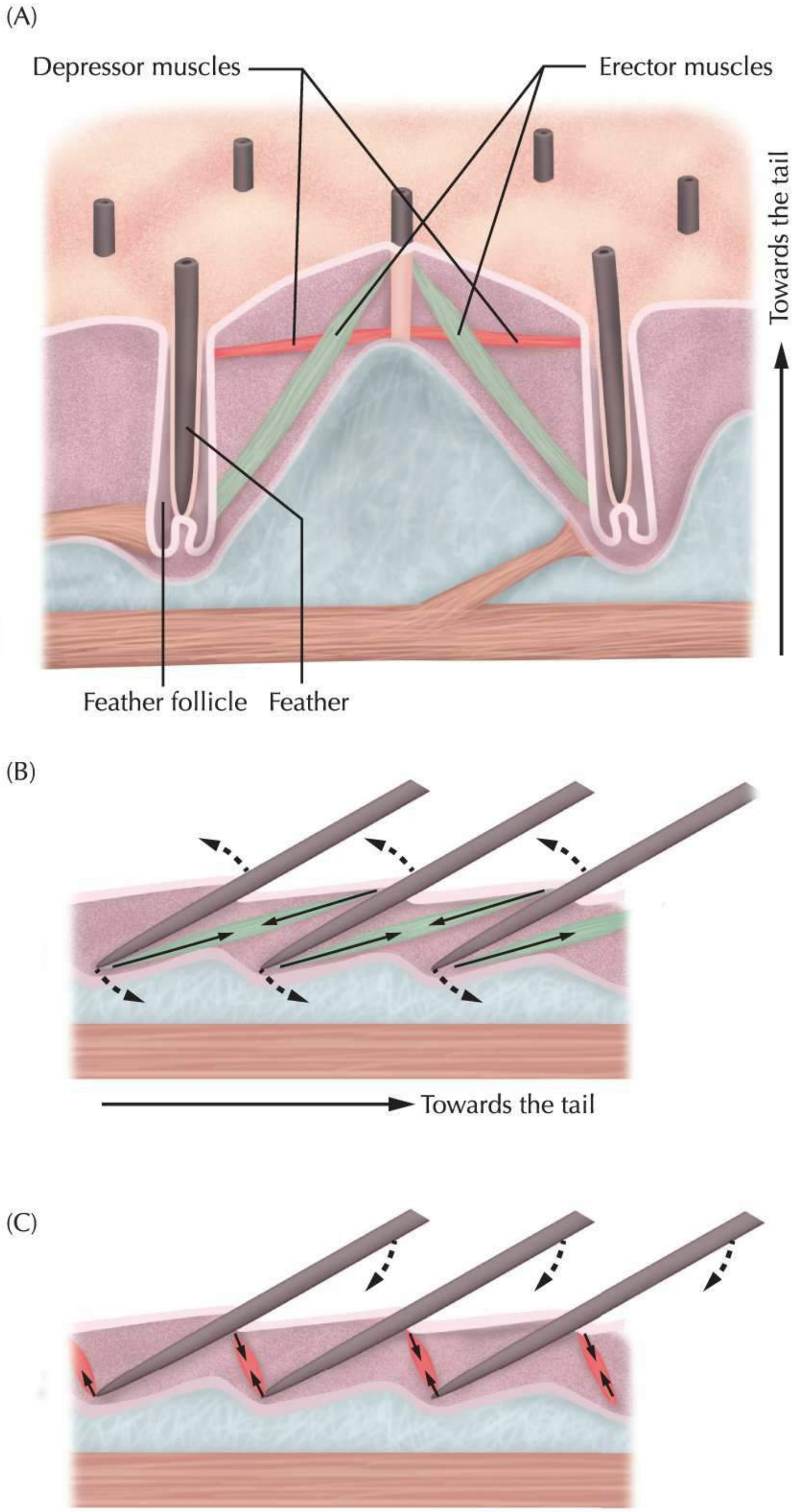
DATA FROM VAN TYNE AND BERGER 1976

Figure 4–23 The nine major feather tracts, or pterylae, of a Loggerhead Shrike. Bare or nearly featherless areas between the tracts are called apteria. (A) Dorsal view. (B) Ventral view. (C) Lateral view.

The functional significance of feather tracts and apteria has not yet been established. Most birds have a ventral apterium, which facilitates incubation of their eggs. Penguins lack apteria entirely, perhaps as an adaptation to cold climates and water. For years, ornithologists doubted that pterylae had functional significance and hence were good taxonomic characters. However, no one has yet returned to investigate the evolution of pterylosis in the context of modern phylogenetic hypotheses.

Within a feather tract, feathers are distributed in a spatially efficient hexagonal pattern. This hexagonal spacing also facilitates feather movements, which are accomplished by pairs of tiny networks of antagonistic muscles that interconnect the follicles of neighboring feathers. Mammals have only single muscles that raise their hairs. By contrast, birds have muscles that both raise and lower the feathers (Homberger and de Silva 2000; Figure 4–24). The feather-raising muscles run from the base of one feather follicle toward the tail to insert on the upper surfaces of the follicles of the two neighboring feathers. The feather-lowering muscles run from the upper surfaces of the follicle toward the tail to insert at the bottom of the follicles of the two neighboring feathers. Contracting either one of these networks of antagonistic muscles will raise or lower the feathers within a plumage patch. The movement of the feathers within the skin is facilitated by a layer of cutaneous fat that moves fluidly without compression (Homberger and de Silva 2000).



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DATA FROM HOMBERGER AND DE SILVA 2000

Figure 4–24 (A) Birds move their feathers using pairs of (green) erector and (red) depressor muscles that run between the follicles of neighboring feathers within a feather tract. (B) Contraction of the erector muscles (arrows in green muscles) rotates the feathers upward (dashed arrows). (C) Contraction of the depressor muscles (arrows in red muscles) rotates the feathers downward. Contraction of the depressor muscles in flight keeps the contour feathers from moving around and creating excess drag.

4.6 Feather Care

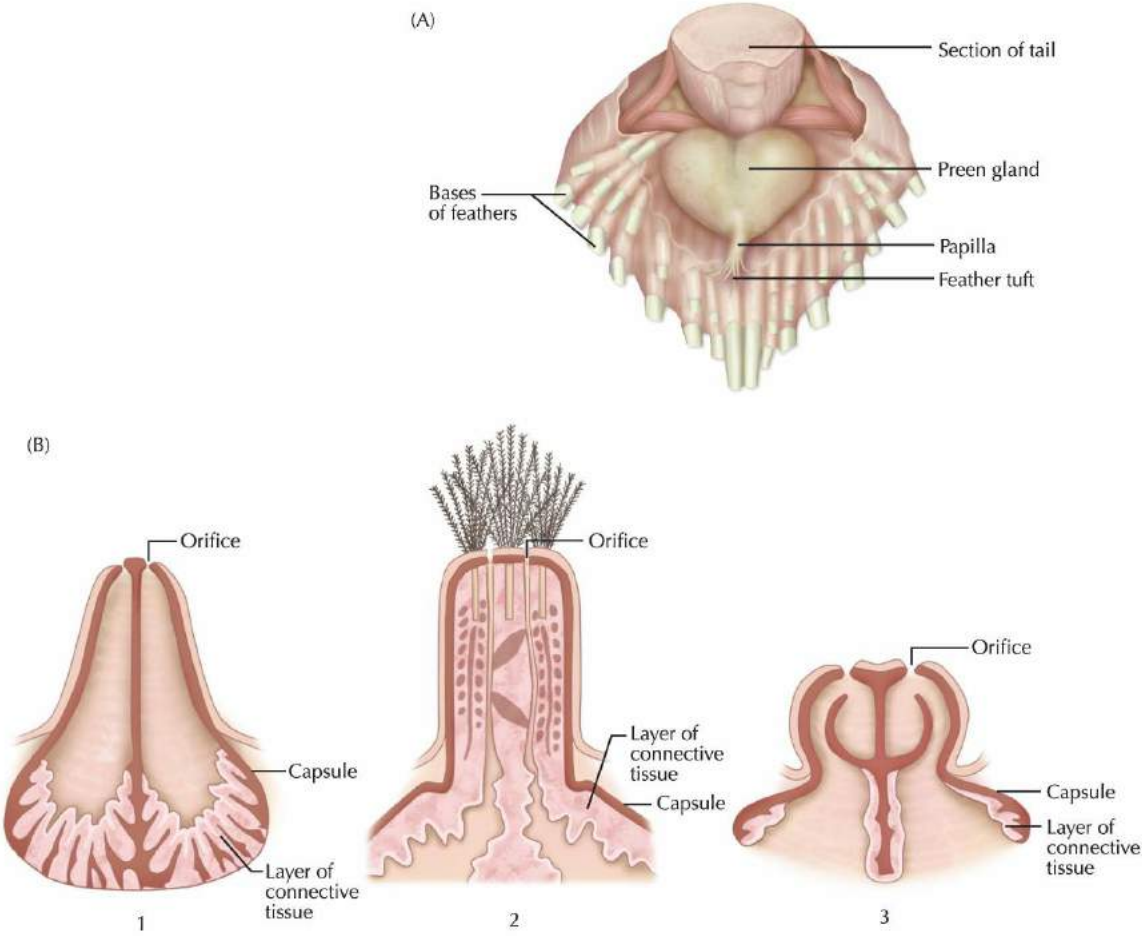
Daily care of feathers is essential. Birds preen their feathers with their beaks and toes to maintain their pennaceous feather vanes and to fight parasitic mites, lice, and bacteria.

Preening is important to birds, and it can occupy a significant portion of their daily activity budget. Birds systematically rearrange their plumage with their bills and reposition out-of-place feathers. They also draw the long flight feathers individually and firmly through the bill to restore the vane's integrity and to remove parasites. Birds groom and delouse head and neck feathers, which they cannot reach with their bills, by vigorous scratching. The vital preening function of the avian beak may have constrained the evolution of avian beak shapes. To augment the beak, herons, nightjars, and barn owls have evolved miniature combs on the inner margins of the claws of their middle toes that are used in grooming. Most birds scratch their heads directly, reaching up under the wing with a foot, although some scratch indirectly, over the wing. The advantage of one method over the other is not apparent but may be due to phylogenetic relationships. Crippled and one-legged birds cannot scratch their heads properly and, as a result, can accumulate large, uncontrolled populations of lice on their heads.

Many bird species also preen their mates or other social partners—a behavior called **allopreening** (Figure 11–1B). A phylogenetic comparative study indicates that allopreening is more frequent in cooperatively breeding species and is also associated with the higher likelihood that mates will remain together in future breeding seasons

(Kenny et al. 2017).

While preening, birds apply to their feathers the waxy secretions of the **uropygial gland,** or preen gland, located on the rump at the base of the tail (Figure 4–25). This skin gland is a unique evolutionary novelty of birds, and it is found in most extant birds. Most preen glands are bilobed structures with a small tuft of downlike feathers encircling the glandular orifices of a well-differentiated papilla.



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(A) Data from Lucas and Stettenheim 1972. (B) Data from Jacob and Ziswiler 1982

Figure 4–25 At the base of the tail on the lower back of most birds is the preen gland, which produces oily secretions that are essential for feather care. (A) Dorsal view of the gland and its environment on a White Leghorn Chicken. (B) Details of papilla: (1) delicate type; (2) compact type; (3) unique passerine type.

The preen gland secretes a rich oil of waxes, fatty acids, fat, and water, which, when applied externally with the bill, cleans feathers and preserves feather moistness and flexibility. Regular applications of the secretion to the plumage sustain its functions as an insulating and waterproofing layer. The largest preen glands are found in birds that swim, dive, or rest on water, such as petrels, pelicans, ducks, and grebes (Johnston 1988). Whether their secretions are essential for keeping feathers dry and pliable and for maintaining buoyancy remains to be verified. However, as noted earlier, the water repellency of feathers depends chiefly on the fine structure of the barbs, not on the uropygial secretion.

The waxy secretions of the preen gland may also help to regulate the parasitic bacteria and fungi that grow on feathers. Certain preen-gland lipids can kill fungi and bacteria that digest keratin in in vitro experiments, thus potentially influencing both insulation and color (Shawkey et al. 2003). However, experimental removal of the uropygial gland in House Sparrows led to an increase in total plumage bacteria but not to a specific increase in **feather-degrading bacteria** (Czirják et al. 2011). Other secretions may promote the growth of nonpathogenic fungi and discourage feather lice. Such chemical hygiene is among the most important functions of preen-gland secretions. The foul-smelling preen-gland secretions of hoopoes and wood hoopoes of Africa may also repel mammalian predators.

Results of studies of the impact of feather-degrading bacteria on plumage and color quality are mixed. Tail feather wear is significantly correlated with the prevalence of feather-degrading bacteria but not with the total prevalence of bacteria, indicating that feather-degrading bacteria have a specific impact on the integrity of the plumage (Kent and Burtt 2016).

Living among the feathers themselves are diverse communities of feather **ectoparasites,** including chewing lice, louse flies, and feather mites (Proctor and Owens 2000; Clayton et al. 2008). These parasites have been with birds for a long time: the fossil record includes a 44-million-year-old bird louse with feathers in its gut (Wappler et al. 2004). Chewing lice, or mallophaga, feed on the feathers themselves as well as on blood or tissue fluids. At the tiny size scale of these parasites, the plumage is an entire ecosystem. As many as 12 species of lice may inhabit the plumage of one bird, with each species specializing on different kinds of feathers or parts of the body. Louse flies are flat, tough, clawed, bloodsucking flies specialized for living in the feathers of birds and the fur of mammals. More than 150 species are known to parasitize birds. They are the important vectors of blood parasites and aid the transport of chewing lice and feather mites from one host to another. Eight-legged feather mites are relatives of spiders. They live their entire life cycles on their avian hosts and include many species specialized for particular feather microhabitats. Some live on the feather surfaces; others live inside the feather shaft.

Feather-chewing parasites damage the structural integrity of feathers, which can reduce both the winter survival and the attractiveness of male pigeons (Clayton 1990, 1991). Feather damage also reduces the insulating quality of feathers and thereby causes metabolic heat production to increase by as much as 8.5 percent (Booth et al. 1994).

Preening by birds creates strong natural selection on feather parasites to become camouflaged against the host plumage. For example, sister species of feather lice that live and feed on the Yellow-crested Cockatoo and Yellow-tailed Black Cockatoo have rapidly diverged in color to be either brilliant white or dark black to match the plumage colors of their host (Bush et al. 2010; Figure 4–26). Cryptic coloration evolves commonly in lice that live on the body, wings, and tail plumage, where preening with the beak is guided by vision, but it does not occur among lice that infest the plumage of the head, where birds have more limited ability to preen and cannot guide their preening visually.

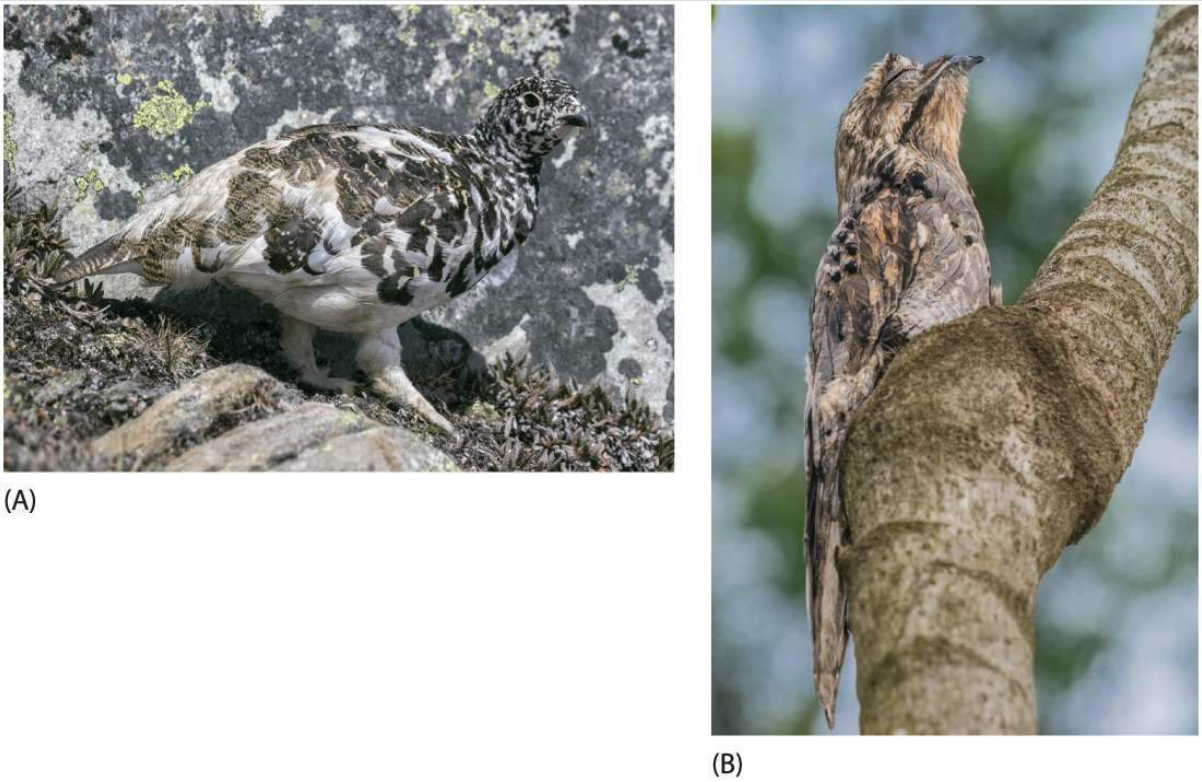
(A, B, D) Courtesy of Sarah E. Bush, Clayton-Bush Lab, Department of Biology, University of Utah. (C) Trevor Hampel.
(E) Brooke Whatnall/Shutterstock

Figure 4–26 (A) Damage to abdominal contour feathers done by feeding lice: (*top*) no damage, and (*bottom*) severe damage. The barbs and shaft are not damaged, apparently because they are too large to ingest. (B, D) Closely related feather lice have evolved body colors that match the plumage colors of two closely related species of Australian cockatoos, Sulphur-crested Cockatoo (C) and Yellow-tailed Black Cockatoo (E), to escape visual detection by the hosts during preening.

Until recently, birds were thought to lack poisonous chemical defenses, such as those of some brightly colored frogs and insects. However, certain New Guinea forest birds—the three species of shrike-thrushes called pitohuis and an unrelated songbird, the Blue-capped Ifrita—are extremely toxic. Jack Dumbacher and his colleagues (1992) discovered that the skin and feathers of pitohui shrike-thrushes contain high concentrations of a deadly alkaloid neurotoxin called homobatrachotoxin, which was first discovered in poison dart frogs from the Neotropics. The Hooded Pitohui, in particular, carries large amounts of poison (see Figure 4–15B). Indigenous New Guinea peoples knew that pitohuis made them sick if eaten without special preparations. The feather toxin is apparently incorporated into the body by ingesting *Chloresine* beetles (Melyridae), which produce this toxin to defend themselves against predation (Dumbacher et al. 2004). The source of these feather toxins was discovered serendipitously because in the region of Herowana, a tiny village in the Central Highlands of Papua New Guinea, these toxic beetles are referred to by the same name—*nanisani*, referring to the tingling, numbing sensation that occurs from handling them—as one locally common species of toxic bird.

4.7 Plumage Color Patterns

Plumage colors, the great composite of individual feather colors, vary in hue from drab to bright and in pattern from **cryptic** (concealing) to bold. Concealment is an important function of many bird color patterns, not just of those that are obviously cryptic but also of many bold or bright patterns that match a bird’s usual environment. Ptarmigan are nearly pure white in winter, when they blend with the mountain snows. In spring, when patches of snow remain on the alpine meadows, the birds are white and brown (Figure 4–27A). In summer, when herbs and lichen cover the rocks, ptarmigan are finely barred black and brown. Woodcocks and Whip-poor-wills resting on a forest floor of dead leaves are invisible to us. Parrots disappear among the greens of tropical leaves and the reds of tropical flowers. The American Bittern points its bill skyward, aligning its body contours and the stripes on its breast with the surrounding vertical marsh grasses. The wood-colored Common Potoo of tropical America conceals itself by assuming the posture of a dead stump (Figure 4–27B).



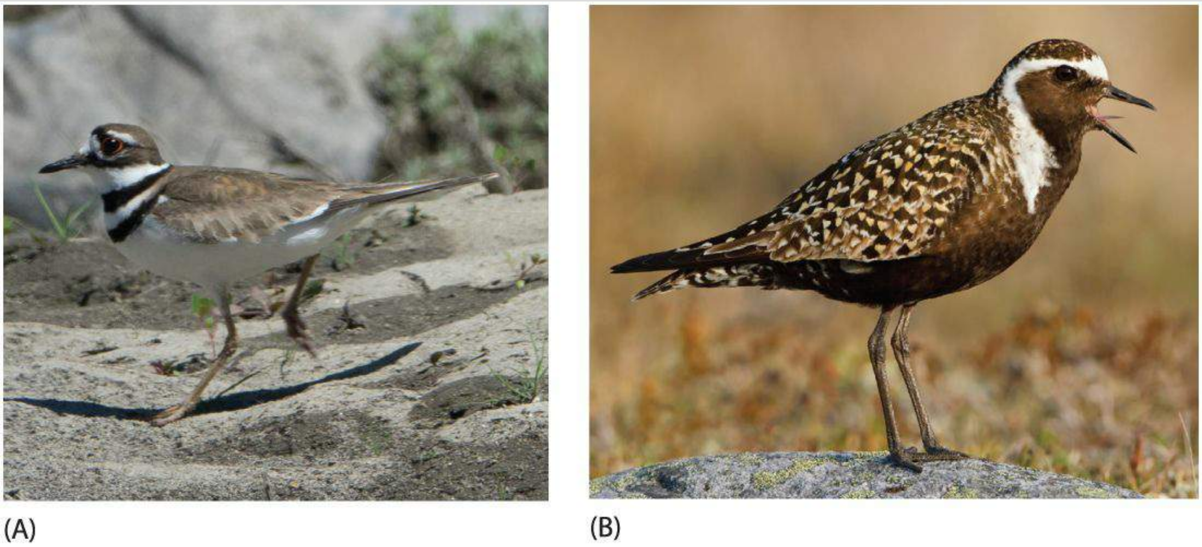
(A) David Osborn/Shutterstock. (B) Rafael Martos Martins/Shutterstock

Figure 4–27 Plumage coloration provides excellent camouflage. (A) The White-tailed Ptarmigan blends into an alpine meadow. (B) The Common Potoo looks like a dead stump.

Some bold color patterns reduce the contrast between a bird’s shape or outline and its background. The double breast bands of the Killdeer, a small plover, are a classic example of a disruptive pattern. The bands visually separate the outline of its head from that of its body. To be most effective, the contrast between disruptive patches on a bird’s body should be as great as that between the bird and its background. The finely patterned summer plumage of a ptarmigan blends with the finely patterned alpine grasses and lichens, and the boldly patterned plumages of the arboreal wood warblers of North America blend with the small leaves, branches, and lighting of trees.

Abbott Thayer and his son Gerald (1909) were the first to identify the principle of **countershading** in concealment. Because the body casts a shadow on itself when illuminated from above, having a darker dorsal surface and a lighter ventral surface will compensate for the effect of body shadows and conceal the outline of the body. The value of contrast increases with the intensity of illumination from above. Thus, many open-country birds, such as plovers, often have strongly contrasting colors on their upper and lower surfaces (Figure 4–28A). White underparts work particularly well as a neutral (achromatic) reflector that takes on the hue of the nearest surface.

The advantages of bold color patterns for visual display used in social and sexual communication can supplement or take precedence over the need for concealment. Whereas countershading enhances concealment, reverse countershading (white upperparts and dark underparts) renders the breeding male Spectacled Eider, Bobolink, and American Golden Plover strikingly conspicuous (Figure 4–28B).


(A) (B)

(A) LISA PARSONS/SHUTTERSTOCK. (B) GLENN BARTLEY/AGE FOTOSTOCK

Figure 4–28 (A) The plumage pattern of a Killdeer (a plover) combines countershading, the achromatic reflectance of substrate by white underparts, disruptive head and breast markings, and breast bands that help match horizontal breaks in the shoreline or horizon. (B) The breeding plumage of an American Golden Plover is an example of reverse countershading for higher visibility.

4.8 Molts and Plumages

Every bird replaces all of its feathers with a series of new plumages, or feather coats, during its lifetime. Accidental feather loss triggers the growth of replacement feathers, but feathers are typically replaced in a comprehensive and controlled way through molt, both seasonally and with age. The first natal down plumage may consist of a few scattered down feathers, as in many young passerines, or it may be a dense, fuzzy covering, like that of ducklings. The fragile down feathers rarely last more than a week or two. A more substantial set of downy or vaned feathers then replaces them.

In most birds, the natal down is pushed out of its follicles by the incoming pennaceous **juvenal plumage** in the first weeks of life. Wisps of down may remain for a time attached to the new juvenal feathers. A baby bird's first set of wing and tail feathers appears at this time and grows rapidly in preparation for flight. As the young bird—now called a juvenile—approaches independence, it exchanges parts of its juvenal feathers for new plumage.

Immature or adult plumage replaces the juvenal plumage of most of the feather coat, although not always that of the wings or tail. The young American Robin, for example, begins in midsummer to replace its spotted juvenal plumage with unspotted adult plumage (Figure 4–29). The first wing feathers remain. A few months later, its original flight feathers will propel the young robin on its first migratory flight. The bird will not molt again until it is just over one year old.

JPBC/SHUTTERSTOCK

Figure 4–29 The spotted juvenal plumage of an American Robin, with residual tufts of down still attached to the tips of incoming contour feathers.

An adult bird typically molts after breeding, replacing its entire plumage. It may keep its new set of feathers for 12 months, or it may replace some plumage before nesting the following year, which allows it to convert somber camouflage plumage into brightly colored plumage for territorial and sexual display.

Feathers of some plumages may change in appearance because of feather wear. The Common Starling, which is spotted in the winter, loses its spots as the feather tips wear off; by spring, it is sleek and glossy. Meadowlarks also wear off the buffy feather tips of their winter plumage, exposing bold black and yellow underparts in the spring. The male Velvet Asity molts into a scaly green and black plumage that changes gradually to a deep velvety black as the green tips wear off (Figure 4–30).


(A)

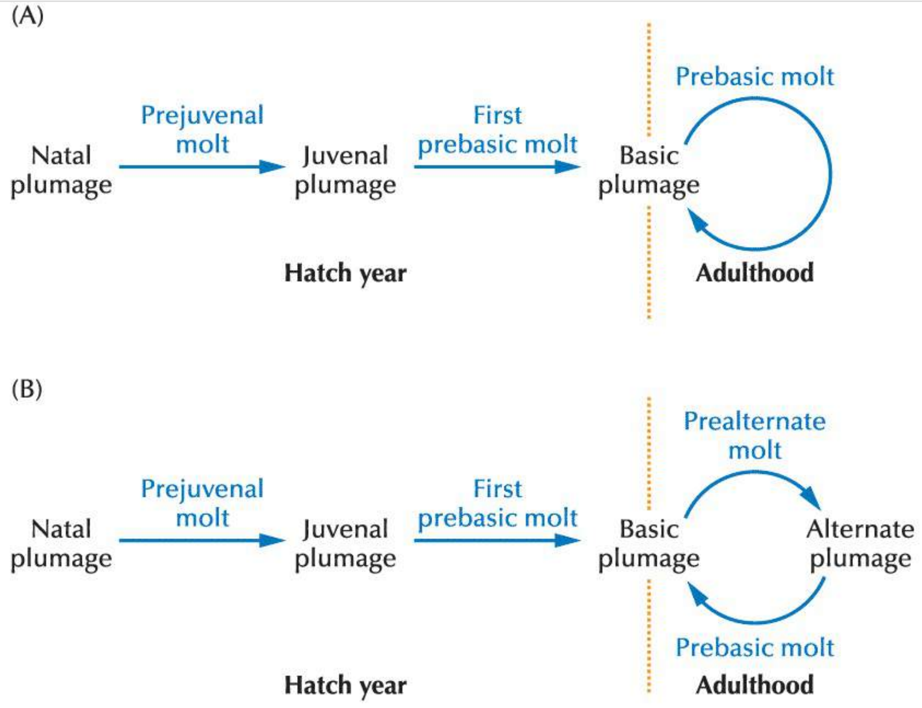
(B)

(A) B. Miller/VIREO. (B) © Dominique Halleux/Biosphoto

Figure 4–30 Plumage color change with feather wear. (A) The freshly molted basic plumage of the male Velvet Asity is scaly green over a black background. (B) When the green tips wear off as the breeding season approaches, the male appears pure velvety black.

Molt and Plumage Terminology

The terminology of molts and plumages relates each generation of feathers to the molt that produced it (Humphrey and Parkes 1959; Pyle 1997; Figure 4–31A). All birds have at least one complete (or nearly complete) new plumage a year, which is usually renewed after breeding. This plumage is present in all birds and is called the **basic plumage.** Many different groups of birds have independently evolved a distinct, second annual molt and plumage, often occurring before breeding. Because it is an evolutionary addition to the ancestral condition of a single basic plumage, this plumage is called the **alternate plumage** (Figure 4–31B). The terms “breeding” or “winter” plumage are considered ambiguous because they may refer to either the same or different plumages, depending on the molt sequence of the species.



Plumage and Molt Terminology

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Figure 4–31 The molts and plumages of birds are named according to their sequence in the life cycle of the bird. Each molt (blue) is named for the plumage (black) that it produces. (A) The simplest molt pattern begins with the natal and juvenal plumages during the first, or hatch, year, which are followed by the basic plumage that is produced once annually by a prebasic molt. (B) Another common, more complex molt pattern is characterized by the addition of an alternate plumage produced by an annual prealternate molt. Typically, the alternate and basic plumages are displayed during the breeding and nonbreeding seasons, respectively.

The distinct molts and plumages during the first year of life, or hatch year, may have distinct names, but subsequent years repeat the same cycle of plumages and molts. Different groups of birds have evolved additional plumage complexity by inserting an additional molt and plumage into the hatch year or into all years (Howell et al. 2003; Jenni and Winkler 2004; Wolfe et al. 2011).

Multiple annual molts can be an adaptation to severe feather wear or infestation by parasites. For example, in deserts, where wind and sand rapidly destroy feathers, some African larks molt completely twice a year. European larks, which suffer less abrasion, molt only once a year. Species that live in coarse grass habitats, such as the Bobolink and Saltmarsh Sparrow, also may molt twice a year. Shedding parasites is one apparent result of the double molt in the Saltmarsh Sparrow. It has fewer feather parasites than the Seaside Sparrow, which lives in the same marshes but molts only once a year.

Body molt proceeds in a characteristic spatial and temporal wave over the body. The molt of flight feathers must proceed in regular sequence, feather by feather, in order to avoid big gaps in the wings that would compromise flight capacity (Figure 4–32). Most commonly, primary feather molt begins with P1, the innermost primary at the base of the carpometacarpus, and proceeds outward to P10 or P9. However, many molt sequence variations are possible, including molt from higher primaries inward and molt in both directions away from a central feather. Perhaps the most complex is the wing molt of certain cuckoos, which proceeds in two waves, skipping even and then odd feathers: for example, P9–7–5–3–10–8–6–4 and so on (Payne 2005a).

Waterfowl (Anatidae) and Magpie Geese (Anseranatidae) are unique in exhibiting simultaneous molt of all of their flight feathers after breeding, rendering them flightless for several weeks. The seasonal molt pattern of waterfowl is the source of both the idea that it is unsporting to “shoot a lame duck” and the colloquial tradition of referring to a politician or legislature during the period between an election and the next term as a “lame duck.”

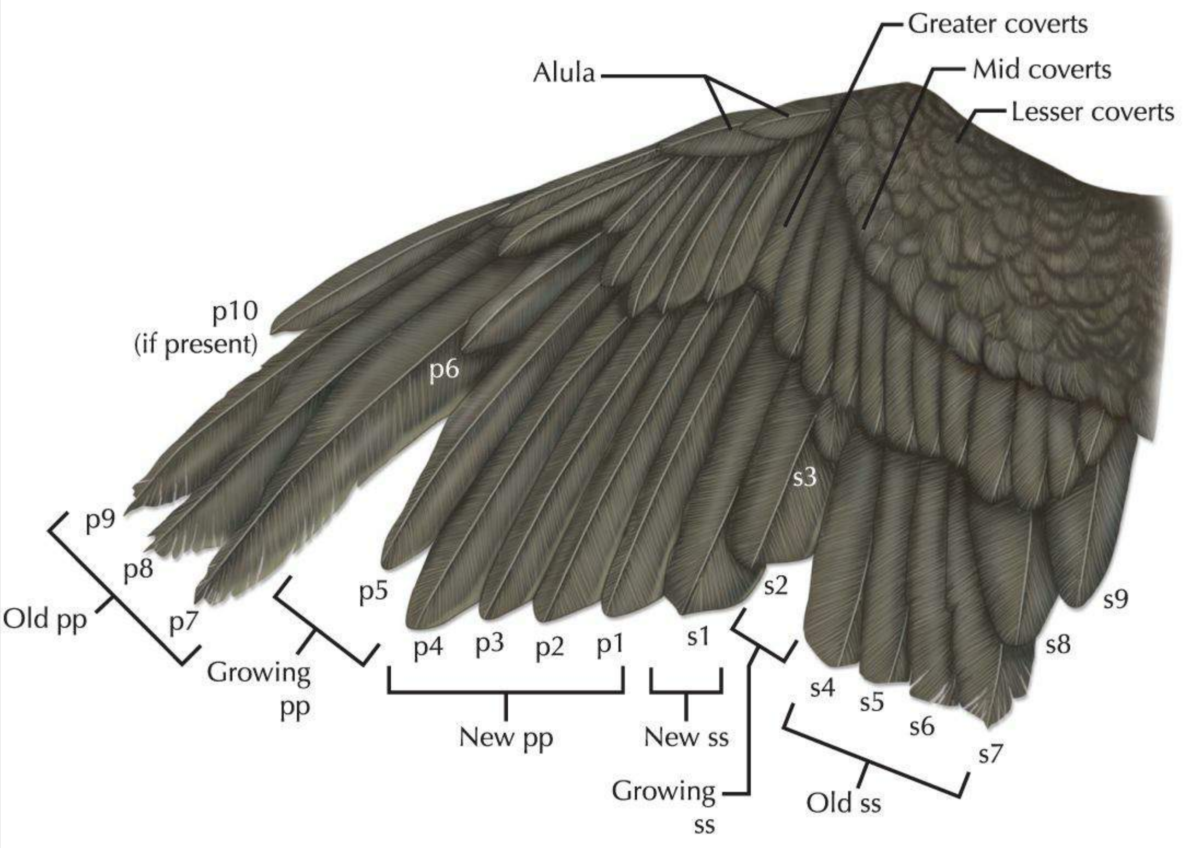

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Figure 4–32 Molt of primary and secondary flight feathers proceeds in a stereotyped spatial pattern across the wing. During active molt, the distribution of worn, actively growing, and newly replaced feathers provides evidence about the molting pattern.

Because molting can be metabolically demanding, most birds have evolved to molt when they are not breeding. Albatrosses have such long wings with so many flight feathers to regrow that they cannot complete a full flight feather molt in the one nonbreeding season. As a result, albatrosses cannot molt all their flight feathers in a single bout, and the largest albatrosses breed every other year so that they can completely replace all their flight feathers (through two intervening prebasic molts) before breeding again (Rohwer et al. 2009).

Instead of molting into an adultlike **definitive plumage** in their first prebasic molt, many different birds have evolved **predefinitive plumages** with distinctive appearances for some years after the first hatch year. For example, some species of *Larus* gulls do not acquire definitive plumage for four or five years. These predefinitive plumages may signal the younger age and lower status of the individual to older social competitors in order to escape social competition or aggression.

Many bird species are **sexually dimorphic** in plumage coloration or feather shape. Sexual dimorphism usually evolves by sexual selection for ornamental plumage in one sex or the other (Chapter 13). In some sexually dimorphic species, such as *Chiroxiphia* manakins, young but sexually mature males molt through a series of distinctive plumages before reaching definitive male plumage in year 4 or later. These predefinitive male plumages may signal lower social status to other males that compete with each other for mating.

A few birds molt three or four times a year, but the extra molts are only partial ones. The Ruff, a large shorebird with an unusual lek mating system (Figure 13–11), produces a variety of striking male breeding plumage in stages. Male Ruffs undergo a standard prebasic molt in the fall to assume a brown camouflaged basic plumage; a prealternate molt in the spring, which produces most of its breeding plumage; and then a third, partial, supplemental molt, which produces the “ruff,” which varies in color from white to rust to black and many combinations of these colors. The males return to a drab, female-like basic plumage in the next prebasic molt. The same set of follicles generates feathers of colors and shapes in the successive molts. To match their camouflage to the seasonal changes in the tundra, ptarmigan have three partial molts a year, and some populations of the Willow Ptarmigan have four.

REVIEW KEY CONCEPTS

4.1 Feather Structure

Feathers are complex, branched structures that are made mostly of the protein beta-keratin. The main shaft of the feather is the rachis, and the smaller branches are barbs. The barbs have even smaller branches called barbules. The tubular base of the feather, or calamus, is retained in the skin by the feather follicle. The coherent surface of a feather vane is created by the zippering interactions between hooklets and grooves on the overlapping barbules of adjacent barbs. The diversity of feathers over the body vary in the structure of these fundamental feather parts and in their consequent functions in the lives of the bird. The main classes of feathers are the contour (or body) feathers, flight feathers, downs, filoplumes, bristles, and powder downs.

Key Terms: beta-keratin, contour feather, vane, calamus, follicle, rachis, barbs, ramus/rami, barbules, cortical cells, medullary cells, barbicels, distal barbules, proximal barbules, plumulaceous, nodal prongs, afterfeather, aftershaft, remex/remiges, rectrix/retrices, primaries, secondaries, pennulum/pennulae, down, natal down, filoplumes, bristles, powderdown

4.2 Feather Development

A bird’s feather follicles and its first feathers develop while the embryo is still in the egg. All the feathers of the bird are replaced periodically throughout its life through molt (section 4.8). The development feather, or feather germ, is basically a tube of epidermis that grows out of the skin. The various branches of the feather develop from specific sections or layers of this tube. Feathers are branched like a tree, but they grow from their base like a hair; the tip of the feather is older than its base, and each barb is older than its connection to the rachis. To create the vane, new barb ridges form on the ventral side of the follicle, grow helically around the tube toward the dorsal side, and ultimately fuse to the rachis. When the feather is mature, it emerges from the tubular sheath, and the barbs expand to form the planar vane.

Key Terms: molt, epidermis, dermis, follicle collar, placodes, feather germ, sheath, barb ridges, barbule plates, rachis ridge, dermal pulp, pulp caps, inferior umbilicus, fright molt

4.3 Evolution of Feathers

The top and bottom surfaces of a feather are not homologous with the top and bottom surfaces of a scale. Thus, feathers could not have evolved from elongate scales through natural selection for gliding or flying. The process of feather growth predicts that feathers evolved through series of distinct stages, each of which involved an innovation in developmental mechanisms. The “Evo-Devo” theory predicts that the first feathers were simple tubes, followed by downlike tufts of barbs, followed by more complex, multiply branched feathers. Feathers evolved nearly all of their structural complexity in theropod dinosaurs before the origin of birds or the origin of flight.

4.4 Feather Colors

Feather colors are produced by light-absorbing pigments, color-producing nanostructures, or an interaction of both of these mechanisms. Different feather pigment molecules produce different feather colors. Melanins produce black, gray, and brown plumage colors. Carotenoids produce yellow, orange, red, and purple plumage colors. The unpigmented cells of white feathers scatter all light wavelengths. In contrast, wavelength-specific structural colors are produced by constructive interference of light by arrays of melanosomes in feather barbules or by air bubbles in the medullary cells of the barb rami. In general, the former are iridescent (i.e., they change with angle of observation or illumination), while the latter are not.

Key Terms: light, pigments, structural colors, melanins, carotenoids, psittacofulvins, porphyrins, melanocytes, melanosomes, eumelanin, pheomelanin, turacin, turacoverdin, "honest signaling", nanostructures, constructive interference, iridescence

4.5 The Plumage

The entire plumage of the bird is composed of 2,000 to more than 25,000 feathers. The contour feathers are not distributed uniformly over the body of the bird. Rather, they grow from specific tracts, or pterylae. Between the pterylae are regions of skin that lack contour feather follicles, called apteria. Birds can move their feathers dynamically using networks of antagonistic muscles that connect neighboring feathers.

Key Terms: pterylae, apteria, pterylosis

4.6 Feather Care

The plumage of birds can be damaged by abrasion, feather-degrading bacteria, and feather-eating ectoparasites, including feather lice and mites. Birds care for their feathers daily by preening them with their beaks and their claws. While preening, birds apply to their feathers the waxy secretions of the uropygial gland, or preen gland, located on the rump at the base of the tail. Feather ectoparasites are diverse and have an ancient evolutionary history with birds. The plumage is an entire ecosystem to these tiny feather ectoparasites. Many species are endemic to individual bird species and may be found only on specific classes of feathers.

Key Terms: allopreening, uropygial gland, feather-degrading bacteria, ectoparasites

4.7 Plumage Color Patterns

Plumage coloration varies in pattern from cryptic (concealing) to bold. The complex plumage color patterns have evolved through natural selection for protection from predation and through social and sexual selection for communication. Because a bird in direct sunlight will cast a shadow on its own belly, many open-country birds have evolved countershading—plumage patterns with dark colors above and light colors below.

Key Terms: cryptic, countershading

4.8 Molts and Plumages

Birds replace all their feathers with an entirely new plumage through molt. From the natal down feathers of the embryo and the first juvenal plumage, each bird proceeds through a series of specific molts. The simplest molt pattern is a single annual prebasic molt that produces the basic plumage. Many birds that have a different appearance in the breeding and nonbreeding seasons have evolved an additional prealternate molt before the breeding season, which gives rise to the alternate plumage. Patterns and timing of molts are complex and often highly stereotyped within species, but they have evolved to be highly variable among species with different ecologies, breeding systems, and migration patterns.

Key Terms: juvenal plumage, basic plumage, alternate plumage, definitive plumage, predefinitive plumage, sexually dimorphic

APPLY YOUR KNOWLEDGE

1. Describe the functions of the following feather types: contour feathers, down feathers, filoplumes, bristles, and powderdown.
2. Explain the developmental theory of feather evolution and how a tubular outgrowth of the skin progressed through stages to produce a vaned, asymmetrical flight feather. What may have been the functions of the precursors to modern feathers?
3. Compare and contrast the structures of outer contour feathers and the underlying feathers and feather structures that provide insulation.
4. Describe how feather growth proceeds and how barbs fuse to the rachis.
5. Describe how feather development indicates that feathers did not evolve from elongate scales.
6. Compare and contrast the features of the chemical structures of pigments. How does the organization of double bonds, ring

structures, and the lengths of carbon chains produce different colors in bird feathers?

7. Describe the sources of carotenoid and melanin feather pigments.
8. Structural colors depend on the interaction of light with the physical structures of feathers instead of the differential absorption of light by pigments. Explain how light interacts with structures to produce white feathers, blue feathers, and iridescence.
9. Describe the factors that influence the number and nature of molts of birds throughout their lives. What factors influence the frequency of molting, the timing of molting, and the sequential changes to a bird’s appearance?
10. How do preening and allopreening increase the health and fitness of birds?

CHAPTER 5 *Flight*

ALL CANADA PHOTOS/ALAMY STOCKPHOTO

Flying in V-formation allows Canada Geese to save energy and fly more efficiently.

5.9 Evolution of Flight

> The pure acrobatic ability of birds far exceeds that achieved by the most sophisticated aircraft. [DIAL 1994, P. 301]

Powered flight is an amazing evolutionary innovation of birds. Only three groups of vertebrates have ever evolved this ability: the bats, the extinct pterosaurs, and the birds. Yet birds do not merely fly. They are masters of the fluid that is air, just as fishes are masters of the fluid that is water. Birds can hover in one place, dive at breathtaking speeds, and fly upside down and backward. Foraging frigatebirds and migrating swifts can fly continuously for months on end (Liechti et al. 2013; Weimerskirch et al. 2016). Birds are one of nature's finest locomotor designs (Dial 1994).

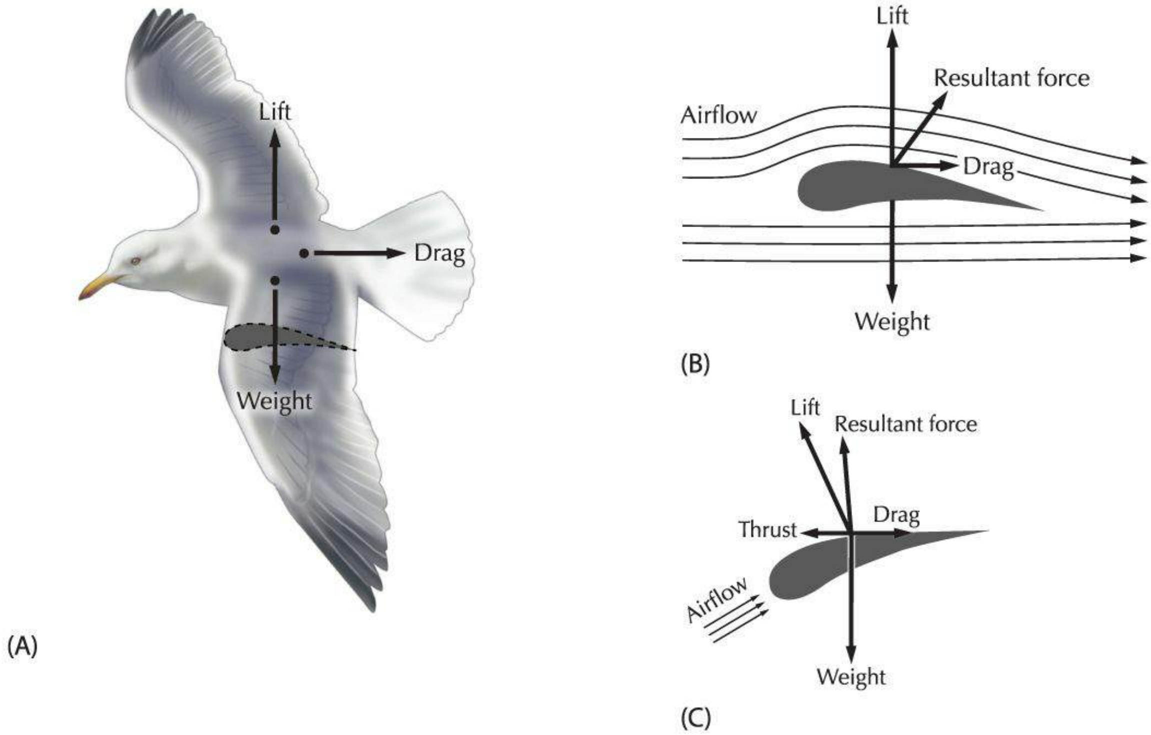
Basic bird flight has many components—taking off, maneuvering, stabilizing, and landing—each of which is complex in its own right. Flight requires rapid and constant adjustments of the wings and tail. The sensory system sends information from thousands of individual feathers in a bird's plumage (see section 4.1 in Chapter 4) to the flight-control center in the brain and neural receptors throughout the body (see section 7.5 in Chapter 7).

Flight is expensive in regard to energy used per unit time but makes up for those costs with savings in energy per unit distance covered. Flight is the most economical form of locomotion. A 10-gram bird in flight, for example, expends less than 1 percent of the total energy required by a 10-gram mouse to run the same distance. The high, moment-to-moment costs of flight, however, favor efficient designs of a bird's wings, muscles, and skeleton.

This chapter first discusses the elementary aerodynamic principles of flight, including the role of wings as airfoils, the phenomenon of lift, the countering forces of thrust and drag, and forward thrust in powered flight. Different modes of flight—the gliding flight of soaring birds, flapping flight, and the hovering of hummingbirds—help to illustrate these principles further. Then we review the anatomy of avian flight, particularly the skeleton and the highly developed breast muscles that power flight. Flightless birds also highlight the adaptations and trade-offs required for flight. Some diving birds (such as penguins) have traded aerial flight for underwater flight with the use of highly modified flipperlike wings. Finally, we return to the topic of the evolution of avian flight with greater appreciation of the mechanics and anatomical specializations involved.

5.1 Elementary Aerodynamics

To understand bird flight, we must consider the physics, or **biomechanics,** of avian movement in terms of the forces acting on the bird (Figure 5–1). All objects are subject to **gravity,** the force that pulls the mass of an object toward the earth. In moving air, objects are also subject to the frictional force of air molecules moving over its surface—a force called **drag.** We experience drag in a high wind or when riding a motorcycle at high speed.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
Data from Burton 1990

Figure 5–1 (A) The three idealized aerodynamic forces acting on the body of a flying bird: weight, drag, and lift. During flight, the force of lift counteracts the forces of gravity and drag. (B) Cross section of the cambered wing. Lift is created perpendicular to the flow of air over the wing. (C) Forward thrust is the forward component of lift. Thrust is created by rotating the wing forward during the downstroke (to a negative angle of attack).

To stay aloft in flight, a bird must counteract the potential energy lost to gravity and to drag by generating an equal and opposite force: **lift.** Lift is the upward force produced by airflow over the wings. To understand how lift is produced, we will begin by looking at air moving over a stationary wing, or **gliding** flight. Like the wing of a plane or the sail of a sailboat, the bird wing is cambered in shape; the upper surface of the wing is curved outward, or convex, while the lower surface is curved inward, or concave, usually more weakly than the upper surface. Because of these differences in shape, the flow of air is also different on either side of the wing. Cambered bird wings produce lift because air flows faster over the upper surface than the lower surface (Anderson and Eberhardt 2001; Kunzig 2001). However, there are several different ways to analyze the physical mechanism of lift production.

These differential airspeeds across the wing produce lift, in part, through the **Bernoulli effect.** The seventeenth-century Swiss physicist Daniel Bernoulli realized that the pressure of a fluid, including air, could be decomposed into the static pressure pushing against a surface and the dynamic pressure moving along the surface. According to the Bernoulli equation, the sum of the static pressure (p_S) and the dynamic pressure (p_D) is constant:

$$p_S + p_D = C$$

When air moves faster along one surface, the static air pressure pushing down on that surface will decrease. When air moves faster over the top surface than over the bottom over a cambered wing, the static pressure on the upper surface of the wing will be lower than the static pressure on the bottom surface of the wing. The difference in static pressure creates a net upward force. You can observe this process yourself if you blow gently over the horizontal, upper surface of a piece of tissue paper; the tissue will rise up and flutter because of the greater net static pressure on the lower surface of the paper. However, the classic, Bernoulli effect explanation is just one component of the circulation pattern generated by the airfoil that creates lift.

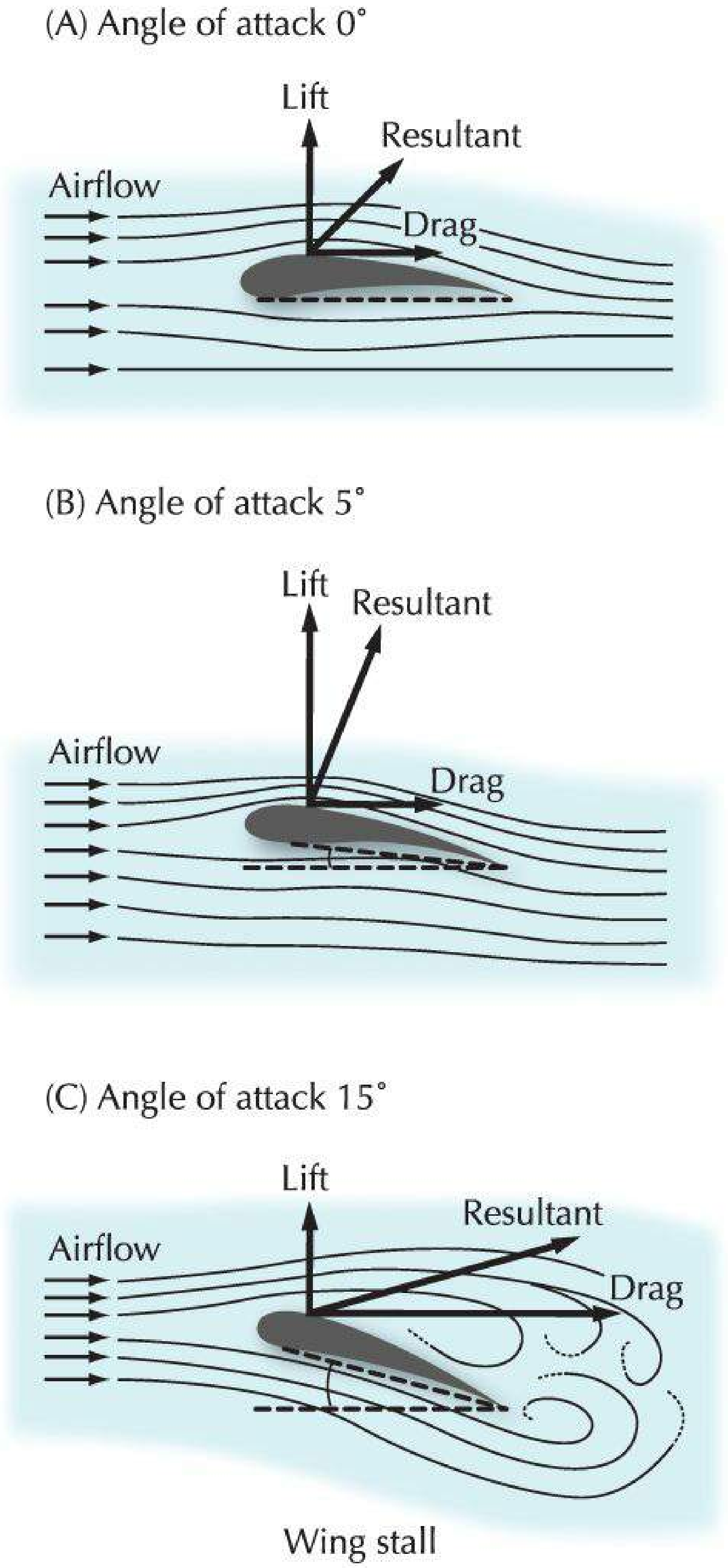
According to a different analysis, lift is produced by the wing as the asymmetrically curved shape of the airfoil deflects the airstream downward (Long 1999; Videler 2005). Elementary physics (Newton's third law) tells us that for every action there is an equal but opposite reaction. The downward deflection of air by the airfoil, therefore, produces an opposite upward force of lift.

From a third perspective, differential movement of air over the surfaces of the wings also produces rotating currents of air called **vortices** (sing. vortex; Videler 2005). When the air flowing more rapidly over the wing meets the air flowing more slowly under the wing at the wing's trailing edge, the airflow begins to shear or twist against itself, creating rotating vortices of air on the edges and tips of the wings. Over time, the starting vortex contributes to **trailing vortices** that are tubular currents of air that trail off behind the tips of the wings (Figure 5–2). As a result of the rotation of the trailing vortices, there will be a downward wash of air immediately behind the wing and an upwash of air just beyond the wing tips. The energy dissipated by the movement of air in these vortices contributes to drag on the flying bird.

Gill/Prum, *Ornithology,* 4e, © 2019 W. H. Freeman and Company
Data from Henningsson and Hedenström 2011

Figure 5–2 As the bird flies, it leaves trailing vortices of circulating air in its wake. The direction of the vortices creates a downwash of air immediately behind the bird. Trailing vortices contribute to induced drag.

The amount of lift the wing produces increases with airspeed and with the wing area. When a large bird, such as a gull or albatross, stands on the edge of a cliff facing into the wind, the flow of air across its outstretched wings generates lift. If the wind is strong enough, the bird rises effortlessly into the air. In still air, the seabird must jump off the cliff with wings outstretched. As the bird drops, its airspeed increases, producing lift and, with it, flight.



(A) Angle of attack 0°

(B) Angle of attack 5°

(C) Angle of attack 15°

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DATA FROM BURTON 1990

Figure 5–3 The angle of attack affects the balance of aerodynamic forces on the wing. The angles of attack illustrated are (A) 0°, (B) 5°, and (C) 15°. Increasing the angle of attack by 5 degrees from a horizontal position increases lift, but increasing the angle by 15 degrees or more causes the airstream to separate from the upper surface of the airfoil, which increases turbulent airflow, or drag, and severely reduces lift. Higher angles of attack will cause a loss of lift and the bird or airplane to stall.

The **angle of attack,** or the orientation of the wing to a current of air, affects the generation of lift (Figure 5–3). More lift is generated as the leading edge of the wing rotates upward, creating a *positive* angle of attack and consequently deflecting more air downward. If the angle of attack is too great, however, the airflow no longer follows the streamlined surfaces of the wing. Instead, the airflow separates from the surface and then swirls chaotically away behind the upper surface of the wings, greatly increasing drag. At very high angles of attack, the increase in drag will overcome the force of lift, causing a stall. When landing a plane, a pilot purposely stalls an airplane by increasing the angle of attack of the wings just before the wheels touch the runway. Birds, too, adjust the angle of their wings to stall just before landing (see Figure 5–12).

After considering how lift is produced by stationary wings gliding through moving air, we will now examine the production of thrust in flapping flight. Because lift is perpendicular to the direction of airflow over the wing, birds can manipulate the shape and direction of their cambered wings during flapping to change the direction or orientation of lift (see Figures 5–1 and 5–3). The **flight stroke** of birds consists of a **downstroke,** or power stroke, and an **upstroke,** or recovery stroke.

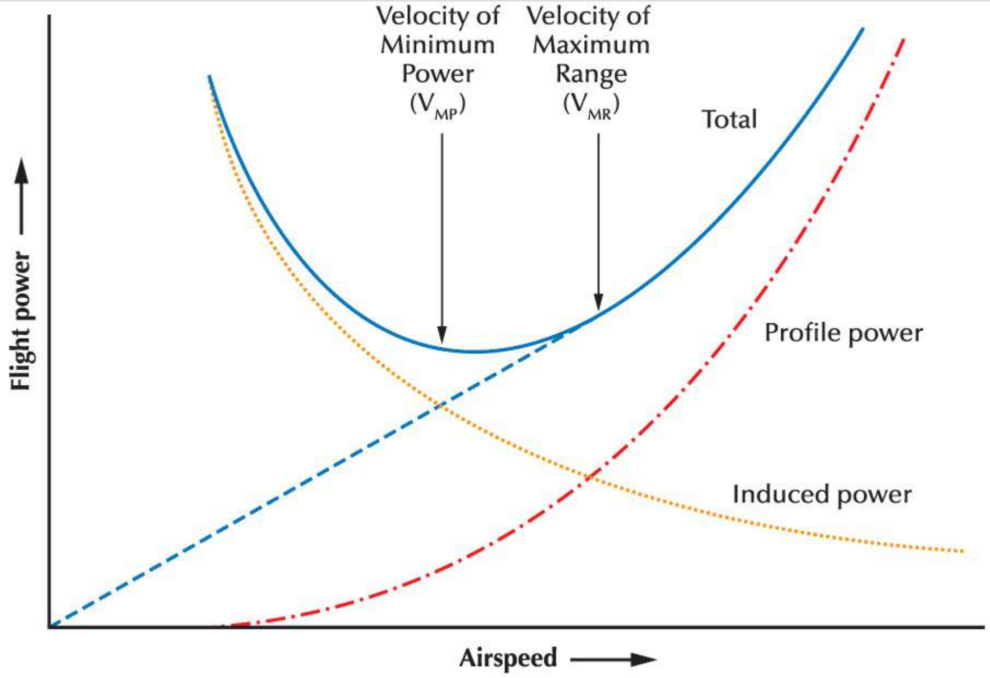
By rotating the cambered surface of the wing downward, or forward, during the downstroke (i.e., a negative angle of attack), the direction of the lift force will also be rotated forward (see Figure 5–1C). The net forward component of lift is called **thrust.** Thus, birds produce forward thrust in flapping flight by rotating the angle of attack downward during the downstroke.

Although an airplane produces lift with its wings and thrust with its propellers (or jets), a bird produces both lift and forward thrust with the same structures: its wings. Propellers can produce thrust continuously by rotating their cambered surfaces around an axis, but bird wings cannot function this way. If a bird used a symmetrical, mirror-image flight stroke, then the forward thrust on the downstroke would be canceled out by the backward thrust on the upstroke, and the bird would not move forward. Rather, just as a rower changes the angle and position of the blades of the oars during the power and recovery strokes when rowing a boat, a bird alters the forces produced during upstroke and downstroke during flapping flight by changing the shape and angle of attack of the wing. Forward flight requires an **asymmetrical flight stroke** in which the bird produces lift and thrust on the downstroke and minimizes the forces produced on the upstroke. Birds do this by changing the shape of the wings, flattening the angle of attack, and reducing the camber of the wing during the upstroke. We will return to consider gliding and flapping flight below (section 5.3).

5.2 Energetics of Flight

To maintain flight, a bird must produce enough lift to counter its weight and its loss of potential energy due to drag. Although the bird’s weight does not change as it flies, the amount and kind of drag produced can change dramatically. Thus, understanding the energetics of bird flight involves investigating how the force of drag and how the resulting energy demands of the flying bird change with flight speed.

The friction of air moving over the surface of the bird’s body and the internal friction of moving air contribute to total drag during flight. The drag produced by the bird’s body itself is called **profile drag.** The thin leading edge of the wing and the smooth contour of the body plumage minimize the profile drag of the bird. The tails of birds also reduce the profile drag by reducing vortices in the wake of the bird’s body (Maybury and Rayner 2001). Conversely, the energy expended in order to move the air itself to produce lift and thrust is called **induced drag.** Interestingly, the magnitudes of both profile drag and induced drag *change* with airspeed but in opposite directions (Figure 5–4). The profile drag *increases* with airspeed because more airflow will produce even more friction and turbulence in its wake. In contrast, the induced drag *decreases* with airspeed because it takes incrementally less energy to create lift-producing vortices when the air is already moving. As a result, the total amount of energy required to maintain powered flight changes with flight speed.



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DATA FROM ALEXANDER 1992

Figure 5–4 The total power requirements of flight (blue) are the sum of the induced power (orange), which decreases with speed, and the profile power (red), which increases with speed. The total power function is J-shaped in relation to airspeed. The velocity of minimum power (V_{MP}) is located at the bottom of the total power curve. This is the flight speed required to fly with the minimum energy cost per unit time. The velocity of maximum range (V_{MR}) is located at where a straight line (dashed blue) drawn from the origin is tangent on the total power curve. This is the speed required to fly with the minimum energy cost per unit distance.

To maintain a certain speed in forward, flapping flight, the lift produced must overcome the force of drag at that airspeed. The **total power** required to overcome the effects of drag is the sum of the lift required to overcome the profile drag, called **profile power,** and the lift required to overcome the induced drag, called **induced power** (see Figure 5–4). Because of the ways that the profile and induced power change with speed, the total power requirement for forward flight varies in a parabolic relation to flight speed. This is the famous J-shaped total flight power function, in which the energetic costs of flying are least at intermediate speeds and greatest at low and high speeds (see Figure 5–4). Flying at slow speeds is energetically expensive because the bird must expend lots of energy to move nearly stationary air with each flight stroke. Likewise, flying very fast also is expensive because the bird will produce lots of profile drag from the friction of airflow over its wings and body at high speeds. Thus, birds fly most efficiently at intermediate airspeeds that reduce the overall costs of flying. As we will see in later sections, different birds have evolved to specialize in flying at different speeds, and many have evolved compensatory changes in wing shape and size and in mode of flight to optimize their energetic costs of flight to their ecological and environmental demands.

The J-shaped flight power function implies further differences in avian flight behavior (Rayner 1985a). For example, the lowest point on the total flight power curve specifies the **velocity of minimum power (V_{MP}),** which is the flight speed at which the bird minimizes the amount of energy used per unit time (see Figure 5–4). Birds that forage in flight, when the energy acquired in food is related to the time they spend flying, are likely to fly at this speed. However, another point on the total power curve is the **velocity of maximum range (V_{MR}),** or the speed at which a bird should fly to go the greatest distance per unit energy. The velocity of maximum range is located where a straight line from the origin is tangent to the total power curve. This is the point where the slope of that straight line, which depicts the ratio of work/distance, is minimized. Birds that fly from one rich food patch to another, like waterfowl, and long-distance migrants (Box 5–1) will minimize their energy expenditures by flying at the velocity of maximum range.

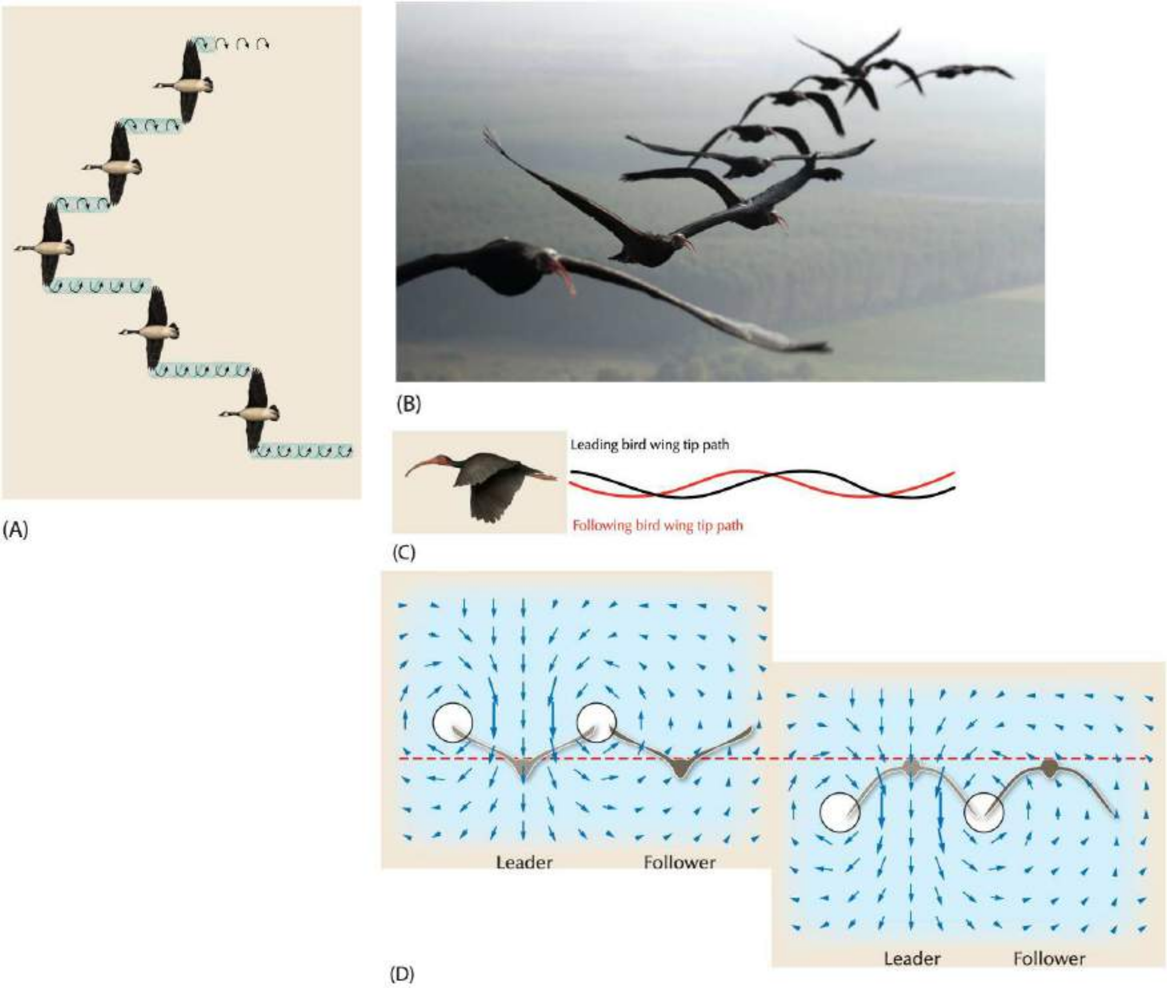
Box 5–1

Flying in Formation

Flying in formation helps to save energy, especially in large or heavy birds, such as geese, with small wings relative to their mass (Badgerow 1988; Alexander 1992). By flying just off the wing tip of the preceding bird, each catches the rising air of the trailing vortex of the bird in front of it, reducing induced drag and saving energy. In the familiar V-formations of migrating geese, each individual bird flies off and behind the wing tip of the bird in front of it (illustration A).

The energetic advantage of formation flight could be as high as 50 percent. Direct measures of the energy output of pelicans trained to fly in formation proved that they use from 10 to 14 percent less energy in flight formation, partly because the group's airstream allows those in back to glide more than the leaders can (Weimerskirch et al. 2001).

Birds flying in V-formation also coordinate their wingbeats and the distances from birds in front of them to exploit the energetic advantage of the upwash from the continuous vortex (see Figure 5–11) trailing behind the leading bird (Portugal et al. 2014, figures B–D). Likewise, birds avoid flying directly behind another bird, where they will experience the downwash from the leader's trailing vortex.



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(A) DATA FROM ALEXANDER 1992. (B) COURTESY OF JOHANNES FRITZ. (C–D) DATA FROM PORTUGAL ET AL. 2014

(A) V-formation of migrating geese. Proper positioning relative to the air currents from the wing tips of the preceding bird saves energy. (B–D) Using highly sensitive GPS tracking devices, Portugal et al. (2014) demonstrated that (B) Northern Bald Ibis fly at (C) the appropriate distance and position behind the leading bird and coordinate the timing of their flight stroke to (D) best exploit the upwash from the trailing vortex of the leading bird.

A single species will fly at different speeds depending on its behavioral and energetic needs. For example, migrating Common Swifts fly at about 40 kilometers per hour, close to their predicted maximum range velocity (V_{MR}). In contrast, while feeding, Common Swifts cruise more slowly at only 23 kilometers per hour, close to their predicted minimum power speed (V_{MP}).

Foraging birds do not always strictly adhere to flight speeds that minimize power costs (V_{MP}; McLaughlin and Montgomerie 1990; Bruderer and Boldt 2001). Hummingbirds, for example, hover expensively as they forage at flowers to extract nectar, and they fly very fast to beat competitors to other nectar-filled flowers (Gill 1985). The advantage to hummingbirds of these costly locomotion strategies comes from increased consumption of sugar-rich nectar. Similarly, Peregrine Falcons dive on prey at breathtaking, high speeds (Box 5–2).

Box 5–2

Peregrine Falcons: Speed Stooping

The Peregrine Falcon achieves breathtaking speeds when diving, called stooping, on its aerial prey. Stoops are executed at angles ranging from 30 to 60 degrees, sometimes starting at more than 1,500 meters from the prey and dropping from 450 to 1,080 meters in altitude (White et al. 2002). Calculations of their airspeed by stationary observers range from 160 to 440 kilometers per hour (96–264 miles per hour). Arguably, the most direct measurements are those by a free-falling parachutist who accompanied his trained falcons in dives from 3,670 meters, or 12,000 feet (Franklin 1999). At 240 kilometers per hour (144 miles per hour), the stooping falcon tucked in its wings and extended its shoulders to assume a diamond shape. At higher speeds (320 kilometers per hour, or 200 miles per hour), the falcon elongated and streamlined its shape to the maximum by pulling its wings in close to its body and extending its head. Keeping an eye fixed on the target prey while diving at such speeds is challenging, in part because the falcon’s acute vision is to the side, not straight ahead. Turning the head would increase drag and slow the bird down. So the falcon instead adopts a spiral path that keeps its head straight and the prey in sight slightly to the side. Better aerodynamics of the body orientation more than compensate for the longer stoop path (Tucker et al. 2000).

SCIENCE SOURCE/JIM ZIPP

A Peregrine Falcon pulls its wings in close to the body while stooping down toward its prey.

5.3 Modes of Flight

Beyond the basics, birds have evolved an extraordinary range of specialized **modes of flight.** To fulfill their ecological needs, birds have diversified to fly in many different ways. These different modes of avian flight are analogous to the different gaits used in terrestrial location by mammals, like walking, trotting, and galloping. In this section, we start with simple forms of flight—soaring and gliding—and proceed to features of complex flapping flight and its variations.

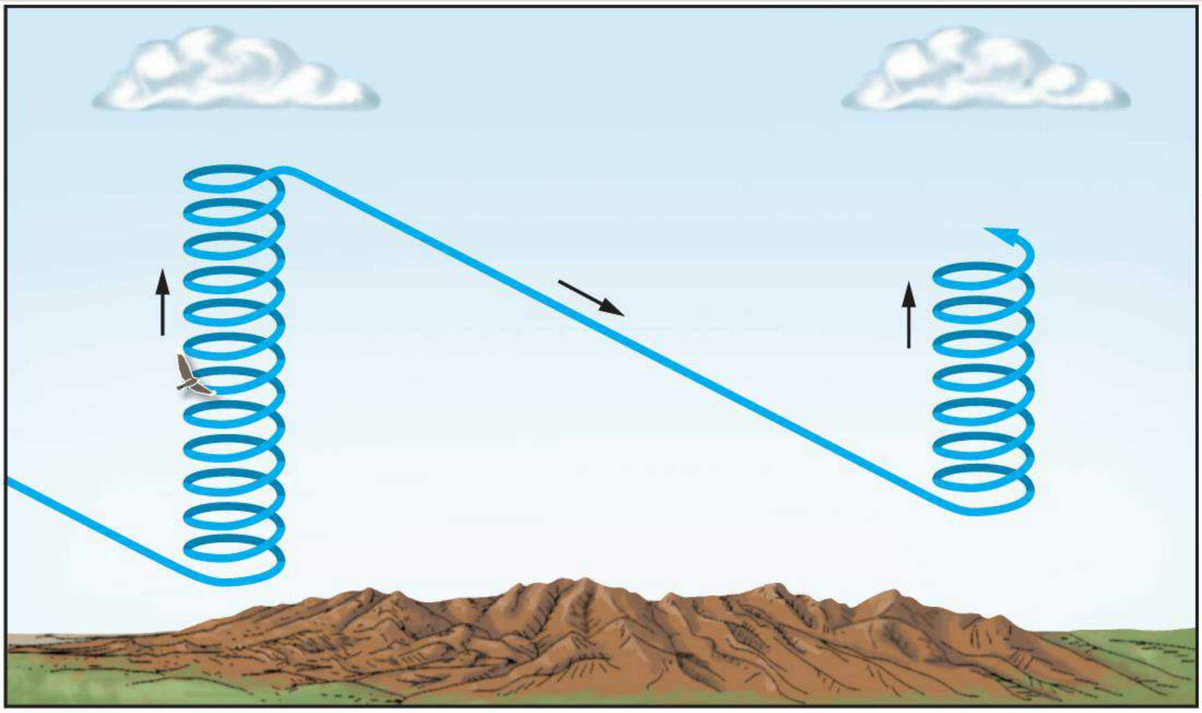
Soaring and Gliding Flight

TATHOMS/SHUTTERSTOCK.COM

Figure 5–5 The Turkey Vulture is a thermal soarer with large, broad wings. Slots between the tips of the primary feathers reduce induced drag at the wing tip. Slight adjustment of the primaries and their associated slots control a vulture’s speed, lift, and aerial position as it searches the terrain for carcasses.

The soaring flight of vultures, albatross, and many other birds illustrates how the forces of weight, lift, and drag work in this simplest form of flight (Figure 5–5). Without flapping their wings to create forward thrust, gliding birds gradually lose altitude in still air—that is, they “sink”—because of drag. Just as in powered flight, sink rates are lowest at intermediate flight speeds when drag is lowest. Both soaring birds and glider airplanes counter their inevitable descent by taking advantage of moving air. The two principal ways of doing so are called **thermal soaring** and **dynamic soaring.**

Thermal soarers exploit columns of warm air that rise when the ground is heated by the sun (Figure 5–6). The soaring bird circles upward within the column of rising air and then glides down to the base of another adjacent thermal. In this way, thermal soaring allows the bird to cover great distances with minimal energy. As the soaring bird rises, it continues to fall relative to the air. But air rises in thermals at the rate of approximately four meters per second, which easily offsets the bird’s sink rate of one to two meters per second or less. Colin Pennycuick (1972) pioneered the study of the gliding flight of birds by following vultures from their roosts to feeding grounds in East Africa from a motorized glider plane. African vultures can rise to heights of 1,500 meters and travel 75 kilometers by using only six thermals (see Figure 5–6). In order to fly with maximum energy economy, migrating hawks, such as the Broad-winged Hawk, use thermal soaring extensively during their annual migrations from eastern North America to southern South America and back. Flocks of soaring Broad-winged Hawks are often called **kettles** because the flocks can be so dense that the spherical outlines of the rising thermal bubble of air are visible (Figure 5–7). Recent use of GPS devices and other sensors have established incredible soaring behavior of Great Frigatebirds, which can stay aloft continuously for weeks or months by soaring on thermal updrafts below or inside cumulus clouds over the Indian Ocean (Weimerskirch et al. 2016). Frigatebirds have been recorded rising as high as 4,000 meters in altitude and gliding for more than 60 kilometers on a single descent.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
Data from Pennycuick 1973

Figure 5–6 Soaring vultures gain altitude in the rising air of thermals and then glide down toward next thermal in order to fly long distances without the energy costs of flapping.

RAUL GONZALEZ/SCIENCE SOURCE

Figure 5–7 During migration, soaring hawks concentrate within rising thermals of air to create a dense flock that is called a kettle.

Many thermal soaring birds, including vultures, eagles, various hawks, storks, and pelicans, have slots between the primary flight feathers at the tip of the wing (see Figure 5–5). These slots permit each primary to act as an individual "winglet," which reduces the induced drag of the wing tip by redistributing the trailing vortices horizontally and vertically (Tucker 1993). Many modern airliners, like the Boeing 737-400 and later models, exploit the same aerodynamic principle by placing winglets extending upward from the tips of the wings.

Dynamic soaring exploits a different kind of moving air—namely, wind. For example, migrating hawks and ravens soar along mountain

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Figure 5–8 Pelagic seabirds, like this Sooty Albatross, are dynamic soarers that fly with minimum energy expenditure by creating lift from nearly constant winds over the surface of the ocean.

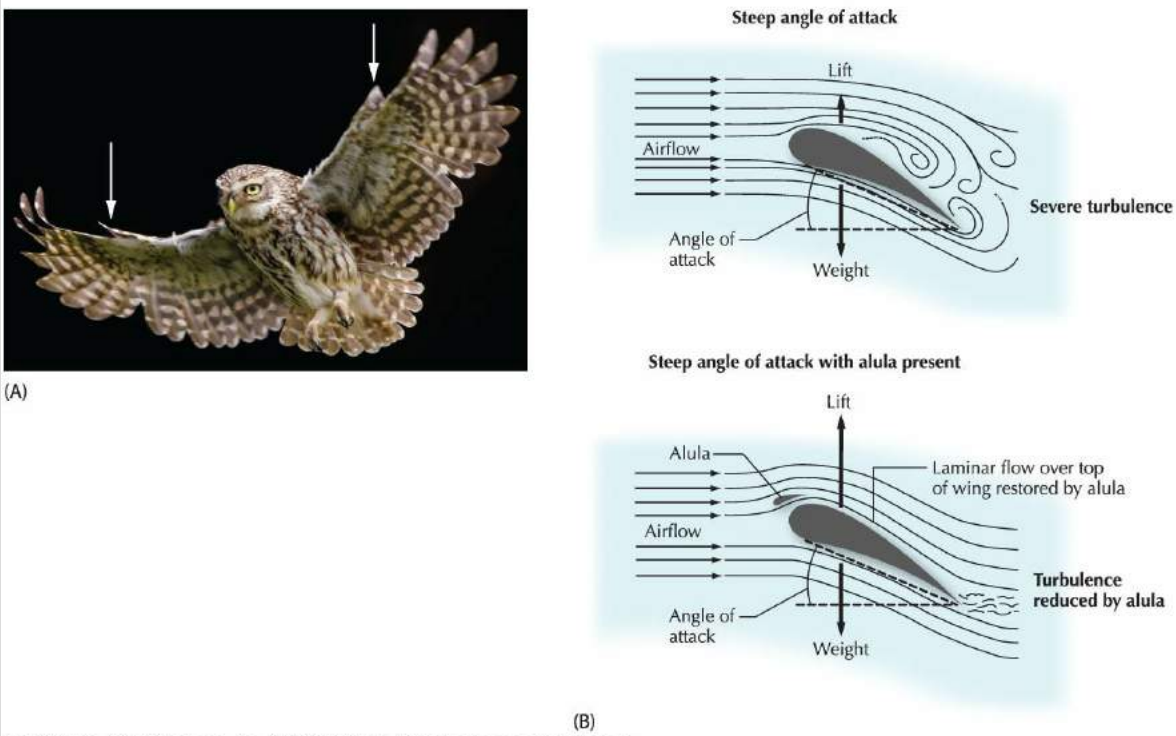
ridges, and gulls hang effortlessly behind boats or above the ocean beach by riding the wind currents that are deflected upward. Raptors that migrate using mountain ridge updrafts often concentrate at particular sites that have become famous "hawk-watch" locations, like Hawk Mountain in eastern Pennsylvania. Seabirds, such as the long-winged albatrosses and petrels, can cruise expertly along to the windward sides of large wave crests (Figure 5–8). These seabirds can also fly continuously across the wind without any expenditure of mechanical energy by alternating their flight direction in an S-pattern: turning into the wind to gain altitude and then gliding down across the wind to gain speed.

Flapping Flight

Gliding flight minimizes the use of thrust to overcome the negative effects of drag. Flapping flight, on the other hand, adds thrust to the aerodynamic forces on the bird. As shown above, birds create forward thrust on the downstroke by rotating the angle of attack downward, producing a forward component to lift (see Figure 5–1C).

The actual shape of the wing can vary tremendously during the flight stroke. The camber and angle of the attack also vary along the length of the wing during various stages of the flight stroke.

Flapping birds maintain control of the flow of air over the top of the wing to maintain lift and prevent stalling at slow speeds or at high angles of attack. The alula, or bastard wing, is the feathered digit I of the hand. Extending the alula creates a slot at the leading edge of the wing that keeps airflow bound to the wing (Figure 5–9). This adjustment helps especially during landing and takeoff, when forward thrust is minimal and extra lift is essential to prevent stalls. Many modern aircraft have these same sorts of slots in the front of the wing, which you can sometimes see opening before landing.



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(A) Mark Smith/Getty Images. (B) Data from Able 2004

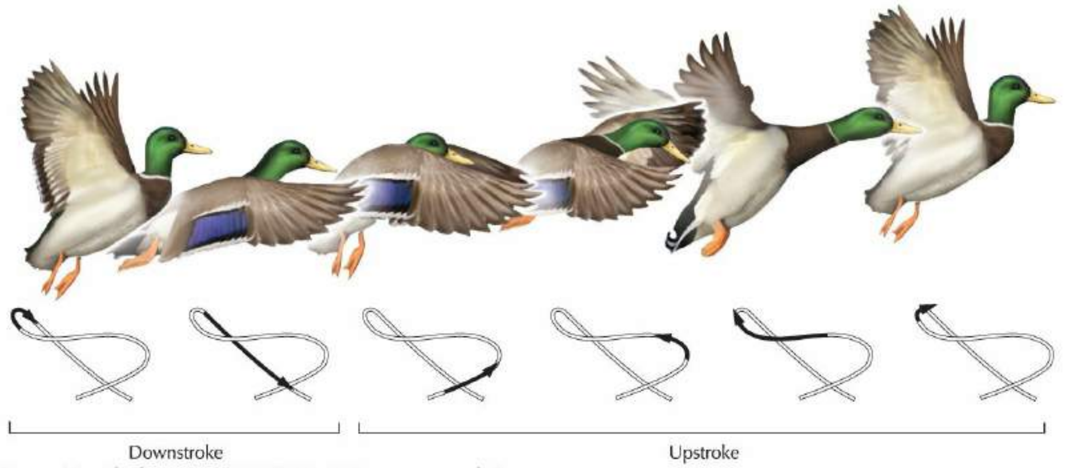
Figure 5–9 (A) The alula, or digit I, of the wing (arrows) is often deployed at slow speeds or during landing. (B) Without the alula (top), steep angles of attack can create chaotic turbulence above the wing and reduce lift. The slot created by the extended alula (bottom) keeps the airflow close to the wing at slow speeds, maintains lift, and prevents stalling.

Birds in flight control lift and thrust in complex, rapid, and continuous patterns (Warrick et al. 1998). No aircraft approaches the average bird’s acrobatic maneuverability (Table 5–1). Slow-motion photographs of birds during takeoff, aerial maneuvers, chases, and landings reveal the precise changes in wing position that control body orientation and airspeed (Figure 5–10). Birds rarely crash. Even more important than the integration of lift and thrust is the independent control of each wing. Asymmetrical wing actions enable a bird to steer, turn, and twist. By flapping with one wing oriented forward and the other wing oriented backward, the bird can execute an abrupt turn.

Setting the wings in a partly folded position reduces the amount of lift, controlling the loss of altitude gradually while gliding. By setting one wing back farther than the other, the bird adds curvature to its glide path.

Table 5–1 *Birds Compared with Airplanes*

Statistic	**Plane (type)**	**Bird (species)**
Travel speed (body lengths/second)	32 (supersonic SR-1)	75 (Common Pigeon) 120 (Common Starling) 140 (swifts)
Roll rate (degrees/second)	720 (A-4 Skyhawk)	5,000 (Barn Swallow)
G forces allowed	4–5 (general aircraft)	10–14 (many species)
	8–10 (select military aircraft)	Note: Hundreds of times per day
DATA FROM DIAL 1994.		



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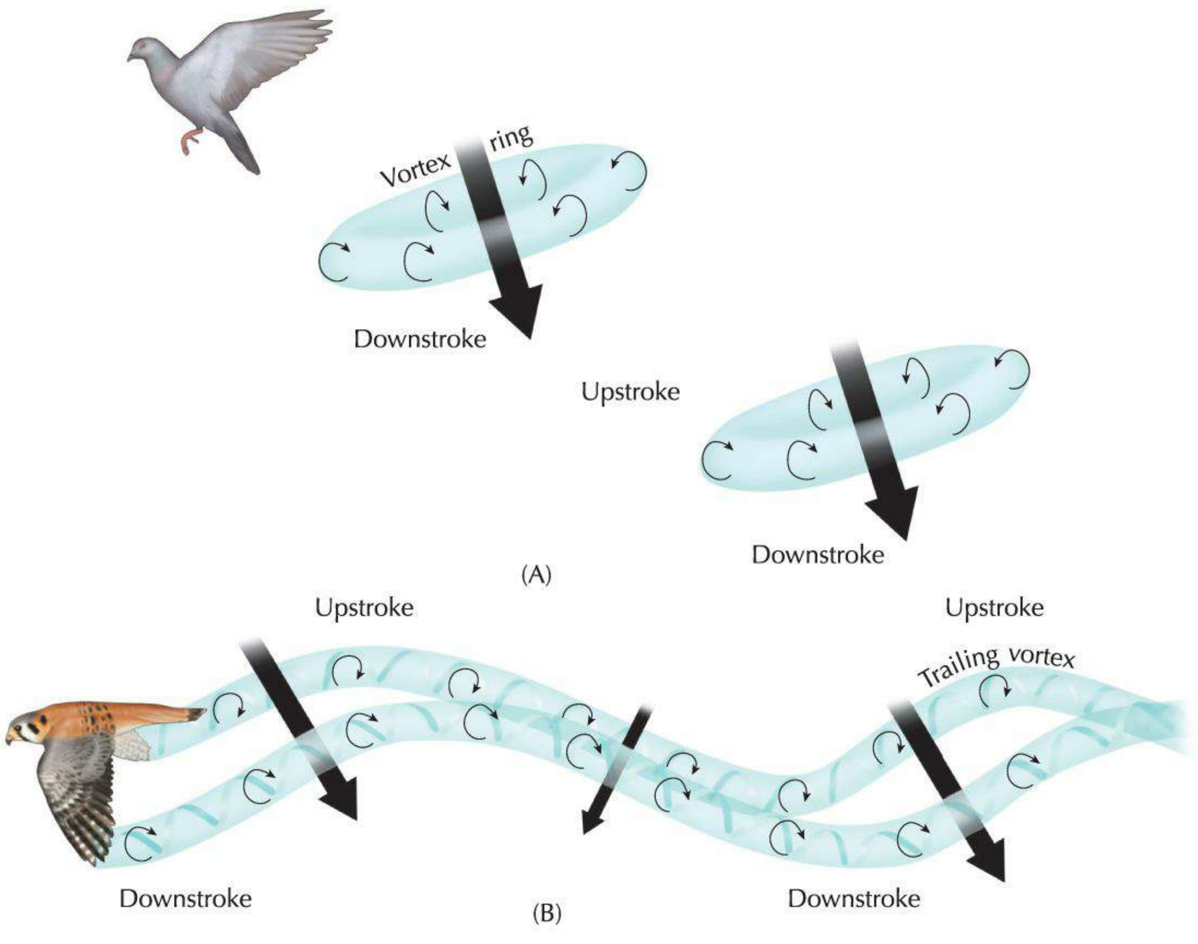
Data from Burton 1990

Figure 5–10 Complete wing stroke of the Mallard during takeoff. Black arrow sections trace the movement of the wing tip through the wing stroke. The downstroke and upstroke are asymmetric to produce maximum lift on the downstroke and minimal forces on the upstroke.

About 50 different muscles control the wing movements. (Sadly, this number is likely larger than the number of researchers in the world who know and can identify these muscles.) Some muscles fold the wing; others unfold it. Some pull the wing upward, others pull it down, and still others adjust its orientation.

Variations in the flight stroke create different modes, or "gaits," of flapping flight. In most small birds, only the downstroke is the power stroke. Little lift is achieved on the recovery stroke, during which the primaries are separated to minimize the forces and turbulence produced. This flight stroke works similarly to a rower who removes the oars from the water during the recovery stroke. Powered downstrokes followed by simple recovery strokes produce a doughnut-shaped, **ring vortex** of turbulent, swirling air in its wake (Rayner 1988; Figure 5–11A). Birds use a ring vortex gait when taking off and at slow speeds when the induced drag is high (see Figure 5–4). At faster speeds, many birds produce lift and thrust on both the upstroke and the downstroke, though the downstroke continues to dominate. This mode of flapping flight produces a **continuous vortex** trailing behind the bird. These continuous trailing vortices oscillate in orientation between the upstroke and downstroke (Figure 5–11B). The wingbeat frequency in the continuous vortex gait is highly constrained. Flapping too slowly causes the turbulence to backlash; flapping too fast causes interference of the turbulence with the next upstroke. As a rule, birds do not increase their airspeed by beating their wings faster. Instead, they increase the amplitude and angle of attack of their wingbeats to achieve greater thrust per wingbeat (Tobalske and Dial 1996).



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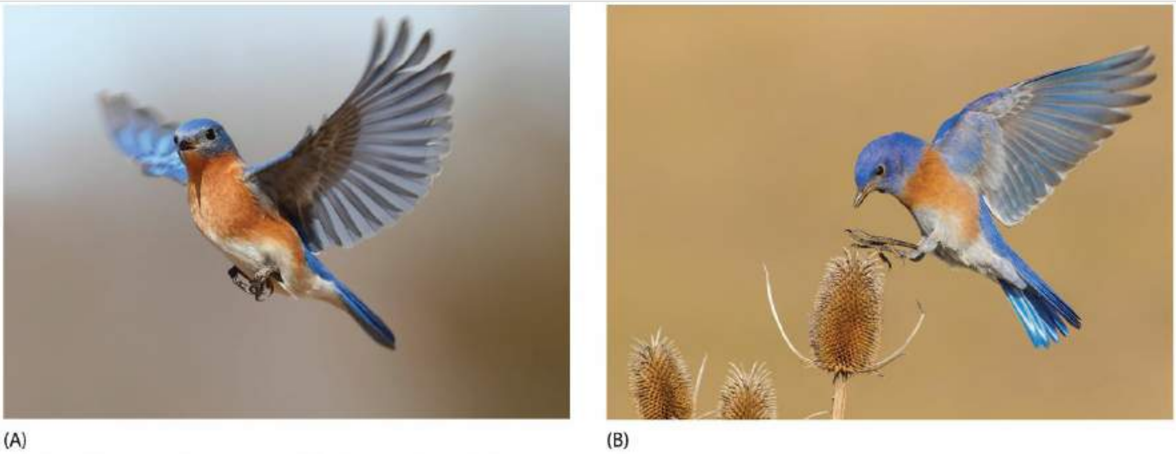
DATA FROM ALEXANDER 1992

Figure 5–11 Wingbeats leave trailing vortices of swirling air that distinguish different modes of flight. (A) The ring-vortex gait of slow-flying pigeons produces a series of separate, doughnut-shaped ring vortices with each downstroke. (B) The continuous vortex gait of the fast-flying American Kestrel produces a trailing vortex that is continuous between the downstrokes and upstrokes.

One dimensionless number, the Strouhal number, specifies the optimum rate of wing (or tail) motions for flapping forward flight (Taylor et al. 2003; Whitfield 2003). Simply multiply wingbeat frequency times wing stroke amplitude and divide by forward speed. Birds, as well as bumblebees, bats, and locusts, all operate most efficiently at the predicted Strouhal numbers from 0.2 to 0.4. So do swimming animals from fish to whales.

Birds maneuver in flight by changing the relative positions of the centers of gravity, lift, and drag with changing the shape of the wings and tail and altering the flight forces created by the two different wings. Landing on elevated or arboreal perches, particularly, requires exceptional control of flight trajectory. Birds are unique among flying vertebrates in the way that they land (Caple et al. 1983, 1984). Aerial species such as bats, flying squirrels, and certain lizards make contact with their forelimbs and then rotate their bodies downward until the hind feet touch the landing surface. Variations exist, but only birds rotate their centers of mass upward to stall directly over the landing site (Figure 5–12).



(A) Steve Byland/AGE Fotostock. (B) Sridatta Chegu/AGE Fotostock. Data from Able 2004

Figure 5–12 Eastern Bluebird landing on a spiny thistle. Note that the bluebird rotates its center of gravity upward to stall in the air and extends its feet forward to control the final touchdown.

Supplementing the wings are the tail’s contributions to flight, which may be minimal in species with small tails but substantial in other species. Tails help to control flight position and stability as well as aid steering and braking. Tails also add lift by improving airflow over the wings, especially at slow speeds, and by reducing turbulence and induced drag as air passes over the body. This contribution may be more important in young birds that are learning to fly than in skilled adults. Immature raptors, in particular, tend to have longer tails than those of adults. The size difference (as much as 15 percent) is most pronounced in short-tailed eagles such as the Bateleur of East Africa as well as in the familiar Red-tailed Hawk of North America. Corresponding to the increased lift, immature raptors have a more buoyant flight than do adults. Extra lift apparently reduces the chance of injury when they strike prey and facilitates their mastery of early flight and hunting skills (Amadon 1980).

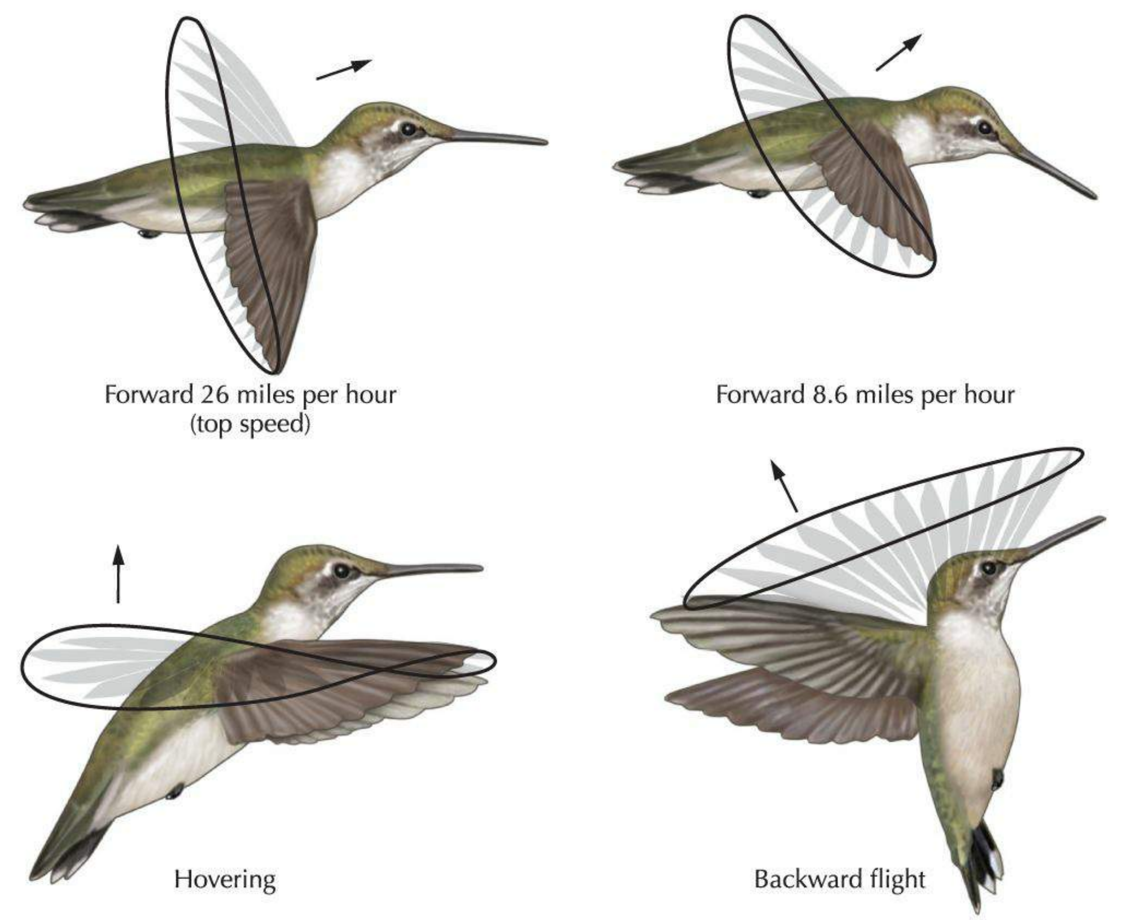
Hummingbird Flight

Hummingbirds are extraordinary flyers that sustain the highest known levels of oxygen consumption and muscle-power output of all vertebrates while hovering (Chai and Dudley 1995). In his pioneering analyses of hummingbird flight using high-speed movies, Crawford Greenewalt (1960a) discovered that hummingbirds are amazingly versatile flyers and that they can produce lift and thrust forces on both the downstroke and the upstroke. Greenewalt wrote,

> In hovering flight the wings move backward and forward in a horizontal plane. On the down (or forward) stroke the wing moves with the long leading edge forward, the feathers trailing upward to produce a small, positive angle of attack. On the back stroke the leading edge rotates

> nearly a hundred and eighty degrees and moves backward, the underside of the feathers now uppermost and trailing the leading edge in such a way that the angle of attack varies from wing tip to shoulder, producing substantial twist in the profile of the wing. [Greenewalt 1960a, p. 233]

A hummingbird can move forward or backward from stationary hovering by just changing the direction of the wingbeat because every wing stroke angle produces a different combination of lift and thrust (Figure 5–13). Forward velocities increase as the wings beat in an increasingly vertical plane. This rotation of the wing is made possible by the unusual structure of the humerus and its articulation with the pectoral girdle. The secondaries of a hummingbird's inner wing are short, and the outer primaries are elongated to form a single, specialized wing shape. The complete stroke of the wing tip describes a figure-eight pattern, which includes a powered upstroke as well as a downstroke.



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DATA FROM GREENEWALT 1960A

Figure 5–13 Hummingbird wing motions during flight. In forward flight, the wings beat vertically to generate forward thrust. In hovering flight, the wings beat horizontally in the pattern of a flattened figure eight. To fly backward, the hummingbird tilts the angle of wing action and inverts the camber of the wing to create rear-directed thrust.

Modern analyses have applied digital particle image velocimetry (DPIV), a technique that uses rapid flashes of sheets of laser light to image the movement of particles floating in the air, to document the vortices produced by hovering hummingbirds (Warrick et al. 2005). These studies document that hovering hummingbirds produce positive angles of attack on both the upstroke and the downstroke by rotating the wing as they flap and reversing the camber of the wing between the upstroke and the downstroke. In this way, hummingbirds produce balancing lift on both the upstroke and the downstroke to stay stationary in the air. However, the two strokes are not fully symmetrical. The downstroke provides more than 70 percent of the weight support during hovering, revealing that this mode of flight is still shaped by its evolutionary origin from a nonhovering ancestor with a highly asymmetric flight stroke.

To create these physical forces, hummingbirds flap their wings very rapidly at rates as high as 78 cycles per second—that is *78 upstrokes and 78 downstrokes per second*—in the Amethyst Woodstar (Greenewalt 1962). The rapid oscillations of the wings create the humming sounds that give the hummingbirds their name.

Like the wings of insects, the wings of birds and their controlling musculature oscillate mechanically with intrinsic elasticity, or springiness (Greenewalt 1960b). The wings of a Ruby-throated Hummingbird, for example, beat at an essentially constant rate of 53 cycles per second. The durations of the upstroke and downstroke are equal. The wingbeat rates of various species of hummingbirds and most other birds decrease predictably with increasing wing length, as oscillation theory predicts. These observations have important implications for the neuromuscular basis of avian flight. After the wingbeat rate has reached its natural oscillating frequency, the nerves and muscle fibers responsible for sustaining the rhythm need to fire only every four beats or so, like a child swinging continuously on a swing with only an occasional push.

Intermittent Flight

Many birds alternate regular bouts of flapping flight with short periods of nonflapping flight. Cooper's Hawks, Black Vultures, and large toucans, for example, flap several times and then glide with their wings open, appropriately called flap gliding. Finches and woodpeckers rise and fall as they alternate flapping and bounding with the wings folded in their characteristic flap-bounding flight. Both of these two main categories of so-called intermittent flight reduce a bird's power costs. They are distinguished by wing positions—wings extended in gliding versus wings folded closed in bounding—and by their advantages at different flight speeds. Flap gliding reduces predicted costs at slower airspeeds, especially those below minimum power speed (V_{MP}; Rayner 1985b). Conversely, flap bounding reduces predicted costs at fast speeds by reducing profile drag, especially at or above maximum range velocity (V_{MR}). Experiments in wind tunnels support these predictions. Mid-sized species, such as the Common Starling, shift from flap gliding at slow airspeeds to flap bounding at high airspeeds (Tobalske 1995). The two modes of intermittent flight also scale differently with respect to body size. Flap gliding is favored in large birds, whereas flap bounding works best in small and mid-sized birds. The European Green Woodpecker is the largest species (176 grams) known to employ flap bounding (Tobalske 1996).

5.4 Wing Sizes and Shapes

Flight speeds, gliding ability, aerial agility, and energy consumption all depend on the size and shape of a bird’s wings (Figure 5–14). A few different measures of the wings and body provide insights into the aerodynamic and energetic consequences of the variation in avian wing size and shape.

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Figure 5–14 Flight abilities vary with the shape of bird wings. (A) Long, narrow wings, such as those of an albatross, are best for high-speed gliding in high winds. (B) The short, rounded wings of grouse permit fast takeoffs and rapid maneuvers. (C) The slim, unslotted wings of falcons permit fast, efficient flight and good maneuverability in open habitat. (D) Slots between the primaries of *Buteo* hawks decrease induced drag during thermal soaring.

The costs of flight are determined, in part, by the relation between a bird’s total **wing area** and its body mass—that is, how much mass, in grams, must be carried by each unit area of wing surface. The relation between body mass and wing area is called **wing loading,** and it is given in grams per square centimeter of wing-surface area. Another fundamental measure of wing performance is **aspect ratio,** which is given by the square of wing span—the distance from tip to tip of the open wings—divided by the total wing area. High-aspect-ratio wings are very pointed, and low-aspect-ratio wings are wide and rounded.

Variation among birds in wing loading and aspect ratio is closely correlated to their ecology, habitat, and predominant mode of flight (Figure 5–15). In general, birds evolve wing shapes that lower the costs of flight at their predominant speed and mode of flight. For example, birds that fly at high speeds have high aspect ratios to reduce profile drag. Thermal soarers, like eagles and vultures, have low-aspect-ratio wings and low wing loadings to make enough lift efficiently at the quite slow speed of the air rising in a thermal. Dynamic soarers, like albatross, have long, high-aspect-ratio wings and low wing loadings so that they can make lift efficiently from the available wind. Ground birds, like grouse and tinamous, have low-aspect-ratio wings and high wing loadings, which are quite inefficient because they usually fly for only short distances to escape predators, and they need to create lots of lift at slow speeds for sudden takeoffs. In contrast, ducks have short, high-aspect-ratio wings and high wing loadings because they are usually flying at rapid speeds (near V_{MR}) between foraging sites. As a consequence, however, many diving ducks must run along the surface of the water in order to gain enough speed to create sufficient lift to take off. Puffins and murres are wing-propelled diving birds that have especially small wings and very high wing loadings because they are under selection to reduce profile drag in both air and water. Parrots and pigeons are examples of aerodynamic generalists with wing loadings and aspect ratios near the average of all birds.

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Figure 5–15 Variation in wing aspect ratio (vertical axis) and wing loading (horizontal axis) describes the tremendous breadth of flight styles that birds have evolved for different ecologies and environments. Flight generalists, like parrots and pigeons, have average wing shapes and loadings.

Wing shape also affects maneuverability. In general, lower wing loadings aid maneuverability. Thus, falcons, swallows, and other aerial foragers have long, pointed wings and low wing loadings. Songbirds tend to have large wings for their body mass and, consequently, low wing loadings, allowing for frequent launches and active maneuverable flight at relatively low cost. Multiple different flight demands can also lead to the evolution of distinct wing shapes. For example, the frigatebirds are thermal soarers with large wing areas and low wing loadings. But unlike vultures and storks, frigatebirds must be highly maneuverable to attack and steal food from other seabirds, so they have evolved high-aspect-ratio wings that also enhance mobility.

5.5 The Skeleton

The skeleton of a bird is highly modified for flight (Figure 5–16; see also Figure 1–3). Fusions and reinforcements of lightweight bones make the avian skeleton both powerful and delicate. Unusual joints not only make flight motions possible but also brace the body against the attendant stresses. The skeleton strategically supports the large muscles that provide the power for flight.

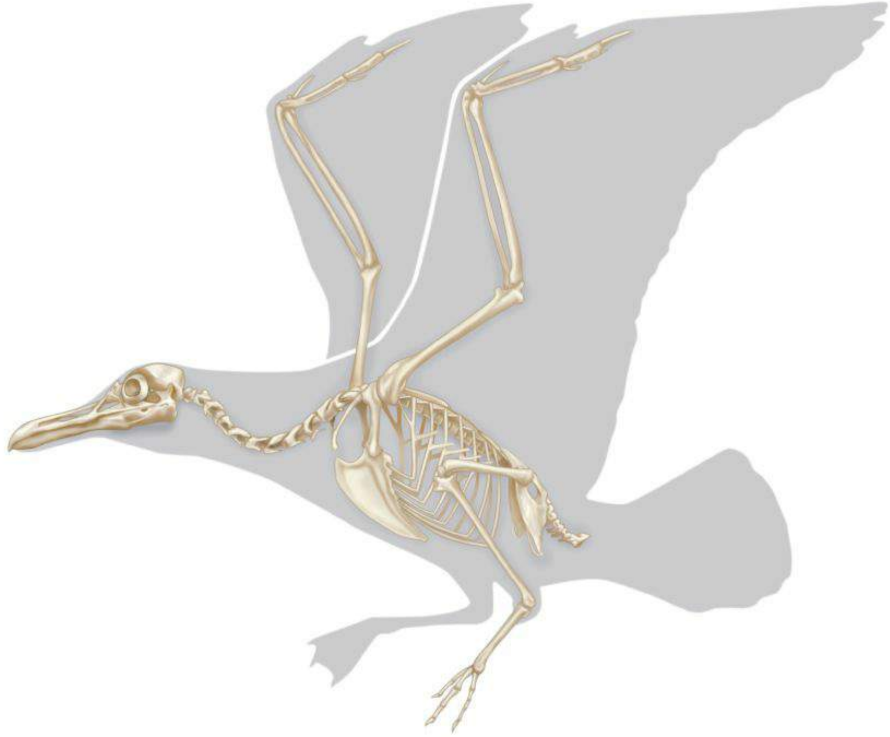

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Figure 5–16 Major features of the skeleton of a Herring Gull in flight.

In cross section, many bird bones are light, air-filled structures unlike the dense, solid bones of many terrestrial animals. The hollow, long bones of the wings may be strengthened further by internal struts. Instead of a heavy, bony jaw filled with dense teeth, living birds have a lightweight, toothless bill. The huge bills of toucans, being hollow, are not the burden they seem.

Despite these adaptations for reduced mass, the bird skeleton withstands the strains imposed by flight. The thorax is more rigid and better reinforced than that of a reptile. The hinged, bony ribs frame a strong bridge between the backbone and the breastbone but allow expansion for breathing. Horizontal bony flaps, called **uncinate processes,** extend posteriorly from the vertical upper ribs to overlap the adjacent ribs and reinforce the rib cage. The **sternum,** or breastbone, typically has a large **keel,** or carina, that anchors the major flight muscles. A bird’s flying ability increases with the size of its keel; some flightless birds lack the keel completely.

The flight muscles act in concert with the bones of the pectoral girdle, which include the **coracoid, scapula,** and **furcula** (see Figure 5–16). On top of the rib cage are the long, saberlike scapulae, each of which joins to the elongate coracoid (which is supported from below by the sternum), and the single furcula, which joins to the two coracoids (Box 5–3). This triangular system of struts resists the chest-crushing pressures created by the wing strokes during flight. An acute angle between the scapula and the coracoid increases the potential exertion force of the dorsal elevator muscles, which help to pull the humerus, or upper wing bone, upward. This angle is oblique in flightless birds.

Box 5–3

The Furcula Is a Flexible, Elastic Spring

The furcula, or wishbone, of the holiday dinner turkey is a fused pair of clavicles, or "collarbones," and serves as a strut, or spacer, between a bird's shoulders. X-ray movies of flying Common Starlings reveal that, in flight, the furcula can act as an elastic spring (Jenkins et al. 1988; Pool 1988). With each downstroke of the wing, the upper ends of the furcula spread widely, becoming as much as 50 percent wider than the normal resting width, and then contract. The furcula repeats this cycle of wide elastic expansion and contraction from 14 to 16 times a second in synchrony with the starling's wingbeats. Exactly how the spring action of the furcula aids flight is unclear, but it may enhance respiratory performance by pumping air through the air sacs (more in Chapter 6). Because it functions as a rapidly vibrating spring, the wishbone "may be one of the most dynamic skeletal units in the vertebrate world" (K. Dial, in Pool 1988).

The avian wing is a modified forelimb. The **humerus, radius,** and **ulna** are homologous to the forelimb bones of other vertebrates, including humans. Large surfaces at the joints between the limb bones allow the resting wing to fold neatly against the body. These specialized joints also permit the wing to change relative positions and angles during takeoff, flight, and landing. When outstretched, these joints are strong enough to withstand the wrenching forces created during wing strokes.

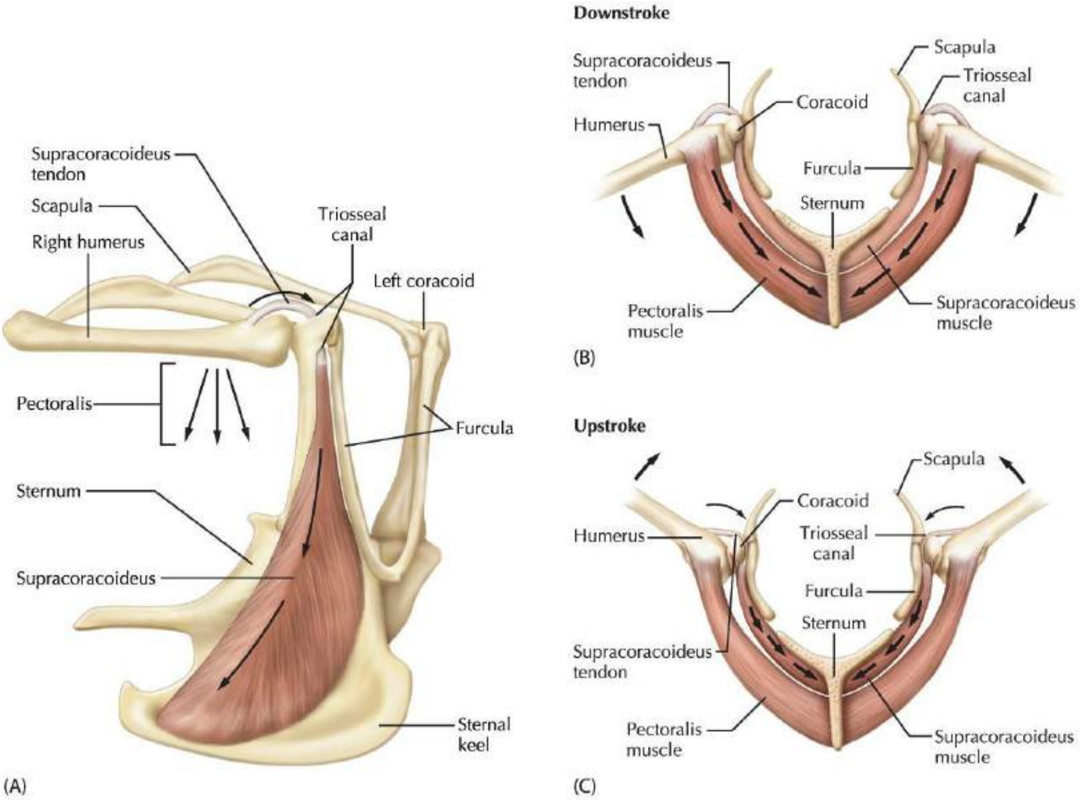
The fused hand bones, or **carpometacarpus,** and finger bones help to provide strength and rigidity in the outer wing skeleton. There are only two free carpals in the avian wrist, far fewer than the 10 or more in most vertebrate wrists. The hand itself includes three digits rather than the five found in most tetrapods. The **alula,** or bastard wing, is the feathered first digit of the avian hand and moves independently of the rest of the wing tip. Within the wing itself are powerful tendons and compact packages of tiny muscles that control the subtle details of wing position.

5.6 Flight Muscles

The two great flight muscles—the **pectoralis** and **supracoracoideus**—originate on the keeled sternum and insert onto the expanded base of the humerus. Their ventral positions help to lower a bird’s center of gravity in flight.

The pectoralis muscle complex accounts for as much as 35 percent of a bird’s total body weight. Contraction of the pectoralis pulls the wing down in the power stroke. Different sections of this architecturally complex muscle enable takeoff, level flight, and landing. The pectoralis muscle originates on the furcula, the strong membrane between the coracoids and the furcula, and the outer surfaces of the sternal keel. In tree-trunk-climbing birds with shallow keels, such as woodcreepers, the pectoralis muscle spreads thinly over the rib cage for attachment.

The supracoracoideus muscles lift the wings on the recovery stroke (Figure 5–17). They are typically smaller than the pectoralis muscles. The supracoracoideus muscles originate on the inner surfaces of the sternum and keel below the pectoralis muscles and extend via a strong tendon that passes upward and forward through the triosseal canals, which are formed by the junction of the coracoid, scapula, and furcula, to inserts onto the dorsal side of the base of the humerus (see Figure 5–17). When the supracoracoideus muscles contract, they pull on the supracoracoideus tendon and raise the wing like a pulley. The supracoracoideus muscles are essential for powering the upstrokes during the initial, rapid wingbeats on takeoff. For example, a pigeon is unable to take off from the ground if its supracoracoideus tendons are cut experimentally (Sy 1936). Once launched and airborne, however, pigeons can fly without functional supracoracoideus muscles because other, smaller dorsal elevator muscles can handle the less demanding recovery strokes of the wings during sustained flight. Thus, supracoricoideus muscles are essential for flying at slow speed using a ring-vortex gait.



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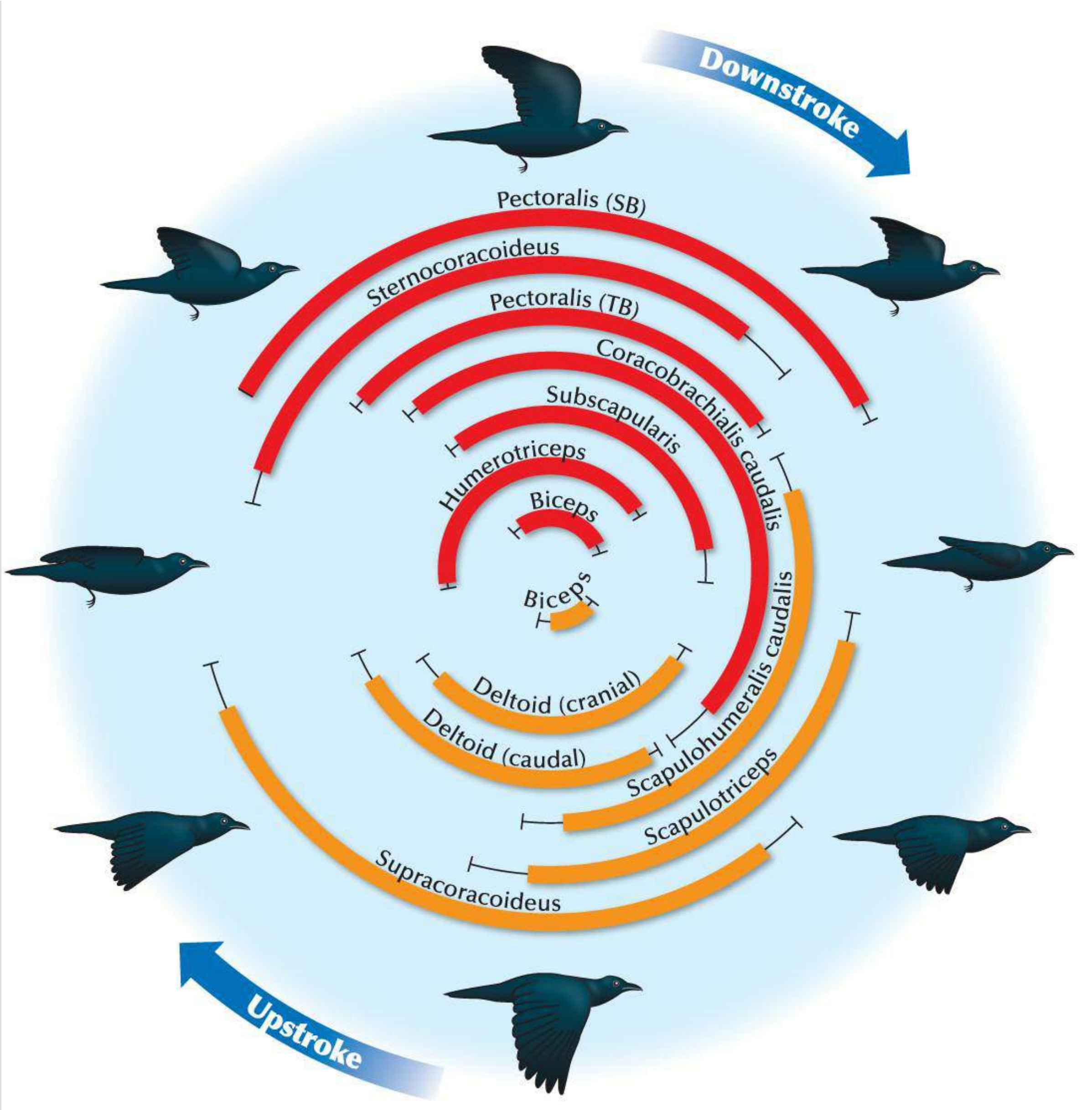
DATA FROM GEORGE AND BERGER 1966, ABLE 2004

Figure 5–17 (A) Right front view of the pectoral girdle and sternum of a pigeon with the pectoralis muscle removed. The supracoracoideus muscle originates from deep on the sternum below the pectoralis. It raises the wing by means of a pulleylike supracoracoideus tendon that passes through the triosseal canal formed by the furcula, coracoid, and scapula to insert on the dorsal surface of the humerus. (B, C) Cross section of the pectoral girdle with the pectoralis intact. (B) During the downstroke, the pectoralis muscle contracts pulling the humerus downward (arrows). (C) During the upstroke, the supracoracoideus muscle contracts, pulling the humerus up (arrows).

Hummingbirds use the upstroke of the wing as a second, lift-generating power stroke rather than as a recovery stroke. As one would predict, the supracoracoideus of hummingbirds is five times as large relative to body size as that of most other birds. It is only half the size of the pectoralis muscle and constitutes 11.5 percent of total body mass, more than in any other bird. The supracoracoideus muscle is also unusually large in penguins, whose flippers propel them forward with a powered upstroke as well as downstroke.

To produce the forward-powered flight stroke, birds must finely coordinate the contraction of their flight muscles to move the wing and appropriately change its shape and angle of attack. For example, each flight stroke cycle in the Starling lasts only 72 milliseconds (Dial et al. 1991). Over this brief time, however, the bird must execute a precise series of independent flight muscle contraction and relaxation events to produce a coordinated flight stroke (Figure 5–18).



Gill/Prum, *Ornithology,* 4e, © 2019 W. H. Freeman and Company
DATA FROM DIAL ET AL. 1991

Figure 5–18 The cycle of contraction and relaxation of 13 shoulder muscles during the flight stroke of the Common Starling, based on electromyography data. Time proceeds clockwise with the downstroke on the right and the upstroke on the left. Average flight stroke is 72 milliseconds long.

5.7 Muscle-Fiber Metabolism

The power for flight derives from the metabolic activity in the cellular fibers of flight muscles, some of which have an extraordinary capacity for aerobic metabolism. Certain muscle fibers are suited to specific modes of flight. Red and white fibers are the extremes of the variation, but intermediate fiber types exist.

Sustained flight power derives from a high concentration of **red muscle fibers** in the flight muscles. The sustained contraction power of red muscle fibers results from the oxidative metabolism of fat and sugar, which is termed aerobic respiration. These narrow fibers have high surface-to-volume ratios and short diffusion distances, which aid the rapid uptake of the oxygen required for aerobic metabolism. They also contain abundant myoglobin, mitochondria, fat, and enzymes that catalyze the chain of metabolic reactions known as the Krebs cycle. Experimental studies of extracts from pigeon breast muscle, which is rich in red fibers and the associated enzymes, have contributed to our present knowledge of aerobic metabolism. The aerobic capacity of the flight muscles of small songbirds and small bats is at the highest level known for vertebrates.

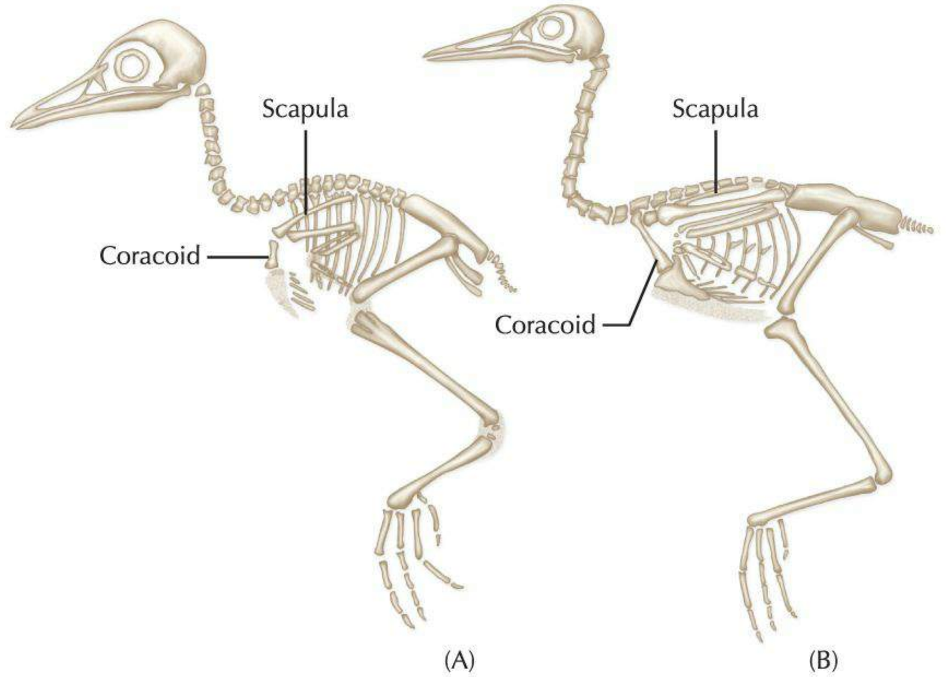
Few birds have muscle that consists entirely of red fibers. Rather, blends of different fibers that combine long-term endurance in flight with short-term power are typical of most birds. **White muscle fibers** provide this short-term power through anaerobic metabolism, which does not require oxygen. Unlike red fibers, they contain little myoglobin, few mitochondria, and a different set of enzymes. The white fibers are capable of a few rapid and powerful contractions, but they fatigue quickly as lactic acid—a product of anaerobic metabolism—accumulates. The light meat of the breast muscles of chickens and grouse consists primarily of narrow, white muscle fibers, the source of power for explosive takeoff. The short-term power of white muscle fibers is useful as well for fast turns and evasive actions in flight, but the birds tire easily and cannot fly long or far.

5.8 Flightless Birds

Not all birds fly. In addition to the well-known ratites (e.g., ostriches, cassowaries, and so on), there are flightless grebes, pigeons, parrots, penguins, waterfowl, cormorants, auks, and rails. The original faunas of remote predator-free islands, such as the Hawaiian Islands and other archipelagos in the Pacific Ocean, the Mascarene Islands in the Indian Ocean, and the Caribbean Islands, included a host of flightless birds: geese, ibises, rails, parrots, and pigeons, like the extinct Dodo (Box 21–1 in Chapter 21). If flight and mobility are so clearly advantageous to the majority of birds, why are some birds flightless?

The answer lies largely in the costly development and maintenance of the anatomical apparatus required for flight. An enlarged, keeled, calcified sternum and large pectoralis muscles, for example, are expensive to produce. Their maintenance and use also require much energy. In the absence of advantageous uses, such as the need to fly from predators or among food sources, natural selection often favors reduced investment in the material and energy for flight (McNab 1994). Rails often evolve flightless forms on islands where predators are absent (Olson 1973). Rails also typically delay until they are nearly full grown the addition of calcium to the (cartilaginous) sternum, strengthening it into a bony structure that supports flight (Figure 5–19). Simple postponement of this conversion would contribute to flightlessness. In the fossil record, evolutionary reduction of the sternal keel and the mass of flight muscles is, in fact, a first sign of reduced flying ability. The angle between the scapula and the coracoid also becomes more obtuse, and ultimately the wing bones become smaller.

The flightless kiwis of New Zealand, for example, have only vestigial wings.



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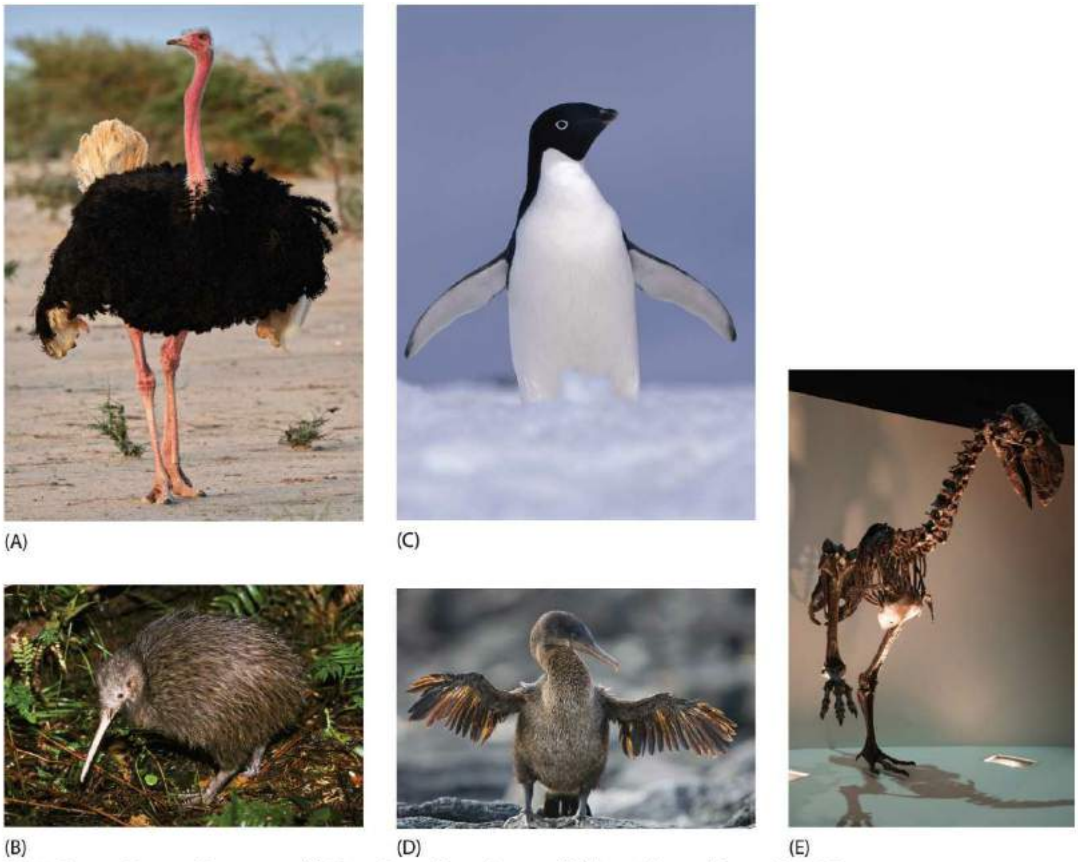
DATA FROM OLSON 1973

Figure 5–19 Skeletons of the King Rail, a flying rail, at (A) 17 days and (B) 47 days after hatching (rescaled so that femur lengths in the two drawings are equal). Stippled areas are cartilage. Note the obtuse angle formed by the articulation of the scapula and coracoid in the younger form and the acute angle in the older form.

Flightlessness has evolved repeatedly in birds with extremely large body sizes (Figure 5–20). The ostrich, the rheas, the extinct moas of New Zealand, the extinct elephant birds of Madagascar, and the emus and cassowaries are five independent origins of flightlessness associated with large body size and herbivory. Eating a diet of low-quality vegetation can favor the evolution of large body size, which can result in the loss of flight capability. During the Cenozoic, there were a large number of fierce, large-bodied, flightless, predatory birds, including *Gastornis* and *Titanis walleri*, from North America (Figure 5–20E).



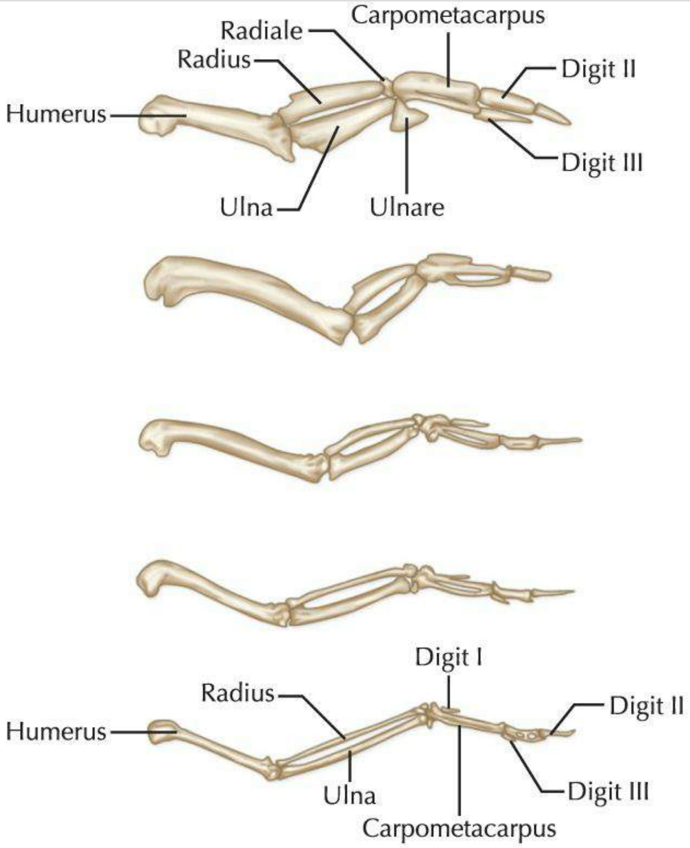
(A) © Olivier Couppey/Biosphoto. (B) Robin Bush/Getty Images. (C) James Urbach/Purest/AGE Fotostock. (D) McPHOTO/ AGE Fotostock. (E) Corbin17/Alamy

Figure 5–20 Flightless birds vary in size and ecology. (A) Common Ostrich, a large-bodied bird with extensively vegetative diet. (B) North Island Brown Kiwi, a medium-sized bird that feeds on soil invertebrates. (C) Adelie Penguin, a large wing-propelled diver feeding on fishes and oceanic invertebrates. (D) Flightless Cormorant, a foot-propelled diver that feeds on fish. (E) Skeleton of *Gastornis*, a large extinct terrestrial predator from the Eocene of North America.

Other routes to the evolution of flightlessness are seen in specialized diving birds. Foot-propelled divers, such as loons, ducks, grebes, and cormorants, have evolved powerful legs and feet that function as paddles. If evolution favors hindlimbs for locomotion, wings and associated pectoral development may regress and render a diving bird nearly or completely flightless. Extreme cases are those of the flightless Titicaca Grebe of Lake Titicaca, Peru; the flightless steamer ducks from southern South America; the Flightless Cormorant of the Galápagos Islands (Figure 5–20D); and the Mesozoic diving bird *Hesperornis* (see Figure 2–16).

Penguins, which are wing-propelled divers, represent another route to flightlessness in specialized diving birds. Their wings propel them through water rather than through the air; their feet act as rudders rather than as paddles. The evolution of other such flightless forms has also occurred in the Great Auk in the Northern Hemisphere. (see Figure 1–16)

The evolution of wing-propelled divers from flying birds proceeds through an intermediate state in which wings are used for both underwater propulsion and aerial flight. Diving petrels represent an intermediate stage in the evolution from flying petrels to flightless penguins. Auks, such as the Razorbill, with dual-purpose wings, represent the intermediate stage in the evolution of specialized divers from flying ancestors to the flightless Great Auk of the North Atlantic. The progressive specialization of wing skeletal structure is evident in the changes from the slim wing bones of a gull through shorter and heavier bone structures to the broad, flat wing skeleton of a penguin’s flipper (Figure 5–21).



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DATA FROM STORER 1960

Figure 5–21 Modifications of the wing skeleton in wing-propelled diving birds: (*bottom to top*) an aerial gull, an auk, the flightless Great Auk, an extinct penguinlike auk, and a penguin.

5.9 Evolution of Flight

With a more detailed understanding of the biomechanics, physiology, and anatomy of flight, we can now reconsider theories of the evolution of bird flight that were introduced in Chapter 2 (see section 2.7). In summary, **cursorial theories** hypothesize that flight started from running locomotion, and **arboreal theories** hypothesize that flight evolved from gliding out of trees.

Many sources of evidence are relevant to evaluating the plausibility of these alternative hypotheses. First, by examining the phylogeny of theropods and Mesozoic birds, we can see that the anatomical components of the modern flight stroke evolved gradually over time through the acquisition of a series of innovations that improved and advanced the flying capacity (Figure 5–22). For example, asymmetrical limb feathers capable of producing aerodynamic forces evolved in the common ancestor of all paravians. The carpometacarpus, short tail, and pygostyle later evolved in the common ancestor of the *Confuciusornis* and living birds: the Pygostylia. A modern flight apparatus finally evolved in the common ancestor of the Enantiornithines and living birds with the origin of the keeled sternum, the alula, and the elongate, strutlike coracoid. Although asymmetrical feathers were the first aerodynamic morphology to evolve, anatomically modern flight feather vanes—with barbs of the leading and trailing vanes at different angles to the rachis—did not appear until the common ancestor of the Enantiornithines and living birds (Feo et al. 2015).

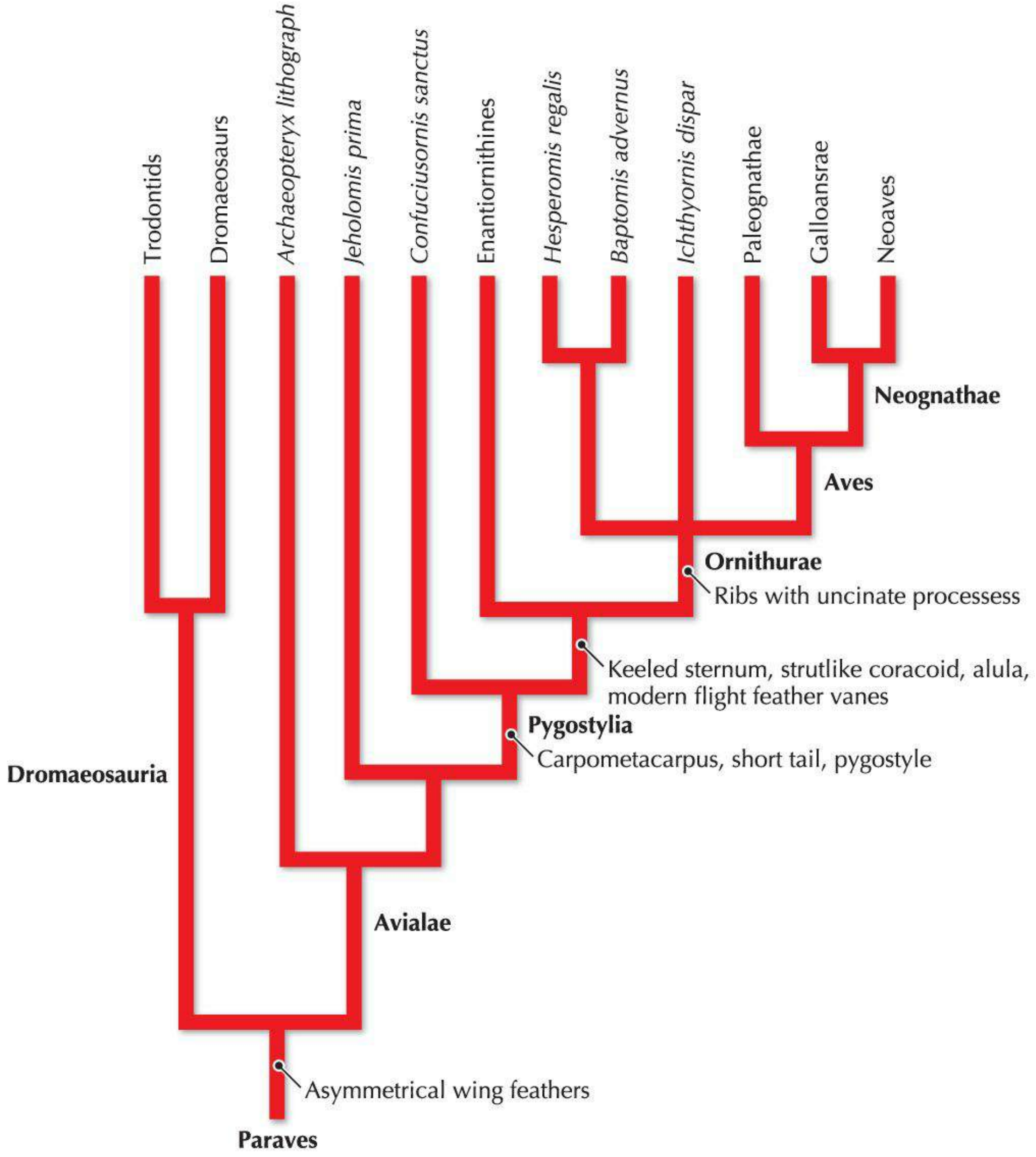

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Figure 5–22 A phylogeny of living birds and their paravian theropod relatives showing the evolutionary origin of the anatomical components of avian flight morphology. The elements of the modern avian flight stroke evolved through a long series of incremental advancements.

The phylogenetic pattern of gradual, incremental advance in flight anatomy implies a parallel pattern of gradual evolution in flight capacity (see Figure 5–22). For example, the supracoracoideus muscle is critical to powering the upstroke required for taking off directly from the ground. Furthermore, flying at slow speeds using a ring-vortex gait requires a highly asymmetrical flight stroke that depends on the supracoracoideus muscle and fine control of the shoulder muscles. Thus, these advanced flight performance capabilities were unlikely to have originated before the elongate coracoid, the triosseal canal, and the keeled sternum in the common ancestor of the Enantiornithines and living birds.

Furthermore, the J-shape flight power function shows that lift is easier to produce at moderate speeds, where induced drag is minimized, than at slow speeds (see Figure 5–4). Thus, the cursorial theory faces two profound biophysical challenges because takeoff by flapping and running along the ground requires both a complex, asymmetrical flight stroke and becoming airborne at the slowest speeds at which the induced drag is highest. *Archaeopteryx* and other early avialians did not have the elongate coracoid and triosseal canal that were likely necessary to produce a powerful, asymmetrical upstroke. It is not clear how relevant the behavior of wing-assisted incline running observed in modern birds may be to the origin of bird flight (Dial 2003a; see Figure 2–17) because modern birds have a modern shoulder girdle, flight musculature, and flight feathers that *Archaeopteryx* and other Jurassic birds lacked.

h

The arboreal or gliding theory of the origin of avian flight is biophysically and anatomically more plausible because gliding down from trees with gravity creates speed without any energetic costs, which would allow the evolution of the first lift production at speeds that require less power without an advanced flight stroke capacity (Dudley et al. 2007). Furthermore, the flight stroke could have evolved gradually from gliding, to simple wing adjustments for maneuvering, to a continuous vortex gait, to an asymmetrical ring-vortex gait. This evolutionary scenario matches the observed phylogenetic pattern and biomechanical data.

Although it is clear that birds evolved from a bipedal, terrestrial group of theropod dinosaurs, the biophysics of flight and the phylogenetic pattern in the flight morphology of birds provide stronger support for the arboreal, gliding theory of the origin of avian flight.

REVIEW KEY CONCEPTS

5.1 Elementary Aerodynamics

In order to fly, a bird overcomes the forces of gravity and drag acting on its body by producing lift with its wings. Lift is created by the movement of air over the asymmetrical upper and lower surfaces of the wing. The direction of the lift is always perpendicular to the direction of air over the wing. In forward-powered flight, a bird must rotate its wings forward during the downstroke, which also rotates the direction of lift forward, creating forward thrust. Forward flight requires an asymmetrical flight stroke in which the bird produces lift and thrust on the downstroke and minimizes the forces produced on the upstroke. Birds do this by changing the shape of the wings during the upstroke and downstroke.

Key Terms: biomechanics, gravity, drag, lift, gliding, Bernoulli effect, vortex/vortices, trailing vortices, angle of attack, flight stroke, downstroke, upstroke, thrust, asymmetrical flight stroke

5.2 Energetics of Flight

To maintain flight, a bird must produce enough lift to counter its weight and its loss of potential energy due to drag. Understanding the energetics of bird flight involves investigating how the force of drag and other energy demands change with flight speed. The profile drag created by air moving over the surface of the bird increases with flight speed. In contrast, the induced drag created by moving the air to produce lift decreases with flight speed. So, the total power required to fly is highest at slow and high speeds and lowest at intermediate speeds. The most efficient flight speed for a bird depends on its behavior. Birds that forage as they fly should use the velocity of minimum power (V_{MP}), which minimizes the amount of energy used per unit time. Birds that fly between one food patch and another should use the velocity of maximum range (V_{MR}), which minimizes the amount of energy used per unit distance.

Key Terms: profile drag, induced drag, total power, profile power, induced power, velocity of minimum power (V_{MP}), velocity of maximum range (V_{MR})

5.3 Modes of Flight

Birds have evolved a wide range of modes of flight. Thermal soaring on rising, warm air and dynamic soaring on the wind are efficient modes of flight that require little energetic investment. In flapping flight, the bird produces its own lift with an asymmetrical flight stroke. At slower speeds, flapping birds fly with a ring-vortex gait in which each downstroke produces its own, separate doughnut-shaped air vortex. At higher speeds, flapping birds fly with a continuous vortex gait, in which both the downstroke and the upstroke contribute to lift. Birds maneuver the direction of flight by changing the relative positions of the centers of gravity, lift, and drag.

Key Terms: modes of flight, thermal soaring, dynamic soaring, kettles, ring vortex, continuous vortex

5.4 Wing Sizes and Shapes

The energetic costs of flight are influenced by wing shape. Particularly important are the relation between a bird’s body mass and its total wing area, called wing loading, and the relative pointiness of the wings, or wing aspect ratio. Birds evolve wing shapes that lower the costs of flight at their predominant speed and mode of flight. All soarers have very low wing loadings, but thermal soarers have low-aspect-ratio wings, whereas dynamic soarers have high-aspect-ratio wings. Ground birds that usually fly for only short distances to escape predators have low-aspect-ratio wings and high wing loadings. Waterfowl and auks have high-aspect-ratio wings and high wing loadings to fly at rapid speeds (near V_{MR}) because they usually are flying between foraging sites.

Key Terms: wing area, wing loading, aspect ratio

5.5 The Skeleton

The skeleton of a bird is highly modified for flight. Many bird bones are light, air-filled structures that are strengthened by internal struts. The sternum of flying birds has a prominent keel for the origins of the major muscles. The shoulder girdle and wing bones are also highly specialized for flight. The bones of the avian hand are fused into the carpometacarpus. The feathered first “finger” of the bird hand is the alula, which stabilizes the airflow over the wing during takeoff and landing and prevents stalling at slow speeds.

Key Terms: uncinate processes, sternum, keel, coracoid, scapula, furcula, humerus, radius, ulna, carpometacarpus, alula

5.6 Flight Muscles

The two great flight muscles—the pectoralis and supracoracoideus—originate on the keel of the sternum and insert on the humerus.

Contraction of the pectoralis pulls the wing down in the power stroke. Contraction of the supracoracoideus muscles lifts the wings on the upstroke. The supracoracoideus muscles accomplish this with a tendon pulley system. The supracoracoideus tendon passes the triosseal canals (which is formed by the junction of the three shoulder bones: the coracoid, scapula, and furcula) before inserting on the humerus.

Key Terms: pectoralis, supracoracoideus

5.7 Muscle-Fiber Metabolism

Avian flight muscles are composed of red muscle fibers, which provide sustained power using aerobic respiration, and white muscle fibers, which provide sudden, short bursts of power using anaerobic respiration. Different birds have evolved different muscle fiber compositions depending on their biology. For example, ground birds, like grouse and tinamous, have more white muscle fibers for occasional explosive flight to escape predators.

Key Terms: red muscle fibers, white muscle fibers

5.8 Flightless Birds

Many different lineages of bird have lost the capacity to fly. Flightlessness has evolved repeatedly in birds with extremely large bodies sizes, in specialized diving birds, and among birds that live on islands where predation is limited.

5.9 Evolution of Flight

Cursorial theories hypothesize that avian flight evolved from running locomotion, and arboreal theories hypothesize that flight evolved from gliding out of trees. The anatomy and phylogeny of Mesozoic birds demonstrates that the anatomical components of the modern flight stroke evolved gradually over time through the acquisition of a series of innovations that improved and advanced the flying capacity. The pygostyle and carpometacarpus evolved in the "short-tailed" birds, or Pygostylia. The modern flight apparatus evolved in the common ancestor of the Enantiornithines and living birds with the origin of the keeled sternum, the alula, and the strutlike coracoid. The cursorial theory faces two profound biophysical challenges. Takeoff by running on the ground and flapping requires a more complex, asymmetrical flight stroke to produce a ring-vortex gait, but the anatomical features for such wing movements were not present in *Archaeopteryx* and other long-tailed birds. Furthermore, lift is energetically cheaper at intermediate airspeeds with lower induced drag. Gliding overcomes both of these problems because it can produce higher speeds with little energetic expenditure and without a complex wing stroke.

Key Terms: cursorial theories, arboreal theories

APPLY YOUR KNOWLEDGE

1. Describe wing shapes in terms of wing loading and aspect ratio and compare wings that best allow gliding flight with those that maximize maneuverability.
2. Describe how wings create lift to overcome gravity and drag and thrust to produce forward motion.
3. Compare and contrast the wing structure and function of songbirds

and hummingbirds. How do the power strokes of these two groups differ?

4. Describe the differences in red and white muscle fibers and their functions in flight.
5. What factors have contributed to the loss of flight in birds from different groups and habitats?
6. How has the skeleton of birds become both strengthened and lighter in support of flight?
7. Describe the J-shaped power function and explain why more energy is required at speeds lower and higher than intermediate speeds.

CHAPTER 6 *Physiology*

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A photo shows two rock ptarmigans roosting in the snow.

> Weight for weight, birds eat more food, consume more oxygen, move more rapidly, and generate more heat than any other vertebrates. [Welty 1982, p. 130]

Feathers and flight are conspicuous features of birds. Less conspicuous but just as fundamental are the internal systems of metabolism and excretion—collectively called **physiology.** These systems sustain daily activities and adapt individual birds to their particular environments, hot or cold, wet or dry.

The advanced physiology of birds provides both power and endurance. Power and endurance derive from the maintenance of high body temperatures. One advantage of high body temperatures is that activity is unconstrained by low ambient temperatures. Birds are fully active in the early morning cold, in midwinter, and in the high mountains. In turn, high body temperatures demand much energy and water, two resources that often are in short supply. Adaptations for heat loss and water economy, as well as heat conservation, enable birds to live in extreme and seasonal environments.

A fundamental function of organismal physiology is to achieve **homeostasis**—the maintenance of a consistent internal environment in response to changes in the external environment and the activities of the individual. We will see how different physiological systems of the bird’s body function to keep the conditions within the body near an internal set point.

This chapter focuses on the fundamentals of avian physiology—metabolism, temperature regulation, feeding and digestion, and water economy. Birds maintain a delicate physiological balance of the conflicting needs for temperature regulation, activity, and water economy. Supporting the demands of sustained aerobic metabolism is a unique and highly efficient respiratory system coupled with a powerful heart and circulatory system. The high body temperatures of birds require active control of heat exchange with the environment to conserve energy in cold environments and to lose heat in hot environments and in flight. Specialized bills and digestive systems garner the required energy and nutrition from the environment. Also essential are water reserves required for heat loss through evaporative cooling as well as the excretion of electrolytes. Metabolic water is an important source of these reserves.

Physiological constraints influence all aspects of a bird’s life. Later chapters treat additional features of avian physiology related to migration, reproduction, stress, disease resistance, and the hormonal control of behavior.

6.1 The High Body Temperature of Birds

The physiology of birds, specifically their metabolism, relates directly to the maintenance of a high body temperature through the production of metabolic heat, or **endothermy.** Most birds, large and small, in the frigid Arctic and in the hottest deserts keep their core body temperature higher than the surrounding air, at about 40°C. High body temperatures enhance intrinsic reflexes and powers. They enable birds to be active, fast-moving creatures. In animals generally, the rates of physiological processes increase with body temperature. For example, the transmission speed of nerve impulses increases 1.8 times with every 10°C increase in temperature. The speed and strength of muscle-fiber contractions triple with each 10°C rise in temperature.

Birds have the highest body temperatures and metabolic rates (relative to mass) among endothermic vertebrates (Gerson et al. 2014). The maintenance of high body temperatures through endothermy, however, is energetically expensive; birds consume from 20 to 30 times more energy than do similar-sized, cold-blooded, or poikilothermic, reptiles. The maintenance of high body temperatures also risks lethal overheating. Desert quail and doves, among others, routinely carry high heat loads and operative environmental temperatures of 50°C to 60°C. Above 46°C, most proteins in living cells are destroyed more rapidly than they can be replaced (Figure 6–1), causing potentially fatal changes in the chemistry of the brain.

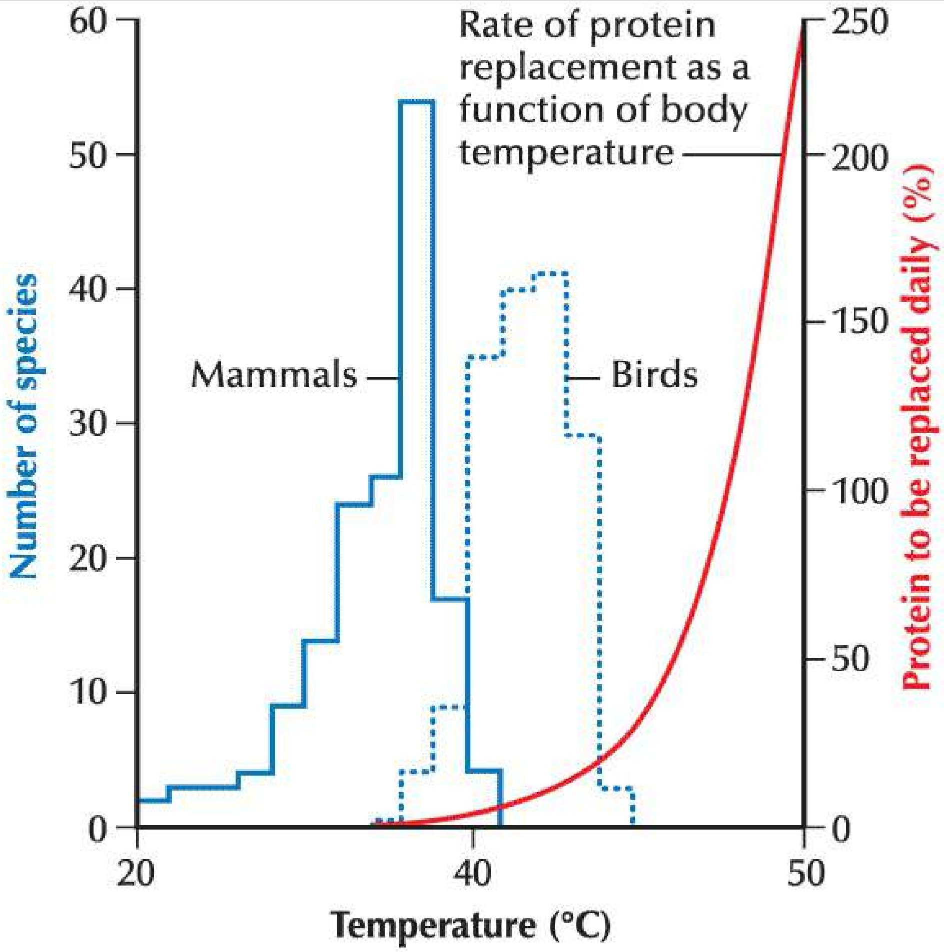

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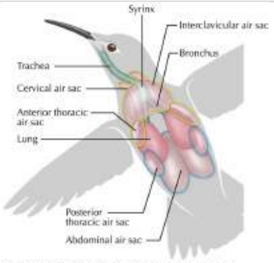
Figure 6–1 Birds and mammals regulate their body temperatures to be just below temperatures that destroy body proteins. Shown here are the body temperatures of many bird and mammal species. The curved line represents the rate of protein replacement as a function of body temperature.

Even more important than the benefits of endothermy for speed or strength are those for endurance. Warm amphibians and reptiles can escape or strike with lightning speed but are quickly exhausted. Some birds fly for hours or days. Increased aerobic metabolism and insulation were among the major changes that accompanied the evolution of reptiles into birds. These changes made possible regulated high body temperatures and the many advantages of dependable rates of muscle function. Higher activity levels, coupled with greater endurance, opened a new range of ecological opportunities for birds. However, challenges accompany the benefits. The high metabolic demands of temperature regulation and of the daily activities of birds require extraordinary delivery rates of energy and oxygen to the body's cells as well as the rapid removal of poisonous metabolic waste products. Efficient respiratory and circulatory systems help to meet these demands and to keep a bird's body chemistry in balance.

6.2 The Respiratory System

The respiratory system of birds is different in both structure and function from the respiratory system of mammals. Bird lungs are small, compact, spongy structures molded among the ribs on either side of the spine in the chest cavity. The dense tissues of their lungs weigh as much as the lungs of mammals of equal body weight but occupy only about half the volume. Healthy bird lungs are well vascularized and light pink in color. They are unique in that the air flows in only one direction rather than simply in and out as in other vertebrates.



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Data from Tyrell and Tyrell 1985

Figure 6–2 Positions of the air sacs and lung in a bird’s body. The interclavicular air sac that surrounds the syrinx is opened here to show that relationship.

Attached to the bronchi and lungs of birds is an elaborate system of interconnected **air sacs** that are not present in mammals (Figure 6–2). These air sacs are thin-walled, nonvascular, membraneous compartments that extend throughout the body cavity and inside the cervical vertebrae and major wing bones. The air sacs are connected to the lungs and bronchi through small accessory channels called secondary bronchi. Birds also lack a diaphragm, the muscle between chest and abdomen that causes mammalian lungs to inflate (inhale) and deflate (exhale). Instead, birds inhale by lowering the sternum relative to the spinal vertebrae, enlarging the chest cavity and expanding the air sacs. Contraction of the sternum and ribs compresses the air sacs, pushes fresh air from them through the lungs, and exhales the air (see below for complete sequence of air movements). During flight, expansions and contractions of the furcula, or wishbone, complement the movements of the sternum that help to pump air through the respiratory system (Jenkins et al. 1988).

Most birds inhale air through nostrils, or **nares,** at the base of the bill. A flap, or **operculum,** covers and protects the nostrils in some birds, such as diving birds, which must keep water from entering their nostrils, and flower-feeding birds, which must keep pollen out. Inhaled air passes into paired chambers (Figure 6–3). Each nasal chamber has elaborate folds, called **conchae** (sing. concha), that increase the surface area over which air flows. The surfaces of the conchae cleanse and heat the air before it enters the respiratory tract. Olfactory tubercles sample (smell) its chemistry. The conchae are also well supplied with nerves and a network of blood vessels—**rete mirabile**—that help to control the rate of heat loss from the body.

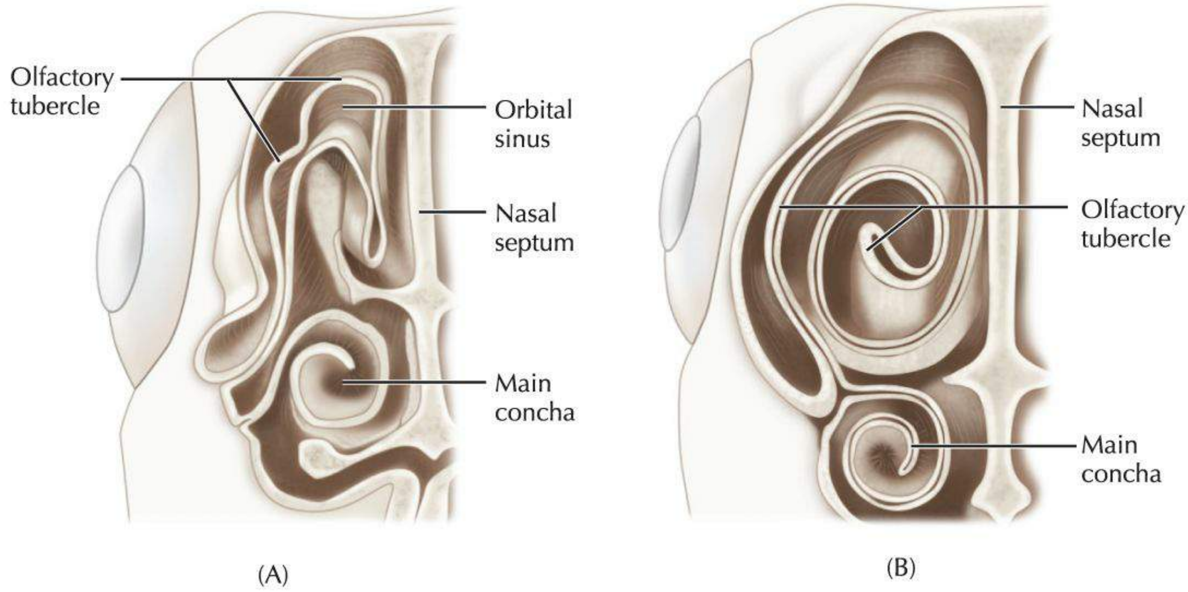

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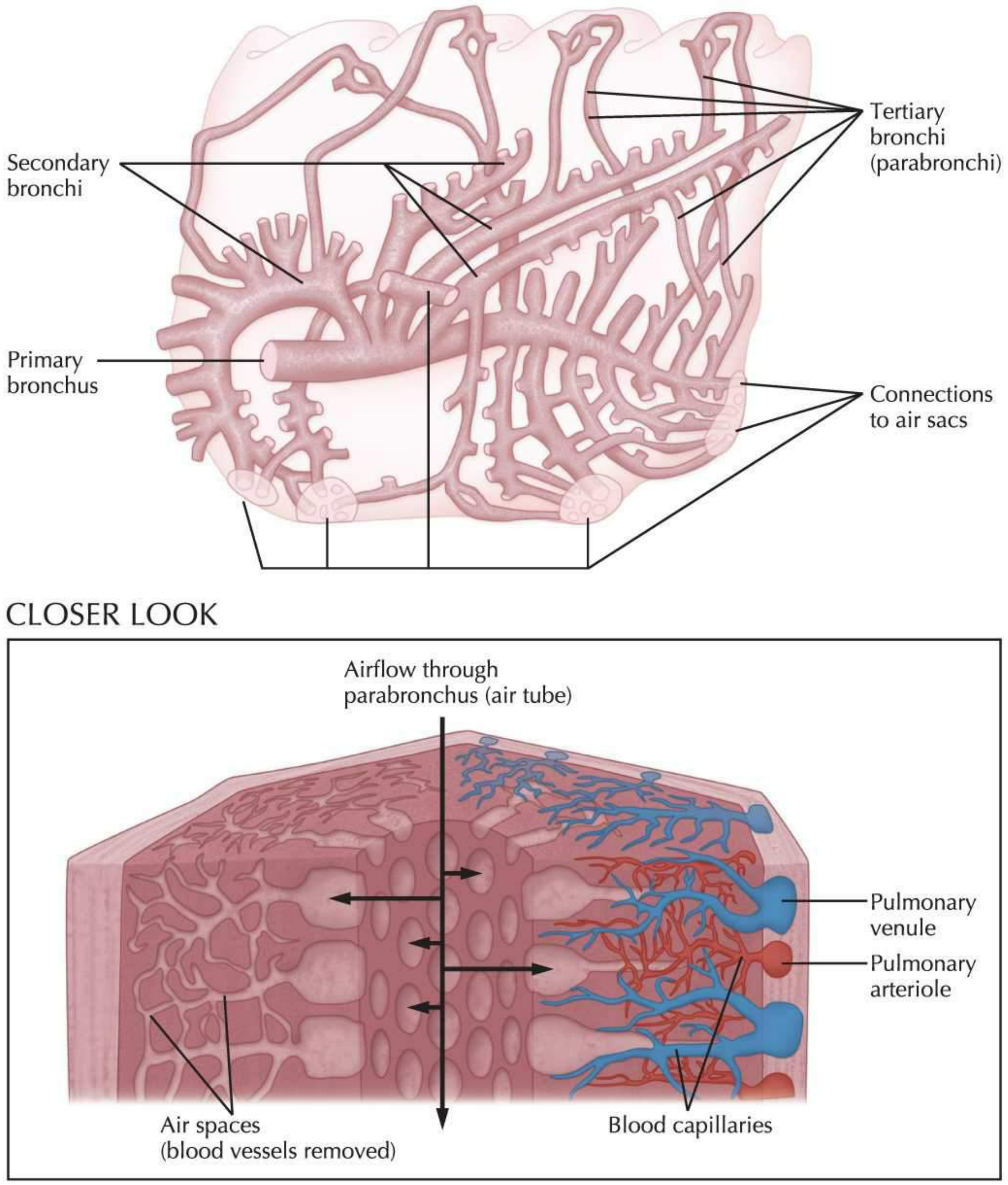
Figure 6–3 Cross sections of the nasal cavities of (A) a Northern Fulmar and (B) a Turkey Vulture, showing the elaborate folds, called conchae, that cleanse and heat inhaled air, remove water from exhaled air, and provide lots of surface area for olfactory receptors in some species.

Inhaled air moves next down the trachea, or windpipe, which divides into two bronchi and in turn into many subdividing stems and branches in each lung (Figure 6–4). Most of the lung tissue comprises roughly 1,800 smaller interconnecting tertiary bronchi. These bronchi lead into tiny air capillaries that intertwine with blood capillaries, where gases are exchanged.



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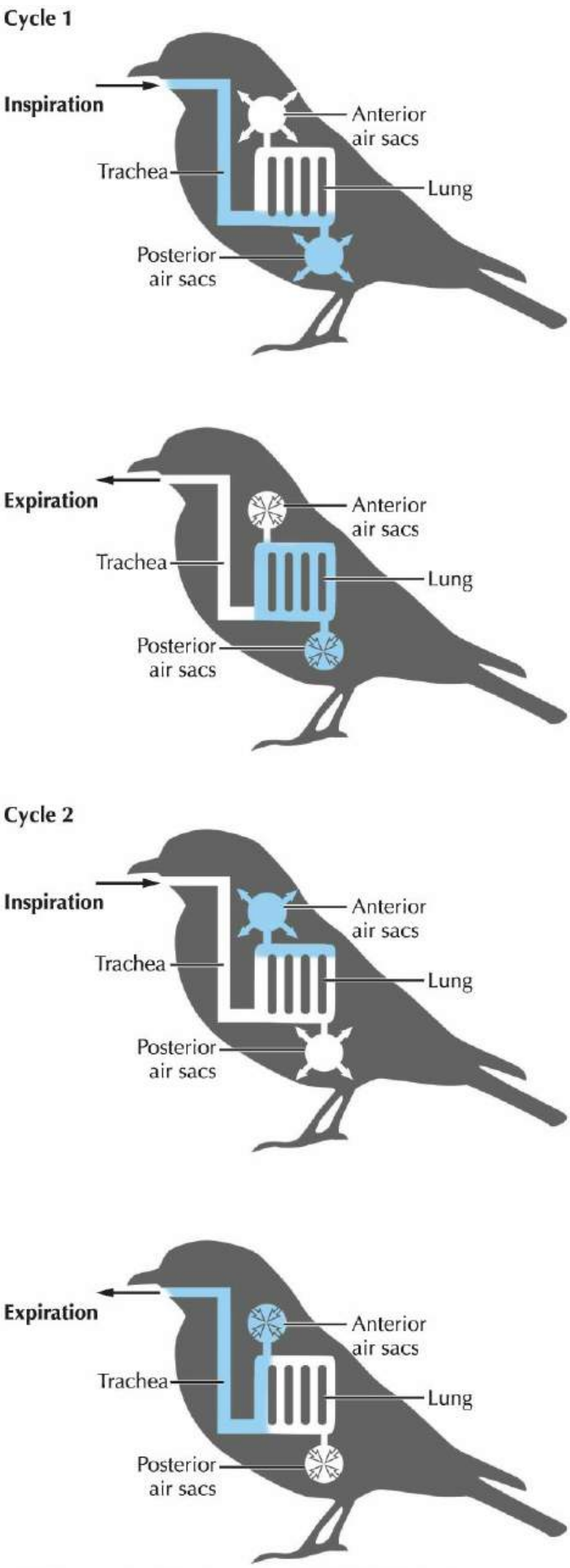
Data from Lasiewski 1972, Evans and Heiser 2004

Figure 6–4 Interconnecting bronchial tubules form the internal structure of a bird’s lung. Tertiary bronchi, or parabronchi, and fine air capillaries constitute most of the lung tissue.

Inhaled air flows continuously through the lungs and air sacs. Two complete cycles of inhalation and exhalation move a single volume of inhaled air through the respiratory system (Figure 6–5). Most of the air inhaled in step 1 passes through the primary bronchi to the posterior air sacs. In step 2, the exhalation phase of this first breath, the inhaled air moves from the posterior air sacs into the lungs. There, oxygen and carbon dioxide (CO_2) exchange takes place as inhaled air flows through the air–capillary system. The second time that the bird inhales, step 3, the oxygen-depleted air moves from the lungs into the anterior air sacs. The second and final exhalation, step 4, expels CO_2-rich air from the anterior air sacs, bronchi, and trachea back into the atmosphere. Of course, this description follows only a single volume of air; in fact, air is following through all parts of respiratory system during each inhalation and exhalation.



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DATA FROM SCHMIDT-NIELSEN 1983

Figure 6–5 The unidirectional movement of a single inhaled volume of air (shown in blue) through the avian respiratory system. One volume of air moves sequentially into the posterior air sacs, into the lung, and into the anterior air sacs and is then exhaled. Two full respiratory cycles—inspiration, expiration, inspiration, and expiration—are required to move one volume of air through its complete path.

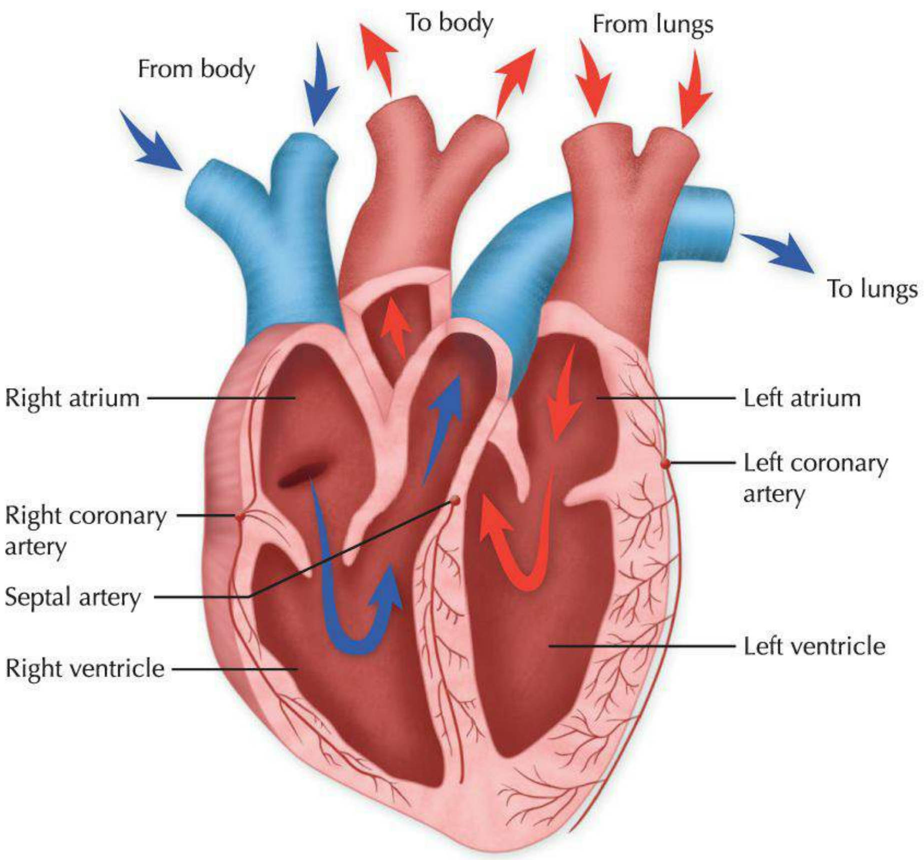
Unidirectional airflow through the lung maximizes contact of fresh air with the respiratory surfaces of the lung. Thus, a bird replaces nearly all the air in its lungs with each breath. No residual air is left in the lungs during the ventilation cycle of birds, as it is in mammals. By transferring more air and air higher in oxygen content during each breath, birds achieve a more efficient rate of gas exchange than do mammals. Interestingly, small regions of unidirectional air flow are found in the lungs of alligators, possibly early precursors of the advanced airflow systems of birds (Farmer and Sanders 2010).

Most birds have nine air sacs, the number of which varies from six in weavers and seven in loons and turkeys to at least 12 in shorebirds and storks. The air sacs of birds not only help to deliver the huge needed quantities of oxygen but also help to remove the potentially lethal body heat produced during flight and protect the delicate internal organs as well. They are an inconspicuous but integral part of the avian respiratory system. Air within the single interclavicular sac, for example, is essential for vocal sound production (Chapter 8). Supporting their ancestral relationship to birds, therapod dinosaurs also had pneumatized vertebrae consistent with the presence of anterior and posterior air sac systems (O’Connor and Claessens 2005).

6.3 The Circulatory System

The high metabolic rates of birds require rapid circulation of high volumes of blood between sites of pickup and delivery of metabolic materials. The circulatory system delivers oxygen to the body tissues at rates that match use and simultaneously removes carbon dioxide for exhalation. It also delivers fuel in the form of glucose and elementary fatty acids and removes toxic waste products for excretion. The demands on the avian circulatory system are far greater than those on the systems of reptiles and exceed those of most mammals.

Like mammals, birds have a double circulatory system and a four-chambered heart (Figure 6–6). Alligators and crocodiles have a three-chambered heart with incomplete separation of the two ventricles. The avian four-chambered heart evolved convergently to that of mammals. The evolutionary advantage of the four-chambered heart is to completely separate the pulmonary circulation from the circulation to the rest of the body. Fresh, oxygenated blood returns from the lungs to the left auricle and ventricle. This blood exits through the aorta to the peripheral arteries to all the cells of the body. After passing through capillary beds in the bird’s organs and tissues, the deoxygenated blood returns through veins to right auricle and ventricle of the heart, where it is pumped back to the lungs. Avian hearts are on average 41 percent larger than those of mammals of the corresponding body size. The heart accounts for 2 to 4 percent of the total mass of a hummingbird; few small mammals have heart masses greater than 1 percent of their mass. Normal resting heart rates in medium-sized birds range from 150 to 350 beats per minute; they average about 220. Heart rates of small birds are higher than those of large birds and exceed 1,200 beats per minute in small hummingbirds.



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DATA FROM JONES AND JOHANSEN 1972

Figure 6–6 The large, four-chambered bird heart supports efficient oxygenation of blood by separating circulation to the lungs and the body.

The performance of the heart is measured in terms of **cardiac output**—or the rate at which the heart pumps blood into the arterial system. Defined as “heart rate times stroke volume (the volume of blood pumped with each contraction) from one ventricle,” cardiac output averages from 100 to 200 milliliters of blood per kilogram of mass per minute in birds. Major organs—the heart, liver, kidneys, and intestines—receive large percentages of the cardiac output, averaging from 8 to 10 percent each. The brain and eyes are next in line, receiving 3 and 4 percent, respectively. When a bird flies or swims, cardiac output allocations to the flight and leg muscles, respectively, increase dramatically.

Although bird hearts beat more slowly at rest than do the hearts of similar-sized mammals, their larger stroke volumes create comparable cardiac outputs. Not only is the avian heart larger, but its ventricles empty more completely than do those of mammals on each contraction. At high heart rates, ventricles fill more completely between contractions. The avian ventricles are also made up of more muscle fibers than is the mammalian ventricle. Each fiber (cell) is thinner than mammalian heart-muscle fibers and contains more mitochondria—energy-producing organelles that depend on the supply of oxygen. The thinness of avian heart-muscle fibers speeds the transfer of oxygen and increases the capacity for aerobic work and endurance at high activity levels.

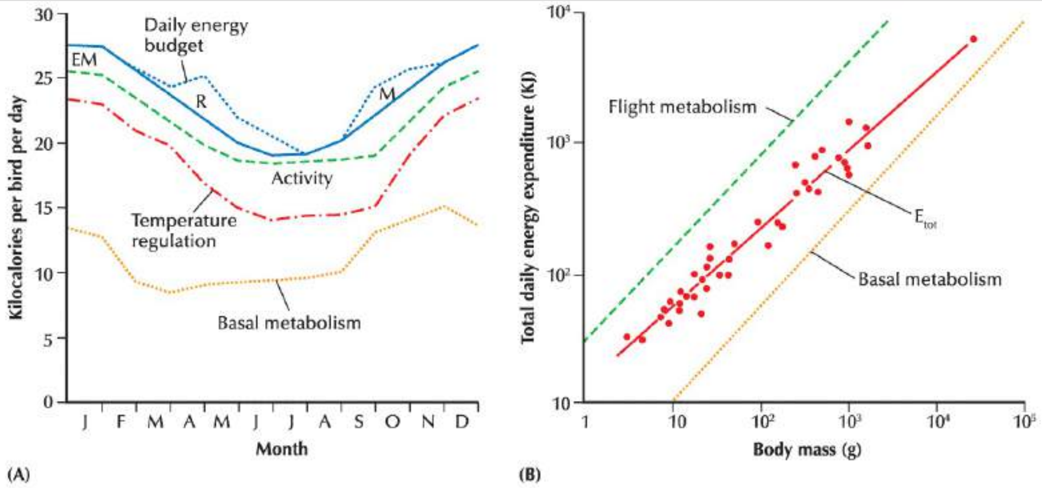
The high-performance features of the avian heart have their costs. The high tension of avian heart muscles and the strength of the ventricular contractions lead to high arterial blood pressures. Extremes as high as 300 to 400 millimeters of mercury are known in some strains of domestic turkeys—the maximum known for any vertebrate. A blood pressure of 150 millimeters of mercury is high for a human. Not surprisingly, aortic rupture is a common cause of death in these turkeys, which are raised on high-fat diets for weight gain.

6.4 Metabolism

Metabolic rate refers to the amount of energy expended over time to maintain the functions of the body. Metabolic rates change rapidly with different levels of activity, dropping to a minimum when a bird sleeps or rests and rising to a maximum during flight. Intermediate rates of metabolism support the regulation of body temperatures during periods of cold or heat stress. The total daily energy budget of a bird is the sum of these varied expenditures. The following discussions proceed from the minimum, or basal, metabolism to the ways in which birds regulate their body temperatures during cold and heat stress.

Basal Metabolism

Even resting birds use energy, called **basal metabolic rate (BMR).** Carefully controlled measurements of the minimal metabolic requirements of resting birds fasting at nonstressful, or thermoneutral, temperatures give estimates of what is called **basal metabolism.** All birds have high basal metabolic rates relative to most vertebrates. Basal metabolism relates directly to mass but not in a 1:1 relation (Figure 6–7). An eight-kilogram bustard is 100 times as large as an 80-gram falcon, but it expends only 30 times as much energy per unit of time. Just as the surface area of a sphere relates to its volume, large birds have less surface area per unit of volume than do small birds. Thus, a large bird cannot lose heat as fast as a small bird because it has less surface area per gram of heat-generating tissue. If an ostrich's tissues produced heat at the same rate as a sparrow's tissues, the ostrich would not be able to dissipate heat fast enough from its body surfaces and would boil inside.



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(A) Data from Blem 2000. (B) Data from Walsberg 1983

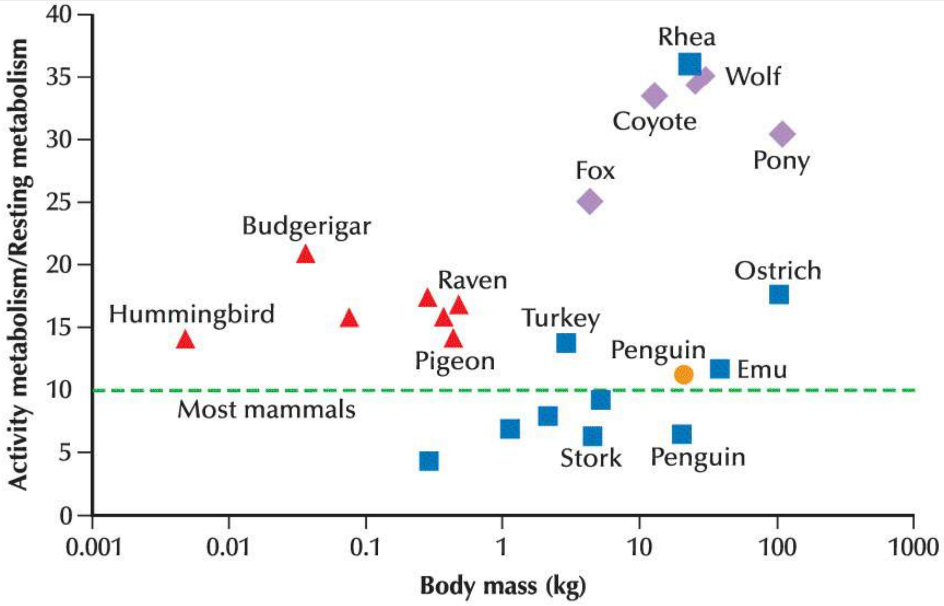
Figure 6–7 (A) Model of seasonal variation of energy expenditure (in kilocalories) of a small temperate-zone bird. The total daily energy budget varies monthly as the sum of different expenditures. Abbreviations: EM, existence metabolism; R, reproduction; M, migration. (B) Metabolism and daily energy expenditures typically increase with body size. The slope of this fundamental physiological relation—the increase in basal metabolism with increased mass—is predictably from 0.72 to 0.73 for different-sized birds as well as for different-sized mammals. Large birds expend less energy per gram of mass than do small birds. Total daily energy expenditures (E_{tot}, in kilojoules) do not increase as fast with increasing body size as does basal metabolism, possibly because small birds are more active than large birds. Energy expenditures of birds during flight—flight metabolism—vary from two to 25 times as high as basal metabolic rate.

Activity Metabolism

A bird usually spends only a fraction of its day at its basal metabolic level—that is, when resting and fasting. Instead, most of its time is spent in activities that require the expenditure of more energy and the use of more oxygen. The simple digestion of a meal, the slight muscle actions associated with awareness and attention, or the powering of a strenuous sprint or vertical takeoff all increase energy expenditures.

Just being awake and resting increases metabolic rate by 25 to 80 percent above the basal rate. Metabolic costs increase more with exertion. Swimming Mallards, for example, increase their metabolism 3.2 times BMR at their most efficient (and preferred) speed and 5.7 times BMR when they swim as fast as they can (Prange and Schmidt-Nielsen 1970).

Matthew Bundle and his colleagues (1999) trained Greater Rheas—large, flightless, South American relatives of the ostrich—to run on an inclined treadmill while wearing clear plastic hoods to measure their oxygen consumption. It took two years to train them to run just as fast as they could to stay in the same place, which would have pleased the Red Queen of *Through the Looking-Glass.* Their aerobic metabolism peaked at 36 times minimum resting rates (not BMR) at an uphill running speed of 4.0 meters per second (14.4 kilometers per hour). At faster paces, they relied increasingly on lactate-producing anaerobic metabolism for running energy. The rhea’s increase in aerobic metabolism, or aerobic scope, exceeded that reported for most mammals, including powerful running mammals, such as wolves and horses (Figure 6–8). More broadly, birds appear to have double the aerobic scope of mammals.



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Data from Bundle et al. 1999

Figure 6–8 Most birds have a greater aerobic scope, measured as the ratio of active to resting metabolism, than do most mammals (dotted green line). Rheas exceed even the most powerful running mammals, like wolves and horses, in the breadth of their aerobic capacity. Metabolic rates are expressed as the ratio of activity metabolism to resting metabolism, or the factorial increase of activity metabolism. Triangles, flying birds; squares, running birds; circles, swimming birds; diamonds, running mammals.

Birds in flight sustain high levels of aerobic metabolism. Small birds in flight can operate at 10 to 25 times their BMRs for many hours, whereas small mammals can sustain an activity level of metabolism of only five to six times their BMRs (Bartholomew 1982). Estimates of flight metabolism range from 2.7 to 23 times BMR, with variations due to flight mode, flight speeds, wing shape, laboratory constraints, or a combination of them (Blem 2000). Low values of flight metabolism are obtained for swallows and swifts in partly soaring flight, and high values are obtained for finches and hovering hummingbirds.

Whether atop the Andes or migrating high over the Himalayas, birds inhabiting high altitudes operate in extreme, oxygen-poor conditions. Making this possible, increases in the oxygen affinity of hemoglobin molecules are a pervasive and predictable adaptation of high-altitude bird species (Natarajan et al. 2016). In one case, a single point mutation that enhances oxygen affinity of the beta-globin gene prevails adaptively in high-altitude populations of Andean House Wrens (Galen et al. 2015). Hummingbirds, especially, thrive in high-altitude environments in the Andes despite exceedingly high oxygen demands of their elevated rates of aerobic metabolism (Projecto-Garcia et al. 2013). Colonization of new elevation zones, followed by speciation, was made possible by predictable and parallel amino acid replacements that enhanced hemoglobin function.

6.5 Temperature Regulation

A bird’s thermal relations with its environment are critical to its survival. Endothermy itself is part of a dynamic relation between internal heat production and heat lost to the external environment. Heat is an inevitable result of the inefficiency of biochemical reactions and so is a direct product of metabolism. Rates of heat production or loss are expressed in watts or joules per hour—the average student at rest produces heat at the same rate as does a 100-watt incandescent lamp.

In special situations (e.g., in a nest hole or a burrow free of wind in which wall temperature equals air temperature), ambient air temperature provides an accurate index to the rate of heat loss or heat gain, but in more realistic environments in which the sun shines and the wind blows, a bird’s thermal relation with its environment becomes a complex function of the intensity of radiation and convection.

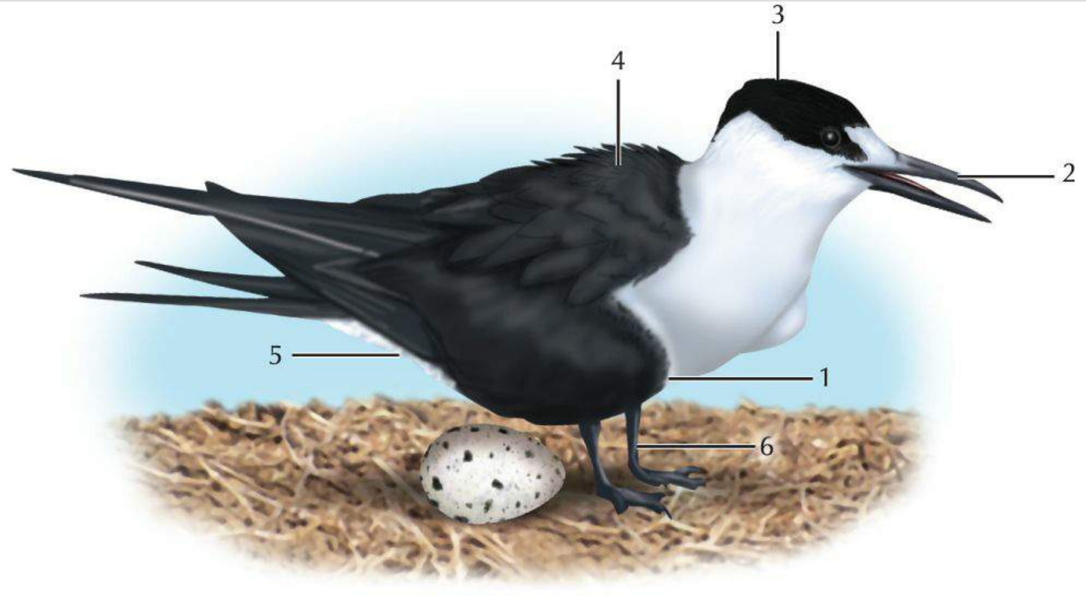
Bird-feather coats are among the best natural, lightweight insulations. Reduced feather insulation increases metabolism. The abnormal feathers of frizzled chickens (Figure 6–9), for example, provide little insulation. Their resting metabolism and the rate of heat loss are twice those of normal chickens at 17°C (Benedict et al. 1932). Contour feathers in the plumage contribute to a bird’s insulation, but the down feathers underneath the contour feathers are the primary sources of insulation. Thus, Arctic finches have dense down, whereas tropical finches do not.

CYNOCLUB/SHUTTERSTOCK

Figure 6–9 “Frizzled” chickens have high metabolic rates because their abnormal plumage does not provide as much insulation as that of normal chickens.

Insulation increases with the amount of plumage. Some birds enhance their insulation during cold seasons by molting into fresh, thick plumage. Nonmigratory House Sparrows, for example, increase plumage weight 70 percent, from 0.9 gram of worn plumage per bird in August to 1.5 grams of fresh plumage in September (Lowther and Cink 1992). Seasonal adjustments in insulation are less pronounced in tropical birds and in migratory species that escape major shifts in environmental temperatures.

Using their feather erector and depressor muscles (see Figure 4–24), birds adjust the positions of their feathers to enhance either heat loss or heat conservation. Fluffing the feathers in response to cold creates more air pockets and increases the insulation value of the plumage. Additional heat savings come from tucking the bill under the scapula feather tract and reducing exposure of the legs. Holding the wings out from the body and extreme elevation of the back, or scapular, feathers enhance heat loss by exposing bare apterial skin to convection. Tropical seabirds that nest in the open sun often elevate their plumage to avoid overheating (Figure 6–10).



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DATA FROM DRENT 1972

Figure 6–10 The Sooty Tern, a bird that is subject to great heat stress at the nest. On a hot day, the bird uses a variety of heat-dissipating mechanisms: (1) exposing the bend of the wing, (2) panting, (3) ruffling crown feathers, (4) ruffling back feathers, (5) wetting abdomen periodically, and (6) exposing the legs.

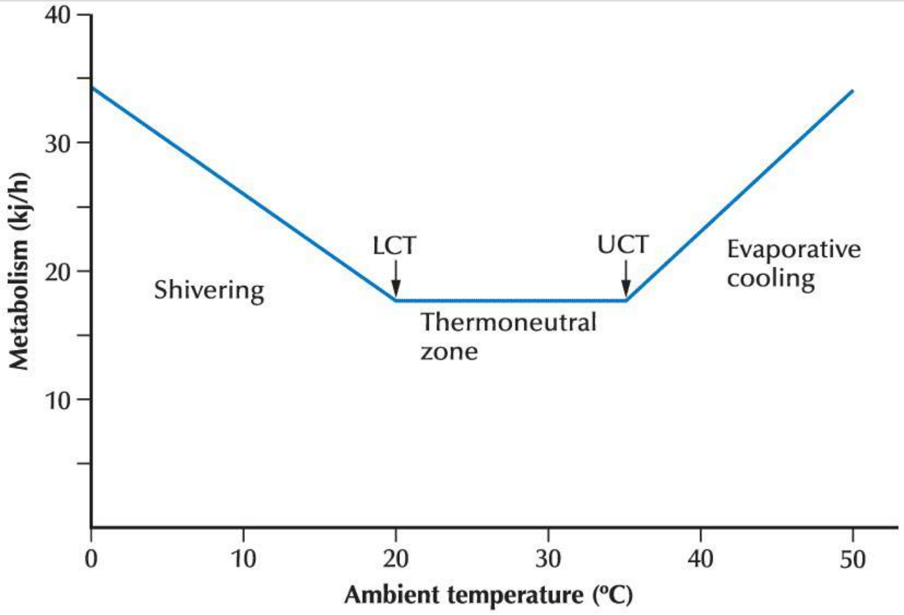
Dark pigmentation aids temperature regulation by absorbing the energy-rich short wavelengths of the solar spectrum. Light-colored plumage reflects rather than absorbs more of the impinging radiant energy than does dark plumage. The Greater Roadrunner erects its scapular feathers and orients its body so that the early morning sun heats strips of black-pigmented skin on its dorsal apteria (Hughes 1996).

The net thermal effect of plumage is influenced by the wind. Wind, or windchill, increases the rate of heat loss and compensatory heat production. The thick plumage of the Snowy Owl provides excellent insulation, but the rate of heat loss triples in winds of only 27 kilometers per hour compared with the rate of heat loss in still air (Parmelee 1992). The use of wind-sheltered sites, including holes or burrows for roosting and nesting, can protect birds from such heat loss.

The cooling effects of wind are most pronounced on black feathers, which concentrate solar heat near the surface of the plumage. Black feathers can increase the amount of heat that a bird’s body absorbs from the environment when there is no breeze. A light breeze, however, removes the accumulating surface heat and reduces further penetration of the radiant heat. The black plumage of desert ravens increases convective heat loss, as do the black robes and tents of Bedouin tribes in the Sahara.

A Model of Endothermy

The classical model of endothermy developed by Per Fredrik Scholander and his colleagues (1950) provides a way of understanding the dynamics of temperature regulation (Figure 6–11). One of the foundations of avian physiology, their model projects that birds expend the least energy on temperature regulation in the **thermoneutral zone**—the range in which the amount of oxygen consumed by resting birds does not change with temperature. Most birds do not have to change their rates of heat production to maintain an average body temperature of 40°C in the thermoneutral zone. Instead, birds can control the rates of heat loss by changing feather positions, by varying rates of the return of venous blood flow from the skin, by manipulating blood circulation in their feet, and by changing the exposure of their extremities, all of which require little direct energy expenditure. Temperature regulation by shivering or panting increases metabolism at lower and higher temperatures outside the thermoneutral zone.



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DATA FROM CALDER AND KING 1974

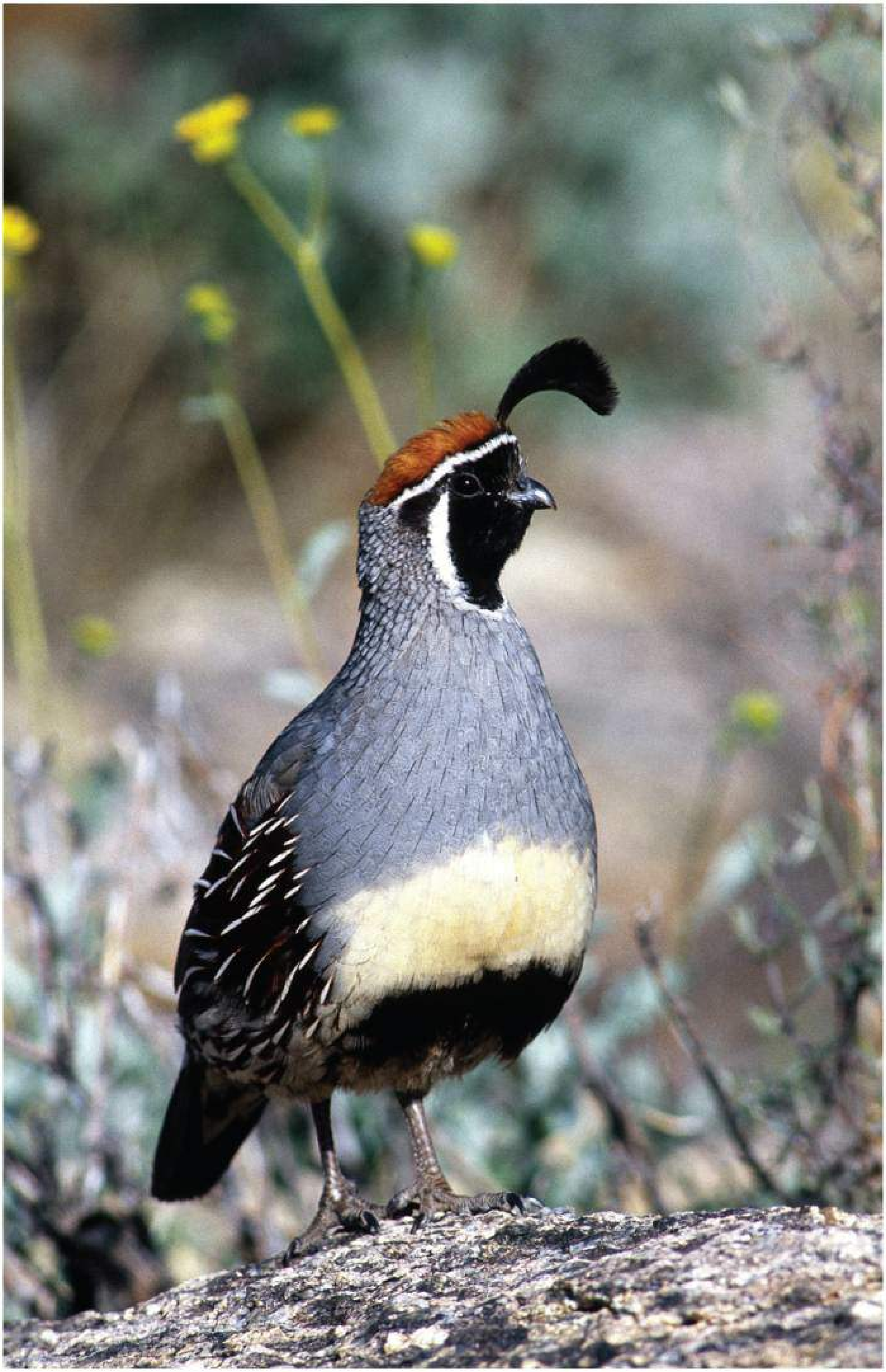
Figure 6–11 Scholander’s model of endothermy. Metabolism increases below the lower critical temperature (LCT) primarily as a result of heat production due to shivering. The slope of this portion of the graph decreases with increasing insulation. Metabolism increases above the upper critical temperature (UCT) due to active loss of heat through panting and evaporative cooling as well as to the direct effects of higher temperatures on cellular functions. Metabolism is relatively insensitive to changing ambient temperature in the thermoneutral zone between the LCT and the UCT.

Gambel’s Quail—a medium-sized game bird with a cute dangling topknot (Figure 6–12)—manages its exposure in the seasonally hot and dry Colorado desert. Their costs of thermoregulation are minor. Nighttime temperatures stay within the zone of thermoneutrality, and the quail avoid midday heat stress by resting in the shade, moving quickly between bushes, and reducing their metabolic heat production (Brown et al. 1998).

Not surprisingly, the critical temperatures of birds correspond to the temperatures that prevail in their primary habitats. Three species of titmice and chickadees (Paridae), for example, divide local habitats and climates in the western United States (Cooper and Gessamen 2004). The Juniper Titmouse of the hottest and driest lowland habitats has higher upper critical temperatures, greater heat tolerance, and lower rates of metabolic heat production than those of the Bridled Titmouse and Mountain Chickadee of higher elevations. Conversely, the thermal neutral zone of the Mountain Chickadee extends to cooler, lower critical temperatures than those of the other species. The distributions of these and other species of North America are predicted to change with global warming (Box 6–1).

Box 6–1

Global Warming



GERALD C. KELLEY/SCIENCE SOURCE

Figure 6–12 The Gambel's Quail reduces metabolic heat production to avoid midday heat stress in the Arizona desert.

The geographical distributions of birds are directly related to their temperature tolerances, water requirements, and other physiological constraints. Changes in the Earth's climate, therefore, have long regulated the distributions of birds. Now, the projected pace of global warming will likely subject birds to unprecedented changes in the location of optimal habitats and climate spaces. Models of how climate changes will affect the distributions of North American bird species suggest major reallocations of bird species from state to state (Price and Glick 2002). Painted Buntings of the South will replace Bobolinks in parts of southern Minnesota. Savannah Sparrows and Sage Thrashers may leave the southwestern states of Arizona and New Mexico. And some states may lose their official state birds, such as the Baltimore Oriole of Maryland.

Responses to Cold Stress

When cold, a bird tenses its muscles and begins to shiver. This response increases oxygen consumption. The temperature at which shivering begins is called the **lower critical temperature (LCT).** The pectoralis muscles are the major source of heat produced by shivering, supplemented by the leg muscles in some species. Mammals can produce heat by nonshivering thermogenesis (heat production) in a particular kind of fat called brown adipose tissue. Birds probably lack such capability for nonshivering thermogenesis (Saarela et al. 1991).

The temperatures included in the thermoneutral zone of bird species are partly a result of adaptations to the average environmental temperatures in which they live. Birds living in colder northern climates start to shiver at lower air temperatures than do species of warmer southern climates. Snow Buntings, for example, cannot maintain their body temperature below −50°C (Montgomerie and Lyon 2011); Northern Cardinals start shivering at 18°C (Halkin and Linville 1999). The LCTs of large birds are lower than those of small birds, a pattern seen also in mammals. In the absence of special adaptations, small birds lose heat faster and are thus more sensitive to cold than are large birds; small birds start to shiver at a higher temperature.

Natural adjustments to seasonal changes in temperature are called acclimatization. Winter-acclimatized American Goldfinches (see Figure 3–1), for example, can maintain normal body temperature for six to eight hours when subjected to extremely cold temperatures of −70°C (Carey et al. 1983). Summer-acclimatized goldfinches, however, cannot maintain normal body temperature for more than one hour when exposed to such frigid temperatures. The ability of goldfinches to withstand winter cold stress stems from an upscaling of their metabolism, including increases both in basal metabolic rates and in short-term heat production. Goldfinches acclimatize by restructuring the metabolic pathways that mobilize and use energy substrates, especially fatty acids (Likenes et al. 2002).

Birds also select **microclimates**—small places where weather conditions differ from the general climate—that reduce their rate of heat loss. Roosting in holes or protected sites, such as evergreen trees, greatly reduces heat loss, which is important during cold winter nights for small passerine birds. Grouse and ptarmigan burrow into the snow to insulate themselves from cold air temperatures; so do Willow Tits, Gray-headed Chickadees, and Common Redpolls.

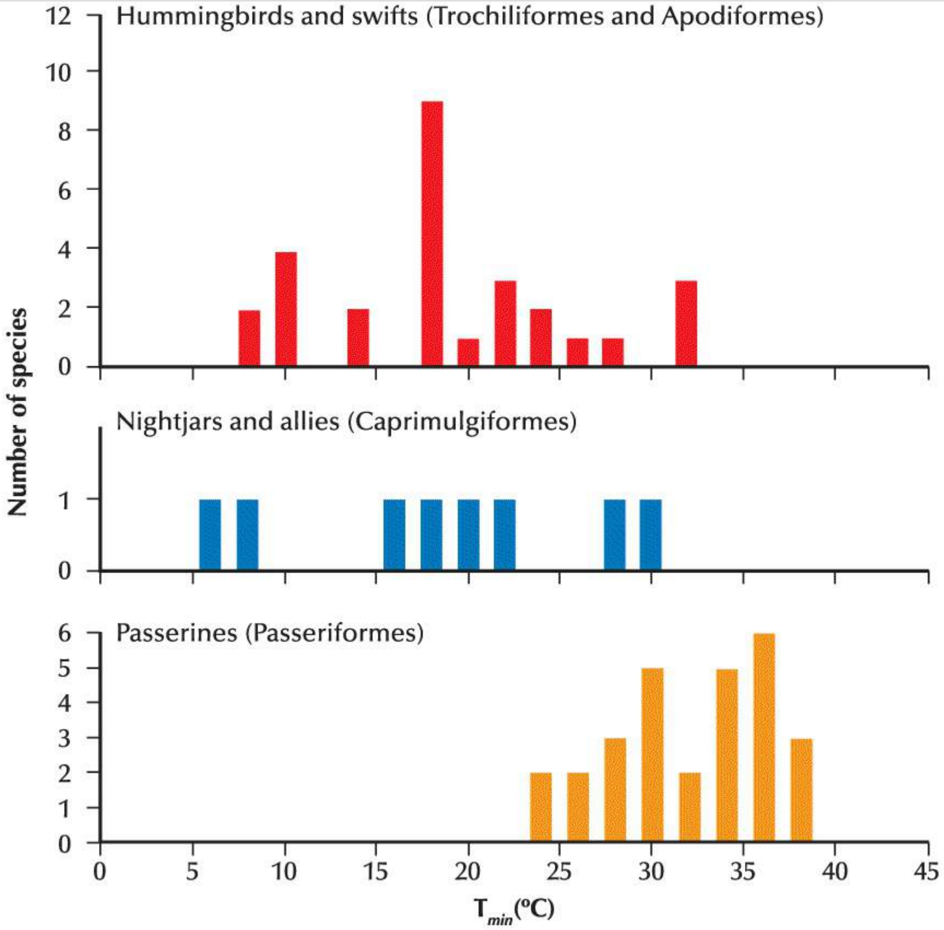
Huddling together also reduces heat loss, but sometimes birds go to extremes: about 100 Pygmy Nuthatches roosted together in one pine-tree cavity, so densely huddled that some suffocated (Knorr 1957). On cold days, Inca Doves sit on top of one another between flock feeding forays, forming two- or three-row “pyramids” of as many as 12 birds (Mueller 1992). With feathers fluffed, pyramiding doves face downwind in a sheltered sunny place. In large pyramids, doves exposed on outside positions try for better positions in the top row and cause the whole pyramid to readjust.

Huddling is also critical to the lifestyle of Emperor Penguins (Ancel et al. 1997). Males of these largest of all penguins incubate their mates’ eggs in total darkness in the dead of the Antarctic winter, enduring frigid air temperatures down to −50°C and winds as high as 180 kilometers per hour. Their LCT is a relatively warm −10°C. By huddling together in a giant side-by-side assemblage, thousands of egg-attentive penguins each cut their rates of energy expenditure and weight loss in half. This reduction buys an extra three weeks of incubation effort and prevents triggering the need to go to sea to feed, abandoning the egg, before the female returns and takes over.

Hypothermia and Torpor

As an energy-saving measure, avian body temperatures fluctuate a few degrees during the day and may drop significantly at night. The physiological condition in which the body temperature drops below normal is called **facultative hypothermia.** Daily cycles of hypothermia—mild or pronounced—may be tied to internal clocks, but facultative hypothermia is also triggered on a day-to-day basis by food deprivation and low energy stores. Facultative hypothermia saves critical energy supplies. Hummingbirds can save as much as 27 percent of their total daily energy expenditures.

Torpor (a state of minimal physiological activity) is known in at least 43 bird species in 14 families. Many birds, ranging from Black-capped Chickadees to Turkey Vultures, can lower their body temperatures by 6°C at night and by even more on extremely cold nights. They become mildly hypothermic. Birds in pronounced hypothermia lower their body temperatures to extremes: hummingbirds to as low as 8°C and the Common Poorwill to 4.3°C (Brigham 1992; Figure 6–13). Deeper still, birds in torpor become comatose and unresponsive to most stimuli. However, they do not abandon control of their body temperature and let it drop to air temperature. Instead, a torpid bird regulates a lower body temperature, increasing oxygen consumption as needed at low air temperatures (Figure 6–14).



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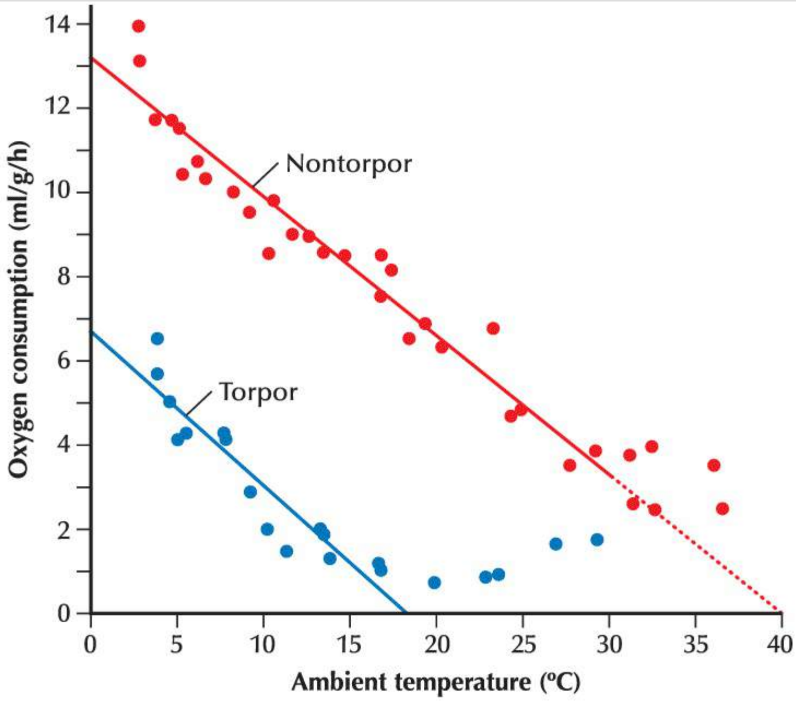
Data from McKechnie and Lovegrove 2002

Figure 6–13 Minimum body temperatures during hypothermia of 28 species of hummingbirds and swifts, eight species of nightjars and relatives, and 28 passerines.



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Data from Hainsworth and Wolf 1970

Figure 6–14 Metabolism of the Purple-throated Carib, a tropical hummingbird, during torpor and nontorpor. Nontorpid birds increase their metabolism (measured here in terms of oxygen consumption) as temperature decreases below the LCT of about 30°C. Torpid birds regulate their body temperatures to about 17.5°C.

Warming up is the main challenge of torpor. Birds waking from torpor begin to show good muscular coordination at 26°C to 27°C but require body temperatures of at least 34°C to 35°C for normal activity. A small hummingbird requires about an hour to arouse from torpor at 20°C, but a medium-sized bird, such as an American Kestrel, requires 12 hours to warm up.

Full torpor is usually neither practical nor economical for short periods in larger birds. Nightjars and their relatives (Order Caprimulgiformes) are an exception. In addition to the daily use of torpor, the Common Poorwill (55 grams) actually “hibernates” for two to three months during the winter. Its body temperature drops to a (regulated) 4.3°C. This habit was long known to Native Americans; the Hopi people refer to the poorwill as Hölchoko, “the sleeping one.” Torpor reduces a poorwill’s oxygen consumption by more than 90 percent. These poorwills are capable of spontaneous arousal at low ambient temperatures but require about seven hours to warm up fully.

Responses to Heat Stress

It is usually easier for birds to stay warm in cold environments than it is for birds to cool down in hot ones. The high metabolisms of birds, combined with their heat-producing activities, render them vulnerable to heat stress, especially in hot, humid tropical climates. Catastrophic die-offs of thousands of birds accompany severe heat waves in Australia and are more likely as global climate change challenges the ability of birds to thermoregulate, with implications for community structure and species distributions (McKechnie and Wolf 2009; Smith et al. 2015a).

Birds reduce heat loads through avoidance behaviors; through controlled elevation of body temperature, called **hyperthermia**; and through active heat loss by means of evaporative cooling. Reduced activity at midday, seeking shade, bathing, and soaring in cooler air are simple ways to reduce heat loads. More cleverly, domestic pigeons can be trained to turn on cooling fans, especially when thirsty (Schmidt and Rautenberg 1975). Desert birds generally tend to have low metabolic rates and highly efficient evaporative cooling systems. Common Poorwills, for example, tolerate severe heat stress when baked by the desert sun by dissipating as much as five times their metabolic heat production.

Controlled hyperthermia has both advantages and risks. In heat-stressed birds, especially dehydrated ones, body temperatures may rise from 4°C to 6°C above normal, approaching the near-lethal threshold of 46°C. Such controlled hyperthermia reduces the rate of heat gain from the environment by bringing body temperature closer to air temperature. If body temperatures exceed air temperatures, the hyperthermic bird can lose heat without evaporative cooling and save water. The body temperatures of ostriches increase 4.2°C during the daily cycle, a response that saves liters of water per day that would otherwise be lost in evaporative cooling. Controlled hyperthermia during the warm daylight hours also allows for the storage of extra heat needed to save fuel at cooler nighttime temperatures, especially in large birds.

Birds actively lose heat by evaporative cooling and other means above the **upper critical temperature (UCT).** Evaporative cooling is a highly effective method of heat loss that can dissipate 100 to 200 percent of heat production. Evaporative water loss, however, is the major source of water loss to the environment; small birds lose five times as much water in this way compared with their loss of water in feces or urine (Williams and Tieleman 2000). Storks and New World vultures increase heat loss through evaporative cooling from the legs by defecating directly onto their own legs.

The body sizes of nonmigratory birds correspond to geographical gradients in temperature and humidity. Climatic rules, such as Bergmann’s Rule—the increase in body size with cooler temperatures—refer to these correlations in a simplistic way. Widespread North American birds, such as the American Robin and the Downy Woodpecker, tend to be smallest in hot, humid climates and largest in cold, dry climates (Figure 6–15). The potential for heat loss by evaporative cooling is lowest in hot, humid climates, which favor small birds with more heat-losing surface area relative to mass. Conversely, cool, dry air favors larger bodies with reduced surface areas that conserve heat (Box 6–2).

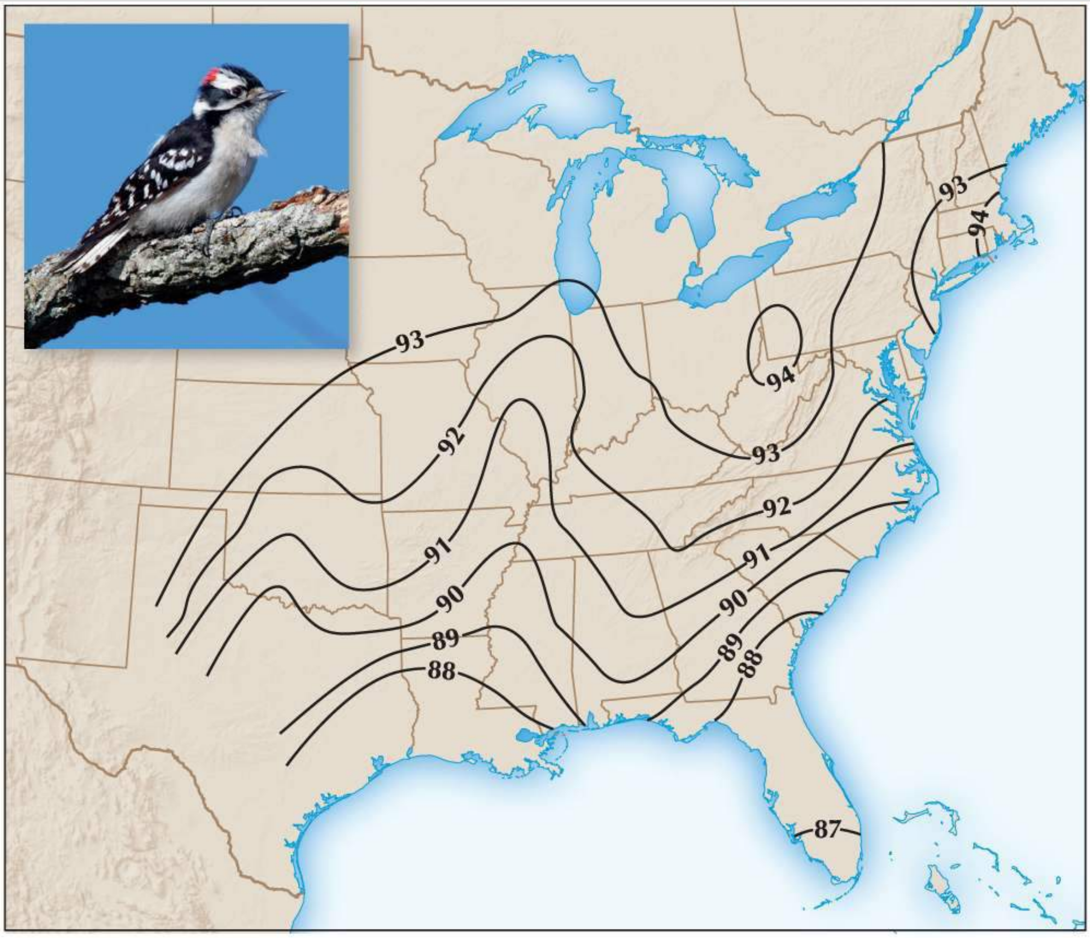

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Figure 6–15 Size variation in Downy Woodpeckers. Body size (which is directly proportional to wing length) increases to the north, but individual birds in the warm, humid Mississippi Valley and coastal areas are small compared with those at other localities at similar latitudes. Numbers indicate average wing lengths in millimeters.

Box 6–2

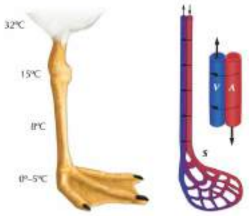
Selection for Larger House Sparrows

Geographical differences in body size as well as plumage color can evolve rapidly among populations—within 100 years for House Sparrows introduced to both North America and New Zealand (Lowther and Cink 1992). The body size of House Sparrows is positively correlated with seasonality and annual temperature range in both North America and Europe. Increased fasting ability appears to be the primary advantage of large size in seasonal environments. Conversely, small size minimizes individual maintenance costs in equable and more predictable or aseasonal environments.

Studies of the effects of severe winter weather have documented the survival advantages of larger House Sparrows. Large-sized males, in particular, survived best because they have superior thermoregulation efficiencies and fasting abilities—and greater access to well-protected roost sites (Buttemer 1992).

Metabolism increases above the UCT because of panting and other efforts that facilitate heat loss. In birds, as in dogs, panting increases evaporative cooling from the upper respiratory tract. Birds typically ventilate faster during heat stress, when body temperatures rise to 41°C to 44°C and above. To supplement panting when they are hot, some birds rapidly vibrate the hyoid muscles and bones in their throats. This action, called **gular fluttering,** increases the rate of evaporative water loss from the mouth lining and upper throat. Many seabirds, both adults and young, regulate body temperature by means of gular fluttering when baked by hot sun shining on their exposed nests. Desert species, including Common Poorwills, achieve more than half of their evaporative cooling in this way.

Evaporative water loss includes loss through the skin as well as in respiration. But birds do not have sweat glands. Instead, they evaporate water directly through the skin, a process called **cutaneous water loss**—a process that is especially well developed in some pigeons and doves and is more efficient than panting with respect to water loss (Gerson et al. 2014). In larks (Alaudidae), cutaneous water loss comprises from 50 to 70 percent of total evaporative water loss at moderate air temperatures.



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Data from Ricklefs 1990

Figure 6–16 Gulls regulate the rate of heat loss from their feet by varying the amount of blood shunted from the base of the leg, where the temperature is roughly 32°C, to veins at the base of the foot, where the temperature may be close to 0°C. They can decrease circulation through the foot, where the rate of heat loss is high, by opening a shunt (S) and constricting the blood vessels in the feet, thereby providing a more direct return of the blood. In addition, heat from outgoing arterial blood can be transferred directly to incoming venous blood. Arrows indicate the direction of arterial (A) and venous (V) blood flow and dashed arrows the direction of heat transfer.

When necessary, birds, especially large-footed waterbirds such as herons and gulls, can lose most of their metabolic heat through their legs and feet (Figure 6–16). Alternatively, when heat conservation is important, they control blood flow to reduce this loss by more than 90 percent. The control of heat loss from the feet is made possible by a network of special blood vessels in the avian leg that act to conserve or dissipate heat as needed. The arteries and veins intertwine at the base of the legs in such a way that heat carried by arterial blood from the body core can be transferred directly to blood returning in the veins. This so-called countercurrent exchange conserves body heat at low air temperatures. For cooling, the blood can completely bypass the network and go directly into the extremities. An overheated Southern Giant Petrel can increase by 20-fold the rate of blood flow through its feet.

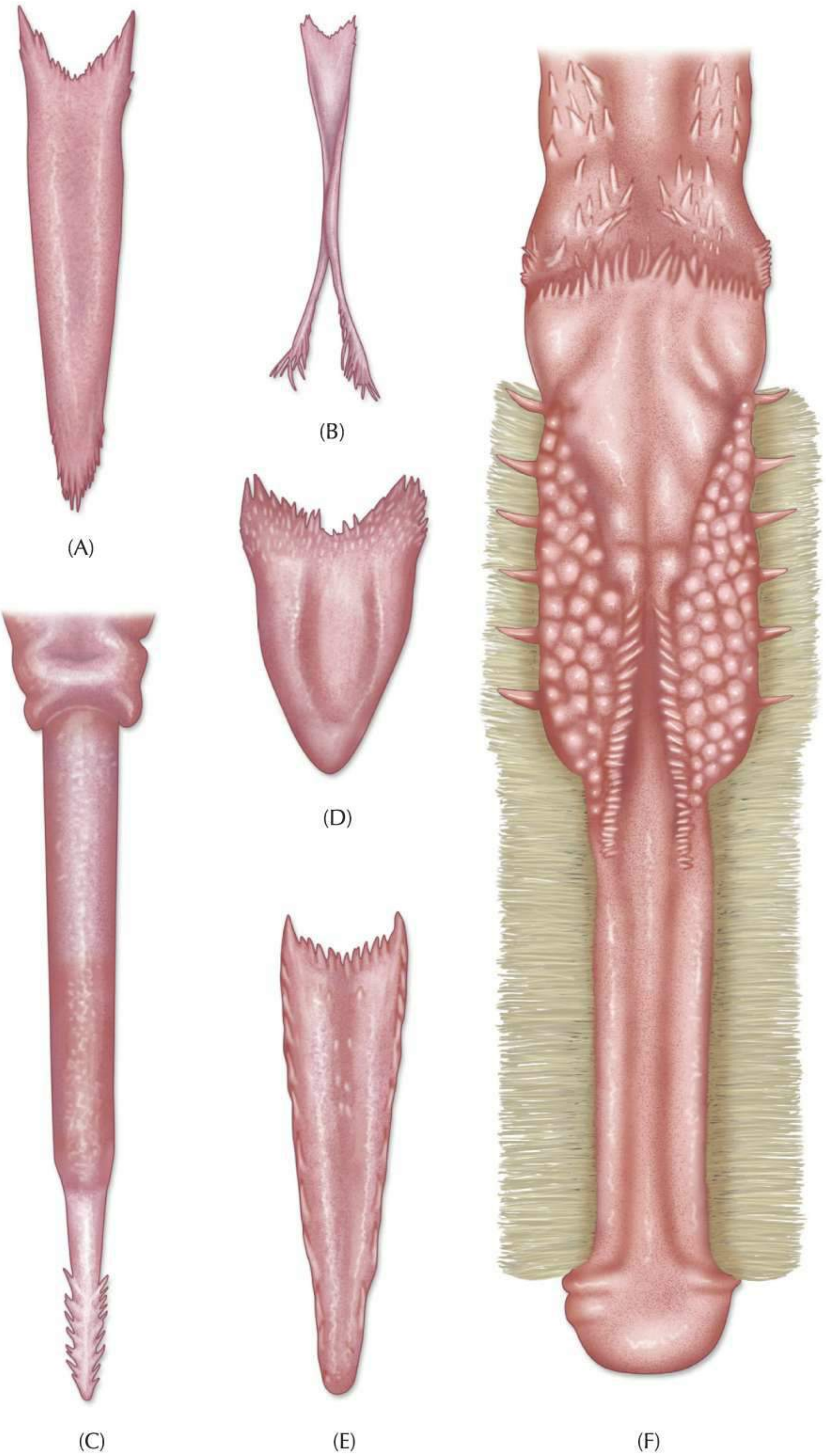
Blood vessels of the head also enable countercurrent heat exchange there. Most birds maintain the temperature of their brains about 1°C cooler than that of their bodies. Helmeted Guineafowl take this maintenance to an extreme. They have colorful, naked heads with large protrusions, or helmets, and wattles that enhance convective heat loss, as do the wattles of chickens and other fowl. Heat loss from these wattles may be so great that a guineafowl’s head cools faster than its body, beyond the ability of increased blood flow from the body core to replace lost heat (Crowe and Withers 1979). Unlike those of most birds, the brain temperatures of guineafowl vary as much as 6.5°C without serious consequence.

The heat produced during flight could cause lethal increases in body temperature. Common Pigeons, for example, produce seven times as much heat in flight as they do at rest, and their body temperatures quickly rise from 1°C to 2°C. Some birds apparently will not fly at temperatures above 35°C because of their inability to control hyperthermia. White-necked Ravens, for example, fly only short distances in the heat or fly in the cooler air at high altitudes (Hudson and Bernstein 1981).

Flight itself increases convective heat loss. The airstream compresses the plumage to the skin, and extension of the wings exposes the thinly feathered ventral base of the wing. As a result, the rate of heat loss by flying parakeets increases to 3.1 times the resting value at 20°C, and that of Laughing Gulls increases to 5.8 times the resting value.

6.6 Feeding and Digestion

Because birds burn energy at high rates, they must feed frequently to refuel themselves. Adaptations for feeding are a conspicuous feature of avian evolution (see Chapter 1). These adaptations include not only the ways in which birds move while feeding and capturing food but also many specializations of the entire digestive tract, starting with diverse tongue structures, which include the woodpecker’s spear tip, the hummingbird’s tube tip, and the duck’s fringed filter (Figure 6–17). Gizzards range from large, hard seed-crushing structures in fowl and finches to softer bags in fish-eating birds such as the Anhinga to miniscule pouches in the Hoatzin, which digests leaves in specialized cervical and thoracic crops. The digestive tract itself changes size and structure seasonally, especially in relation to migration (Karasov 1996; Box 10–3 in Chapter 10).



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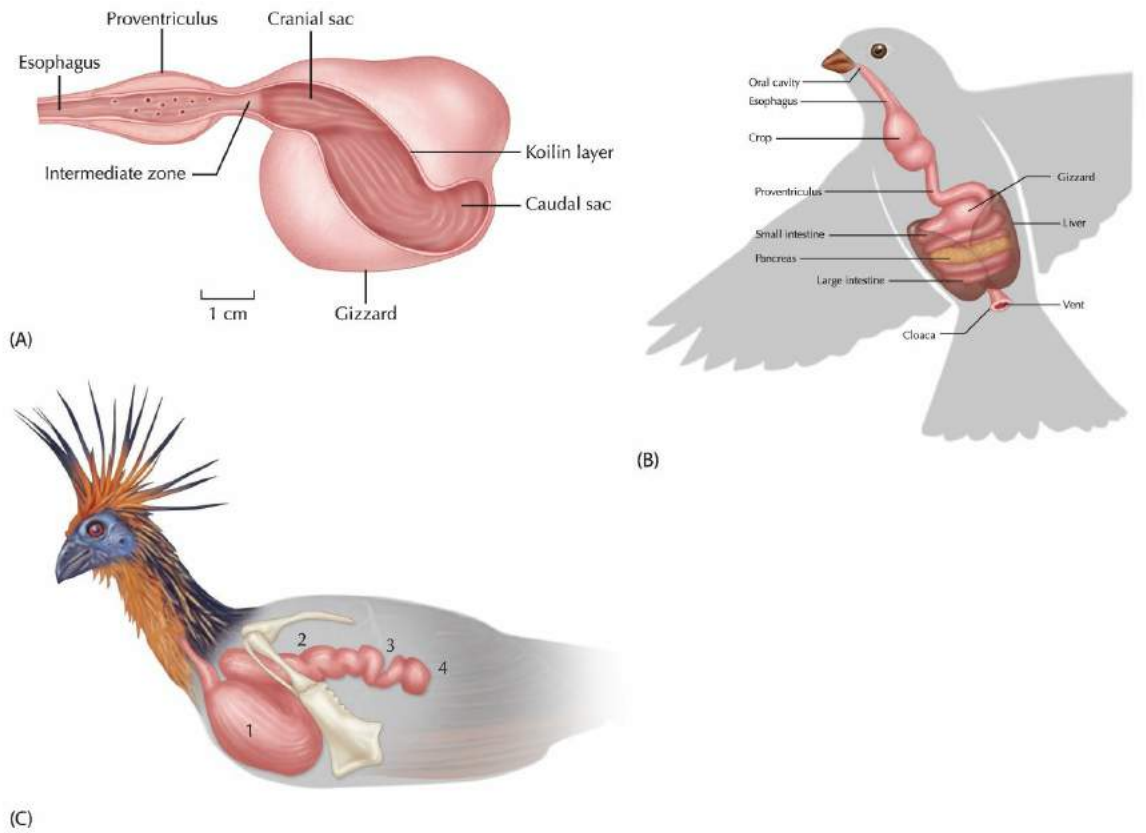
DATA FROM GARDNER 1925

Figure 6–17 Bird tongues (dorsal view): (A) generalized passerine tongue with terminal fringes (American Robin); (B) tubular, fringed nectar-feeding tongue (Bananaquit); (C) probing and spearing woodpecker tongue fitted with barbs (White-headed Woodpecker); (D) short, broad tongue of a fruit eater (Diard’s Trogon); (E) fish-eater tongue with rear-directed hooks that keep slippery fish from wriggling back to freedom (Sooty Shearwater); and (F) food-straining tongue (Northern Shoveler).

Several characters distinguish the digestive systems of birds from those of other vertebrates (Figure 6–18). The lack of teeth means that the bill and mouth function mainly in food getting. Food processing by the bill is limited to such activities as cracking and shucking seeds or tearing prey into bite-size pieces. Birds have little saliva and few taste buds compared with mammals, which chew and physically process food as the first step and then subject it to chemical processing as the second step. Birds reverse this sequence. They start chemical digestion in the **proventriculus,** a unique structure that handles food before it undergoes physical digestion in the gizzard. Some birds also regurgitate undigestible parts of their food—bones or seeds, for example—as pellets.



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(A) DATA FROM MCLELLAND 1975. (B) DATA FROM TYRRELL AND TYRRELL 1985. (C) DATA FROM GRAJAL 1995

Figure 6–18 Bird digestive tracts. (A) Stomach of a domestic chicken. (B) Digestive tract of a bunting. (C) Anterior gut of a Hoatzin, showing (1) large digestive crop, (2) posterior esophagus, (3) proventriculus, and (4) small gizzard. The keel of the sternum of the Hoatzin is reduced in size to make room for the large fermentation chambers, which makes it a very weak flyer.

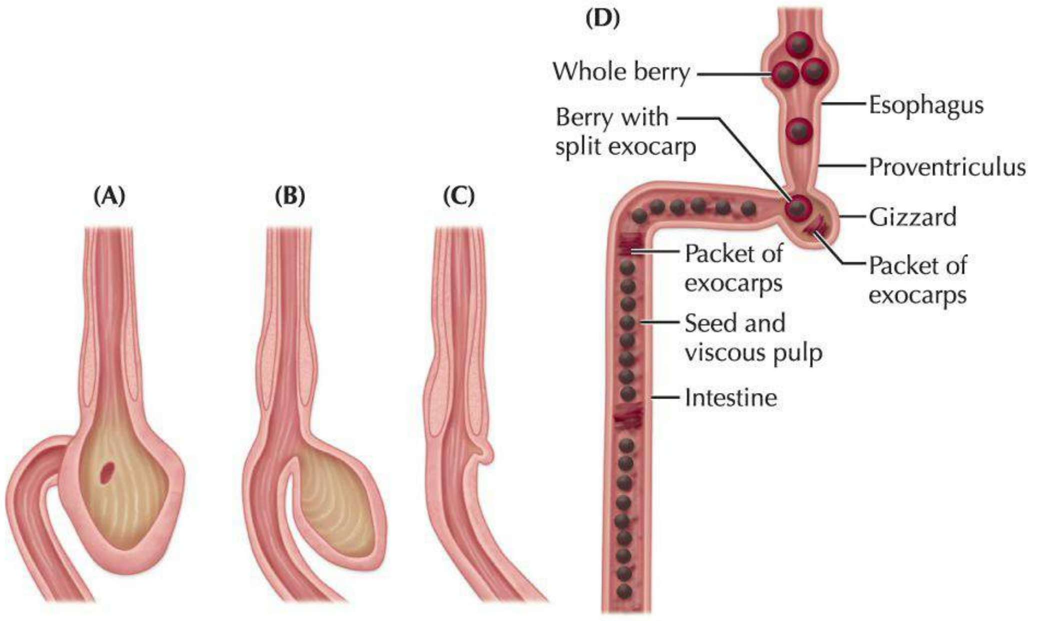
Food passes from the oral cavity to the stomach through the esophagus, a muscular structure lined with lubricating mucous glands. In birds that swallow large prey whole—fish-eating birds, for example—the esophagus expands as needed. No mere passageway, the esophagus is a versatile organ. The esophagus of pigeons produces nutritious fluid, called **pigeon milk,** for their young. The esophagus of pigeons and many other species can also be inflated for display and sound resonance. Some birds have crops, which vary in size and structure. The **crop**—an expanded esophageal section—stores and softens food and regulates its flow through the digestive tract. The chambers of the enlarged crop and esophagus of the Hoatzin, a leaf-eating bird of South America, have evolved into a multichambered, glandular stomach that ferments and digests tough leaves (Grajal 1995; Figure 6–18C).

Most birds have two-chambered stomachs composed of the anterior glandular proventriculus and the posterior muscular gizzard. Shapes and structures of the stomach differ more than any other internal organ, corresponding to the dietary habits of different species. The proventriculus, a structure not present in reptiles, is most developed in fish-eating birds and raptors. It secretes acidic gastric juices (pH 0.2–1.2) from its glandular walls, thereby creating a favorable chemical environment for digestion. Peptic enzymes in the proventriculus dissolve bones rapidly. The Bearded Vulture can digest a cow vertebra in two days. A shrike can digest a mouse in three hours. In addition to the usual functions, a petrel uses its well-developed proventriculus to store oil by-products of digestion, which it regurgitates as food for its young—and sometimes spews at predators and ornithologists.

The length of a bird’s intestinal tract averages 8.6 times its body length but varies from three times body length in the Common Swift to 20 times body length in the Common Ostrich. The intestine tends to be short in species that feed on fruit, meat, and insects and long in species that feed on seeds, plants, and fish.

Near the terminus of the digestive tract, small side sacs, called **ceca** (sing. cecum), are present in many birds. The ceca attach to the posterior end of the large intestine, may be paired or single, and vary from small or absent to prominent in fowl and ostriches. The avian cecum is a multipurpose, vitally important organ (Clench and Mathias 1995). Among their many functions, ceca aid digestion, especially of fibrous plant foods. Bacteria in the ceca further digest and ferment partly digested foods into usable compounds absorbed through the cecal walls. In addition, ceca produce antibodies that fight disease organisms, aid the absorption of water, and aid in the metabolism of uric acid into amino acids (Clench 1999).

Linked to the development of flight and high metabolic rates, the digestive systems of birds extract nutrients and energy with high efficiencies from small volumes of rapidly processed food (Place 1991). The passage time of food through the digestive tract—from the esophagus through the glandular stomach and gizzard into the intestine and finally out the cloaca as feces—varies from less than half an hour for fruit and berries ingested by thrushes and the Phainopepla (Figure 6–19) to half a day or more for less easily digested food.



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DATA FROM DESSELBERGER 1931, WALSBERG 1975

Figure 6–19 Specialized stomachs of fruit eaters: (A) unmodified gizzard of a primitive flowerpecker; (B) more specialized stomach of the Black-sided Flowerpecker, which allows fruit to bypass the gizzard and shunts insects into the gizzard for grinding; (C) rudimentary gizzard of the Violaceous Euphonia; and (D) gizzard of the Phainopepla, which can shuck the outer-layer skin (exocarp) from mistletoe berries and then defecate a pack of skins at intervals between the undigested parts of the berries.

Mammals typically absorb nutrients by active transport into cells that line the intestine. Most birds absorb glucose sugars and amino acids by active transport, but they take up other nutrients passively and nonspecifically into cells along with fluid uptake. The passive absorption of nutrients requires little energy and is directly responsive to concentration, allowing quick uptake of needed energy. But toxins in fruits and seeds also may be absorbed indiscriminately.

Parrots eat seeds and bitter green fruits that are full of toxins that would be distasteful and even lethal to other animals. Parrots of several species, large and small, also gather in large, colorful assemblages to eat dirt, long thought to be clay with minerals that serve as an antidote to toxins. Kaopectate, which consists partly of clay, soothes a person’s upset stomach in similar ways (Gilardi et al. 1999). The negatively charged sites of the clay minerals are hypothesized to bind to the positively charged toxin molecules in the acid environment of the stomach. Mammals, including hunter–gatherer humans, eat soil for this reason (Diamond 1999). However, there is no evidence in favor of this function in avian digestive systems. Alternatively, soil eating by birds may evolve in response to sodium limitation in birds with vegetation diets (Dudley et al. 2012).

The assimilation of digested food through the intestinal walls depends on the nature of the food ingested. Raptors assimilate 66 to 88 percent of the energy contained in ingested meat and fish. Herbivores assimilate as much as 60 to 70 percent of the energy contained in the young plants that they ingest but only 30 to 40 percent of the energy in ingested mature foliage. At the low end, Spruce Grouse assimilate only 30 percent of the energy contained in the spruce leaves that they eat (Boag and Schroeder 1992). Assimilation efficiencies and other digestive responses shift with seasonal changes in diet (Levey and Karasov 1989). For example, American Robins show improved assimilation efficiency of lipids coupled with their increased use of lipid-rich berries in the fall (Lepczyk et al. 2000).

Fruits provide “predigested” nutrients in the form of free amino acids rather than proteins and in the form of simple sugars instead of complex carbohydrates (Levey and Martinez del Rio 2001). This “predigestion” allows rapid processing—as little as 20 minutes to pass through the gut—and the ingestion of large quantities within short time spans. Fruits and fruit-eating birds come in two major categories: carbohydrate-rich and lipid-poor versus lipid-rich and carbohydrate-poor.

The digestion of lipids requires longer retention times in the gut than does the digestion of sugars; lipid digestion and sugar digestion also differ in the enzymes required. Corresponding to their digestive physiologies, some birds, such as North American thrushes, favor lipid-rich berries, whereas others, such as Cedar Waxwings, favor sugar-rich berries. The fast passage of berries through the gut means that lots of glucose is still in the semidigested fruit pulp just before evacuation. The Cedar Waxwing may be unique among birds in that it absorbs glucose in its rectum through active transport at the same high rate as it was previously absorbed in its intestines.

Like junk food, sugar-rich berries may require supplementary nutrition. Cedar Waxwings, therefore, eat the ripe fruits of *Viburnum opulus* only when protein-rich cottonwood (*Populus deltoides*) catkins are available as a supplementary food source (Witmer 2001). In the laboratory, waxwings lose weight when fed only fruit or only catkins. Together, however, they provide a balanced and healthy diet.

The nutrition requirements of chickens are known in detail (Klasing 1998). Less is known about the degree to which the diets and foraging behaviors of wild birds are directed specifically toward nutrition. Birds are usually assumed to passively obtain adequate nutrition to meet their energy needs in the course of their daily foraging and to rarely suffer malnutrition or nutritional stress. Among the known exceptions, the Willow Ptarmigan, an alpine grouse, prefers heather leaves that are rich in nitrogen and phosphorus (Moss et al. 1972). In the laboratory, White-crowned Sparrows are sensitive to concentrations of certain amino acids—namely, valine and lysine—in synthetic diets; they were adept at selecting diets that satisfied their amino acid requirements (Murphy and King 1989).

Many passerine songbirds cannot digest sucrose—a complex sugar that we humans take for granted—because these songbirds lack the enzyme sucrase, which breaks sucrose into smaller sugars—glucose and fructose—that are amenable to assimilation (Martinez del Rio and Stevens 1989). The ingestion of sucrose at high concentrations can cause sickness and diarrhea because of malabsorption. As a result, Common Starlings learn to shun sucrose in laboratory tests (Clark and Mason 1993).

In contrast, hummingbirds feed on sucrose-rich nectar. Hummingbirds assimilate from 95 to 99 percent of the energy in nectar, which consists primarily of sugars and water. Their intestines exhibit 10 times as much sucrase enzyme activity as is evident in passerine intestines (Schondube and Martinez del Rio 2004). They also quickly absorb glucose from their fluid meals at the highest levels known among vertebrates. They achieve this record by means of unusually high densities of sites that actively bind sugar and transport it across cell membranes (Karasov et al. 1986). They appear to function normally at the maximum levels and are unable to absorb sugars faster when stressed by cold temperatures or extreme activity (McWhorter and Martinez del Rio 2000).

Waxes, which consist of saturated, long-chain fatty acids, are among the least digestible of all foods. Several groups of birds, however, use wax as a source of metabolic energy. Seabirds, including petrels and auklets, metabolize the rich wax compounds in the marine crustaceans that they eat (Roby et al. 1986; Place 1991). Waxy foods, together with bile and pancreatic digestive juices, recycle several times from the small intestine back to the churning actions of the gizzard and proventriculus to break the complex fatty acids into smaller, usable elements.

Among the few land-bird species that eat wax are the Yellow-rumped Warblers and the Tree Swallows of North America. They consume large quantities of wax-coated bayberries. Both warblers and swallows are capable of high assimilation efficiencies (80 percent) of bayberry wax (Place and Stiles 1992). Their special gastrointestinal traits include elevated gallbladder and intestinal bile-salt concentrations, slow gastrointestinal transit of dietary lipids, and probably the return of the partly digested food to the gizzard from the small intestine. The ability to use an unusual food source such as bayberry wax allows these birds to occupy northern coastal regions during periods when insects are not available.

Honeyguides are well known for their ability to eat and assimilate pure wax, usually from the honeycombs of bees but occasionally from candles on the altars of Christian missions (Diamond and Place 1988).

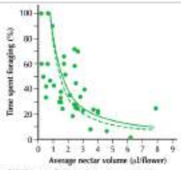
The Greater Honeyguide of Africa leads animals with a sweet tooth, such as the ratel (honey badger), as well as people, to beehives that it has found. First, the honeyguide solicits attention by approaching closely and giving distinctive churring calls. If it gets its helper’s attention, the honeyguide flies a short distance in the direction of the beehive, returning frequently to ensure progress. In this manner, the honeyguide leads its assistant a kilometer or more to the beehive, which it announces with a new set of excited vocalizations. The assistant then opens up the hive, takes the honey (which is prized by many African peoples), and leaves the wax and the bee larvae for the honeyguide.

6.7 Energy Balance and Reserves

Whether hungry or temporarily sated, all birds face the challenge of maintaining their energy balances. Energy balance is the dynamic relation between energy intake and energy expenditure. Ideally, intake and expenditure are roughly equal, so the bird neither gains nor loses much weight. Preceding migration or winter, however, a bird may eat more than it metabolizes each day so that the excess can be stored as fat reserves.

Foraging Time

The amount of time that a bird must feed each day depends on its total energy requirements and its achieved rate of energy intake. Roughly speaking, a bird's foraging time must double when its rate of net energy gain is reduced by half.



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Data from Gill and Wolf 1979

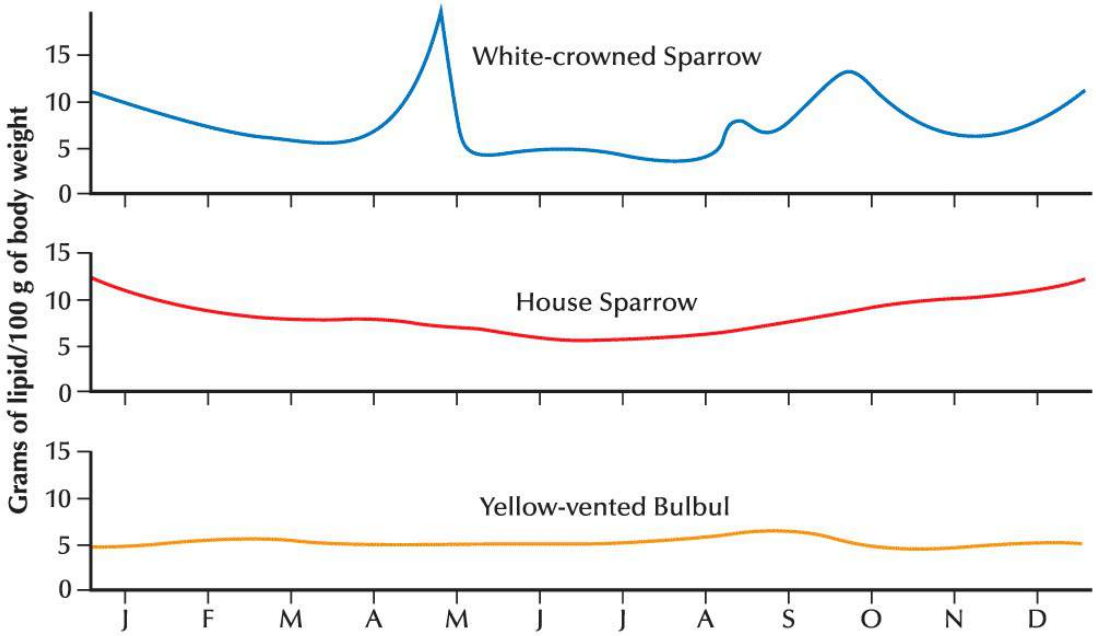
Figure 6–20 The amount of time spent feeding by a Golden-winged Sunbird depends on the average amount of nectar that it gets from a flower. The solid line is the predicted relation, assuming that the sunbird visits only as many flowers as it needs to replace total daily expenditures. The dashed line is fitted to the actual field measurements of foraging efforts.

Sunbirds' daily foraging times, for example, decline with an increase in floral nectar content (Figure 6–20). By providing supplemental food and water, Irene Tieleman and Joe Williams (2002) caused Greater Hoopoe-Larks in the Arabian desert to decrease their foraging time by 13 to 29 percent, resting instead and reducing exposure to the midday heat. Foraging times also vary with seasonal changes in food availability. Small titmice and goldcrests in England may forage 90 percent of the day in winter when food is scarce, their metabolism is high, and days are short (Gibb 1960). At the other end of the spectrum, tropical fruit-eating birds meet their needs in minimum time, less than 10 percent of daylight hours.

If a short foraging time is sufficient for self-maintenance, individual birds can afford to build up energy reserves or undertake energy-expensive activities, such as migration, molting, and breeding (Chapter 9). Low foraging times also allow birds more time to hide from predators, select favorable microclimates, establish dominance and property rights over other individual birds, court potential mates, and rear young. Birds routinely act to increase foraging efficiency and reduce required foraging time.

Fat Reserves and Fasting

Most birds maintain minimal fat (lipid) reserves. Excess mass increases flight costs and reduces agility and the odds of escaping predators. Small, temperate-zone passerines typically have fat reserves of no more than 10 percent of body mass to cover their fasting needs during midwinter. Yellow-vented Bulbuls in tropical Singapore maintain fat reserves of only 5 percent of body weight throughout the year, little more than is needed to survive overnight and to begin feeding the next morning (Figure 6–21).



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DATA FROM BLEM 2000

Figure 6–21 Annual cycles of fat deposition in a temperate-zone migrant (White-crowned Sparrow), a temperate-zone nonmigrant (House Sparrow), and a tropical nonmigrant (Yellow-vented Bulbul).

In general, large birds can store more fat and can fast longer than smaller birds can. At moderately low temperatures (1°C–9°C), a 10-gram warbler, for example, may not survive a day without food, whereas a 200-gram American Kestrel can survive for five days (Calder 1974). Male Emperor Penguins fast for 90 to 120 frigid days during their incubation vigils of the Antarctic winter and may lose 45 percent of their mass during this period (del Hoyo et al. 1992).

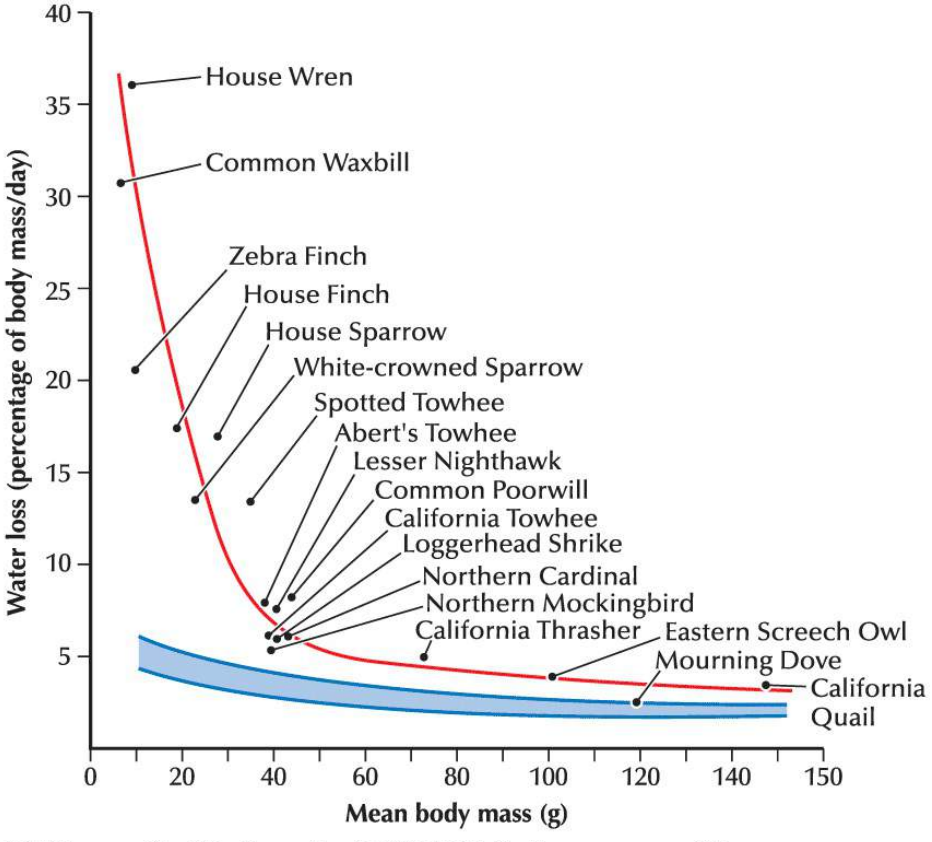
Hoarding food for future use is one way of preparing for food shortages (Källander and Smith 1990; Vander Wall 1990). Groups of Acorn Woodpeckers, for example, build large granaries of acorns for the winter (Figure 11–3 in Chapter 11). Meat eaters, such as hawks, owls, and shrikes, routinely set aside a fraction of their prey for future use. Shrikes impale prey on thorns for later consumption. Crested Tits of Europe obtain as much as 60 percent of their winter food from provisions amassed earlier in the year. These seed caches are more difficult to relocate than other stored foods, such as the acorn granaries of woodpeckers and the impaled prey of shrikes. The recovery of widely dispersed, concealed seed caches requires extraordinary spatial memory, which is processed by an enlarged hippocampal complex of the forebrain (Chapter 7).

6.8 Excretion and Water Economy

Balancing daily energy expenditures is one side of the physiological coin. The other side, water economy, is equally important, especially in arid environments. The potential for debilitating water loss is a corollary of the high body temperatures and activity levels of birds, especially during exposure to midday heat. Enhanced evaporative heat loss is essential to prevent heat stress during strenuous activity. For example, evaporative water loss in a desert sparrow—the California Towhee—quadruples when ambient temperature increases from 30°C to 40°C, whereas oxygen use only doubles (Bartholomew and Cade 1963). Water is used and replaced at high rates as a result of high evaporative water losses and the limited capacity of birds for concentrating electrolytes in the urine.

Birds replace lost water from several sources. Water present in food satisfies the fluid needs of many birds, particularly nectar-eating or fruit-eating birds and meat-eating raptors such as Sooty Falcons, which can nest in arid parts of the Sahara, where midday shade temperatures exceed 49°C. Likewise, insect-eating birds get most of the water that they need from the body fluids of consumed insects; unlike seed-eating birds, they rarely visit water holes. California Quail, a close relative of the aforementioned Gambel's Quail, and Rock Wrens obtain adequate water by supplementing their diets of seeds with insects.

Metabolic water is produced as a by-product of the oxidation of organic compounds containing hydrogen. Metabolic water supplements ingested water and, in some cases, is all that a bird needs. Because of their high metabolism, birds produce more metabolic water in relation to body size than do most vertebrates. The metabolism of one gram of fat yields 38.5 kilojoules of energy plus 1.07 grams of water. Metabolic water production increases directly with oxygen consumption and thus with increased metabolism at both colder and higher temperatures. Large birds can replace more of their evaporative water loss with metabolic water than can small birds (Figure 6–22). Certain exceptional seed-eating birds, such as Zebra Finches, can survive, drinking not a drop, on a diet of air-dried seeds containing less than 10 percent water; they supplement this with metabolic water.



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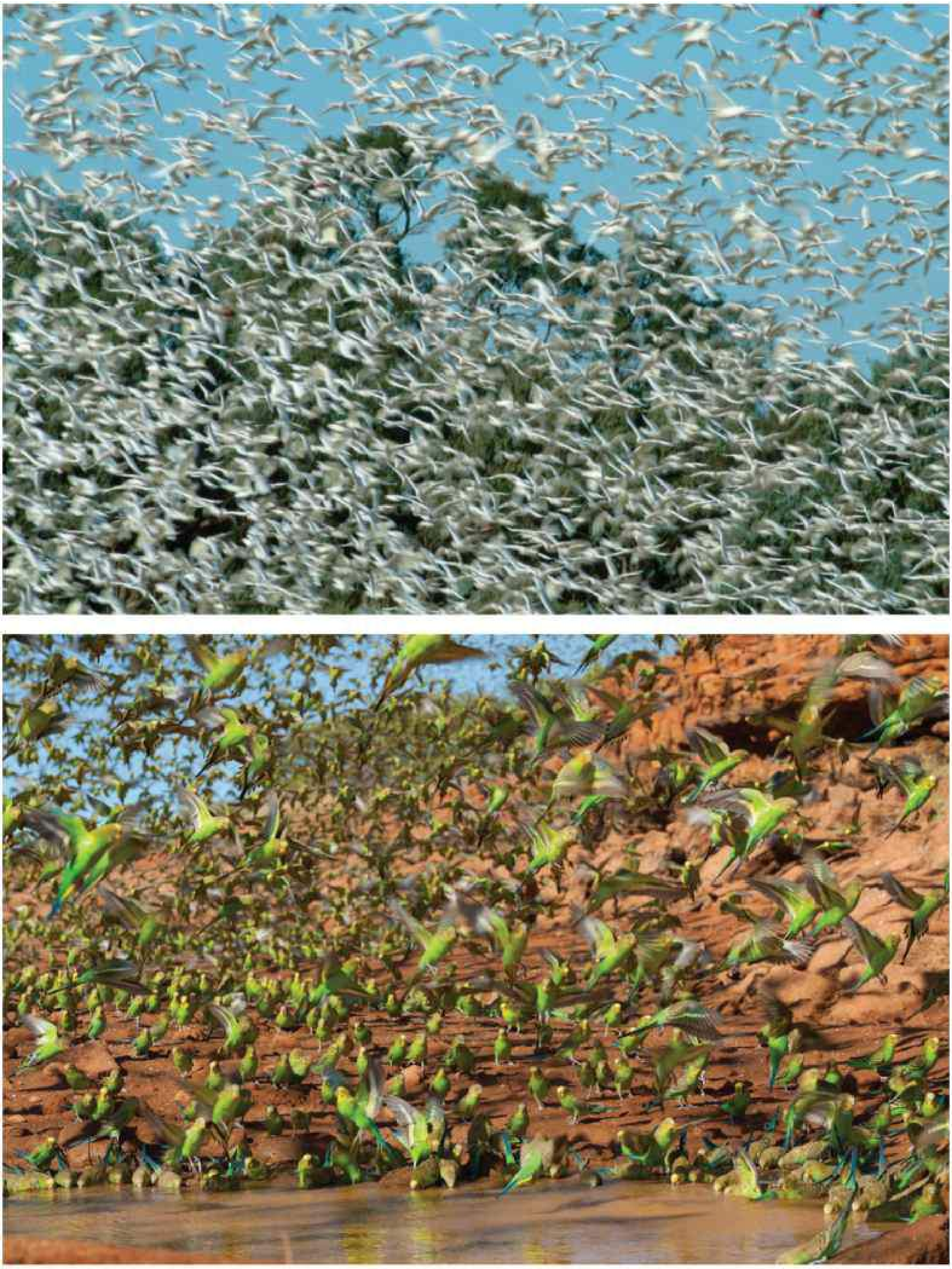
DATA FROM BARTHOLOMEW AND CADE 1963

Figure 6–22 Evaporative water loss (as percentage of body mass lost per day) at nonstressful ambient temperatures (near 25°C) decreases sharply with increasing size (and therefore reduced surface area relative to mass) of small birds. Metabolic water production, the projected range of which is indicated by the blue zone, partly offsets evaporative loss.

Water potentially lost in exhaled air may be conserved by countercurrent cooling in the nasal chambers and respiratory passages. This form of conservation is well established for mammals at low temperatures (Schmidt-Nielsen 1981). Studies of African larks, however, do not support the importance of this form of water conservation in desert birds (Tieleman et al. 1999).

Drinking free water from streams, water holes, dew, raindrops, and even snow is a casual, incidental activity in most mesic habitats—those having a moderate amount of moisture. In deserts, however, daily visits to isolated springs or water holes, where predators wait, may be necessary. Because their diets are limited to dry foods, seed-eating birds experience the greatest need for freestanding water and visit natural water sources in large numbers. Dean Fisher and his colleagues (1972) conducted dawn-to-dusk watches at water holes in the arid regions of western and central Australia. More than half of the 118 species of birds in the area appeared to be independent of surface water. Parrots, however, were not. Their visits to a water hole to drink correlated closely with maximum daily temperatures. Sometimes, they appeared in spectacular numbers (Figure 6–23). One day, during an unusually dry period, Fisher recorded 67,000 bird visits to one water hole.



TOP: ARCO IMAGES GMBH/ALAMY; BOTTOM: © ROLAND SEITRE/NATUREPL.COM

Figure 6–23 (*Top*) Huge flocks of Lesser Corellas, a kind of cockatoo, regularly visit water holes in arid Australia. (*Bottom*) Budgerigars at a water hole.

Excretory Systems

The excretion of water and nitrogenous wastes by birds takes place in the kidneys and the intestines and, in some species, by the action of salt-secreting glands. Avian kidneys—flat structures sited against the fused vertebrae on the dorsal wall of the abdominal cavity—differ in structure and function from those of reptiles or mammals. Urine produced by the kidneys mixes with fecal components in the lower intestine, where additional water can be resorbed as needed.

The most conspicuous physiological adaptation for promoting water economy in birds is the excretion of nitrogenous wastes in the form of uric acid—white crystals that give bird droppings their usual color. This ability is in accord with the reptilian ancestry of birds: uric acid excretion evolved early in the history of archosaur reptiles. The turnover of proteins in the maintenance of body structures produces nitrogenous products that would become toxic if allowed to accumulate. The excretion of nitrogen as urea in aqueous solution, as done by mammals, requires flushing by large quantities of water. Uric acid can be excreted, instead, as a semisolid suspension in which each molecule of uric acid contains twice as much nitrogen as a molecule of urea does. Therefore, birds require from only 0.5 to 1.0 milliliter of water to excrete 370 milliliters of nitrogen as uric acid, whereas mammals require 20 milliliters of water to excrete the same amount of nitrogen as urea. Birds can concentrate uric acid in the cloaca, just before defecation, to amazing levels—as much as 3,000 times the acid level in their blood. Kangaroo rats, among the most efficient mammalian water conservationists, can concentrate urea to levels from only 20 to 30 times those in the blood.

Hummingbirds face a different problem: too much water (Beuchat et al. 1990). Among the many physiological records held by hummingbirds is their claim to the highest rates of water flux of any endothermic vertebrate. Their use of nectar as a primary energy source is the reason for this achievement. To get the energy from the sugars in nectar, a hummingbird must also consume substantial volumes of liquid. When daily energy demands are high, the Anna’s Hummingbird consumes and excretes liquid about 3.3 times its body mass. Most of this water passes through the body at rates that exceed the highest known urine production by freshwater amphibians. A hummingbird’s kidneys are not specialized for unusual levels of water processing; they are essentially the same as a reptile’s kidney (Figure 6–24). Rather, hummingbirds lay claim to the highest rates of evaporative water loss among birds. In addition, as already mentioned, their digestive systems selectively absorb sugar and allow much of the ingested water to pass through rapidly without absorption and processing through the kidneys.

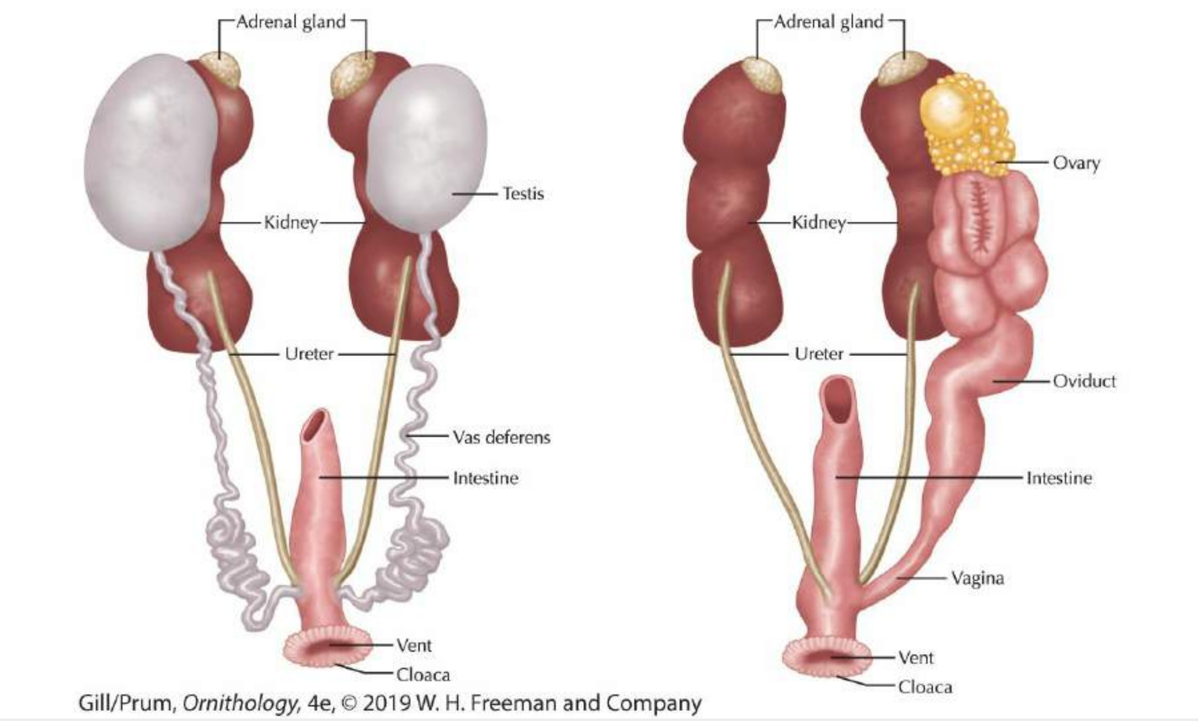


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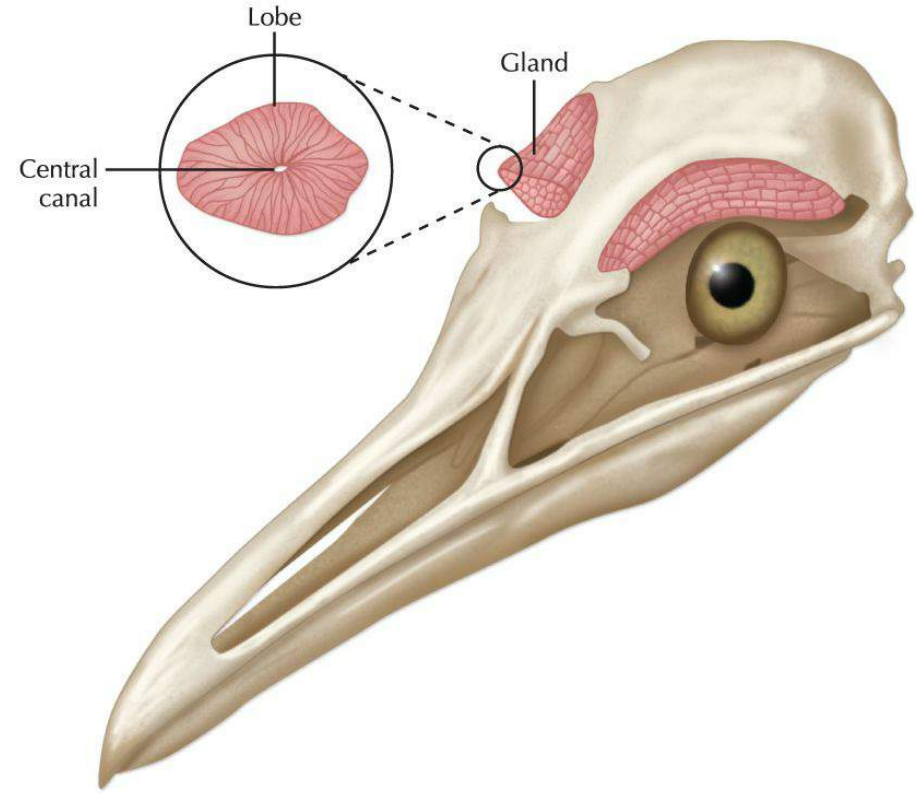
Figure 6–24 Avian urogenital systems. (*Left*) Testes and the vas deferens of the male. (*Right*) Ovary, oviduct, and vagina of the female.

Although avian kidneys can concentrate nitrogenous wastes, they usually cannot concentrate salt or electrolytes much above normal blood levels. Mammalian kidneys, especially those of the kangaroo rat, excel at concentrating salts and electrolytes because of their long loops of Henle—structures that help regulate salt levels and, when necessary, retain water. In contrast, the loops of Henle in the avian kidney are short. This anatomical shortcoming presents a problem, particularly for oceanic birds that drink seawater, which is about 3 percent salt. The body fluids of birds are 1 percent salt. The high salt content of their marine foods further increases their need to excrete electrolytes. For this reason, seabirds, as well as other birds with water-conservation problems, rely on extrarenal structures called **nasal salt glands** (Figure 6–25).



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DATA FROM SCHMIDT-NIELSEN 1983

Figure 6–25 The salt glands of some marine birds are located on top of the head in shallow depressions above each eye.

Salt glands are widespread among birds subject to salty diets. Large, conspicuous structures located in special depressions in the skull just above the eyes, salt glands enable seabirds to drink seawater and to unload the newly ingested salt rapidly through concentrated salt solutions. For example, if a gull drank one-tenth of its body weight in seawater, it would excrete 90 percent of the new salt load within three hours (Schmidt-Nielsen 1983). These amazing glands produce and excrete salt solutions that are as much as 5 percent salt, more concentrated than seawater.

Salt glands are special infoldings of the cellular lining of the nares.

Inside the salt gland are many secretory tubules arranged in lobes. The tubules extract salt from blood in the capillaries of the ophthalmic arteries (which also service the eyes). The tubules then empty directly into a central canal leading to the main duct. Each of the pairs of glands has a main duct that leads to the anterior nasal cavity. The salt concentrate runs out of the nostril and down grooves to the bill tip before dripping off. Some birds, such as storm petrels, eject the fluid forcibly. The activity of the salt gland is stimulated directly by the intake of salt or, sometimes, just by an overload of salt in the blood. These energy-demanding, active-transport processes in the salt gland may increase the resting metabolic rate by as much as 7 percent (Peaker and Linzell 1975).

Salt glands are largest and best developed in oceanic birds, such as albatrosses, which must drink seawater. The size of the gland depends on the number of lobes in it and varies among bird species. Auks and gulls have particularly large glands, with as many as 20 lobes. When individual birds, such as Mallards, drink salt water instead of freshwater, their salt glands increase in size accordingly. Surprisingly, no passerines have salt glands, not even those that live in salt marshes or feed on intertidal invertebrates on the seacoast.

REVIEW KEY CONCEPTS

6.1 The High Body Temperature of Birds

Birds maintain the highest body temperatures and metabolic rates (relative to mass) among endothermic vertebrates. Doing so is energetically expensive; birds consume from 20 to 30 times more energy than do similar-sized reptiles.

Key Terms: physiology, homeostasis, endothermy

6.2 The Respiratory System

Continuous, unidirectional airflow through the avian lung transfers more oxygen and carbon dioxide more efficiently with each breath. A unique system of thin air sacs functions in the unique avian breathing mechanism and helps to remove the body heat produced during flight.

Key Terms: air sacs, nares, operculum, concha/conchae, rete mirabile

6.3 The Circulatory System

Birds have a double circulatory system and a four-chambered heart, as do mammals. But the high-performance, larger avian heart moves blood more efficiently at higher pressures than do the hearts of mammals of corresponding body sizes.

Key Term: cardiac output

6.4 Metabolism

Birds have basal metabolic rates (BMRs) that are higher than those of most vertebrates. Birds in flight sustain high levels of aerobic metabolism 10 to 25 times their BMRs compared to five to six times BMR by small mammals.

Key Terms: metabolic rate, basal metabolic rate (BMR), basal metabolism

6.5 Temperature Regulation

Birds maintain their body temperatures at 40°C to 42°C with little latitude for higher body temperatures: 46°C is lethal. Regulation takes place by adjusting plumage insulation, by increasing heat production through shivering when cold, and by evaporative water loss through panting and gular fluttering when hot. Some birds—notably hummingbirds, swifts, and nightjars—can lower body temperature and become torpid to save energy or elevate body temperature a few degrees to reduce evaporative water loss.

Key Terms: thermoneutral zone, lower critical temperature (LCT), microclimates, facultative hypothermia, torpor, hyperthermia, upper critical temperature (UCT), gular fluttering, cutaneous water loss

6.6 Feeding and Digestion

The digestive tracts of birds are specialized for particular diets that change seasonally. Corresponding assimilation efficiencies range from less than 30 percent for spruce leaves by Spruce Grouse to 99 percent for sugars from nectar for hummingbirds. Some birds digest waxes, particularly the honeyguides of Africa and seabirds, but most birds cannot.

Key Terms: proventriculus, pigeon milk, crop, cecum/ceca

6.7 Energy Balance and Reserves

Birds adjust their foraging efforts in relation to food availability. They build up reserves or cache foods for use when food is scarce or energy expenditures are exceptionally high. Most birds maintain minimal fat (lipid) reserves, as excess mass increases flight costs and reduces agility.

6.8 Excretion and Water Economy

The excretion of nitrogenous wastes as uric acid rather than as urea promotes water economy in birds. Seabirds have well-developed salt glands that void concentrated salt solutions. These glands enable the birds to drink seawater and to eat prey having high salt content.

Key Terms: metabolic water, nasal salt glands

APPLY YOUR KNOWLEDGE

1. What are the advantages and disadvantages of the high body temperatures of birds?
2. Compare the mechanism of breathing and airflow in the respiratory systems of birds and mammals.
3. Describe the unique similarities in structure shared by the hearts of birds and mammals. Explain how bird hearts outperform the hearts of mammals.
4. What is the thermal neutral zone? How do birds survive outside their thermal neutral zones during exposure to ambient temperatures that would lead to hypothermia and hyperthermia?

5. Describe the relationships between temperature, metabolic rate, and oxygen consumption.
6. How do the following organs help to conserve water? (a) digestive tract, (b) salt gland, (c) air sacs.

PART III *Behavior*


Red-winged Blackbird [Ian Plant/Solent News/REX/Shutterstock]

CHAPTER 7 *Senses, Brains, and Intelligence*

STEVE BOER/SHUTTERSTOCK.COM

Crows and their relatives are among the most intelligent birds. They excel at tests of understanding of object permanence, delayed reward, memory, planning for the future, reasoning by exclusion of alternatives, awareness of the own body, and awareness of the mental states of others.

> If men had wings and bore black feathers, few of them would be clever enough to be crows. [Reverend Henry Ward Beecher, mid-1800s, in Savage 1995, p. 1]

Ornithologists once assumed that birds perceive the world in the same way as people do. They don’t. Their daily sensory experience is substantially different and extends beyond that of humans. Their highly developed color vision reaches extensively into the near-ultraviolet range of the spectrum. Birds use magnetic and celestial compasses to migrate (Chapter 10). They are also sensitive to minuscule shifts in gravity and barometric pressure.

Birds have well-developed brains and are more intelligent than most mammals. Tools, behavioral innovation, and culture are all features of the life of birds. Substantial learning by birds guides the mastery of complex motor tasks, social behavior, and vocalizations. Advanced spatial memory guides to food storage as well as the recovery of hidden food. Studies of the avian brain have helped to understand how the central nervous system controls complex behavior and how neural connections restructure themselves.

The sensory world of birds is the initial focus of this chapter, followed by the major features of the avian brain and the scope of avian cognition and intelligence. Advanced behaviors illustrate the abilities of birds to solve, sometimes creatively, the daily and seasonal challenges of gathering food by using their cognitive skills. The concluding sections of this chapter feature the intelligence feats of crows, jays, and their relatives, which challenge those of primates.

7.1 Vision

Vision is light perception. Light comprises the visibly sensible portion of the spectrum of electromagnetic radiation. The visible spectrum of humans includes wavelengths between 400 and 700 nanometers, corresponding to different colors. Birds, however, have much broader visual sensitivity into the near **ultraviolet,** down to around 325 nanometers.

Birds are extremely visual animals. They use their large eyes to search for food and to detect predators at great distances. They also engage in complex, colorful courtship displays, amplified by an exceptional system of color vision. Songbirds and raptors, believed to have the keenest sight of all birds, can resolve details at two-and-a-half to three times the distance that humans can. The American Kestrel, for example, can spot a two-millimeter insect from the top of an 18-meter-high tree (Fox et al. 1976). Wide-angle vision combined with double centers of high resolution in the retina enable some species to capture a whole scene at a glance rather than piecing it together as we do. The visual field of the American Woodcock is one extreme of this ability. With eyes located at the midpoint of its head, the American Woodcock can monitor 360 degrees laterally and 180 degrees vertically (Waldvogel 1990).

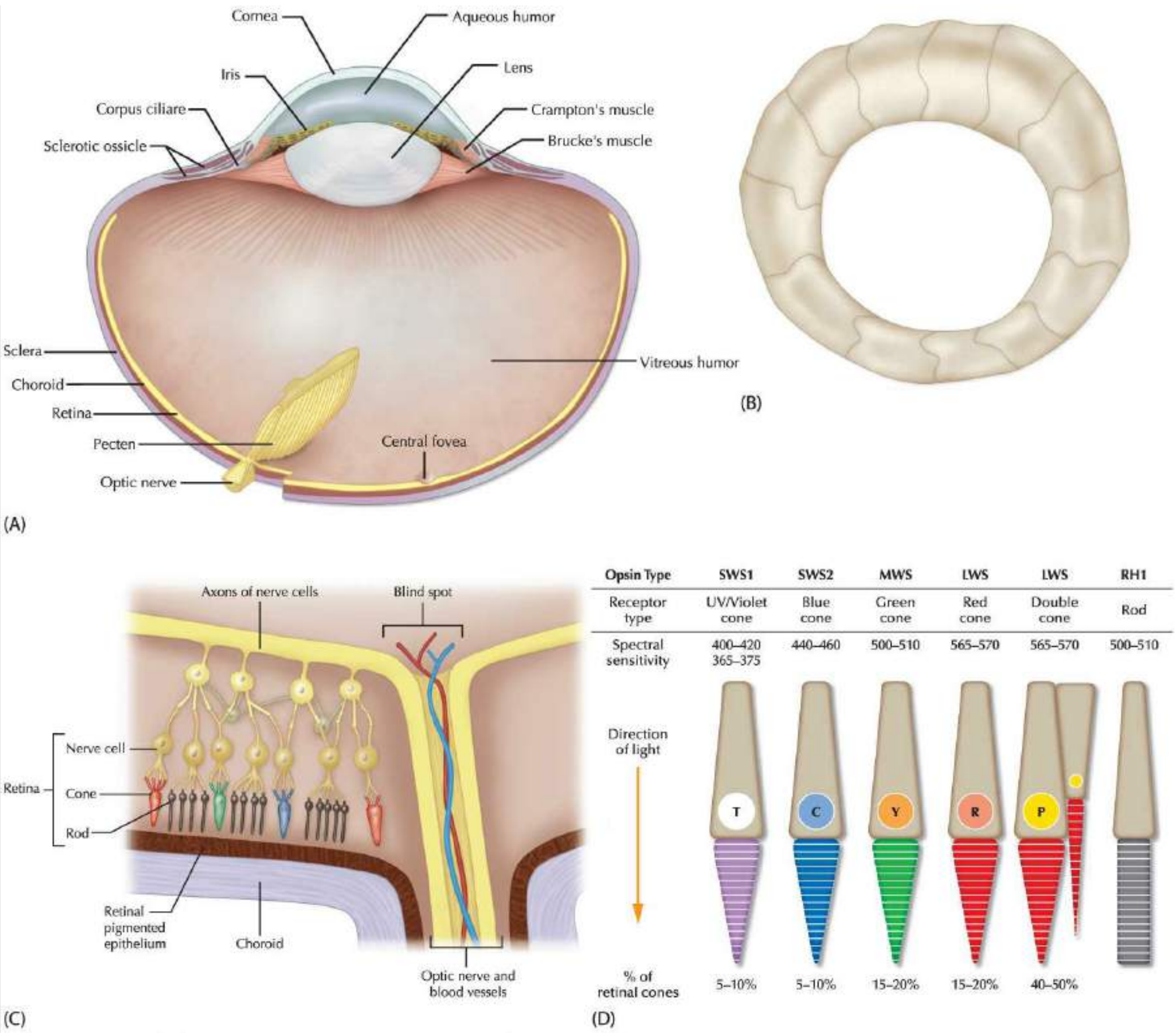
Avian eyes are large, prominent structures. The eyes of eagles and owls are as big as human eyes. The eye of an ostrich is the largest of any land vertebrate (Martin and Katzir 1995). Because birds' eyes are generally set on the sides of their heads, birds see better to the side than to the front. Penguins and passerines, for example, examine nearby objects with one eye at a time. The resulting image is relatively flat because monocular vision does not achieve depth perception with the same accuracy as binocular vision does. Thus, most birds need to use information from within the visual field to estimate the size of objects and their distance from the observer. To compensate, some view an object with one eye from two different angles in rapid succession. Pigeons often bob their heads as they walk to maintain a constant fixed visual perspective between bobs. Pigeons walking on a treadmill at a constant speed do not bob their heads because the visual scene is stationary (Frost 1978).

Some birds, such as swallows, nightjars, hawks, and owls, restrict lateral monocular vision to close objects and use forward binocular vision for distant viewing. Generally, binocular vision is atypical. Among ducks, only the Blue Duck of New Zealand can stare forward; other ducks use one eye at a time. Bitterns stare forward with binocular vision while pointing their bills skyward. Quite the opposite are woodcocks, already mentioned. Their huge eyes are set far back on the head, allowing binocular vision in a narrow range of angles both in front of and behind the head.

Like all other reptiles, birds have three eyelids. Along with the upper and lower eyelids shared with mammals, reptiles have a **nictitating membrane**—a thin, usually transparent membrane that moves horizontally across the surface of the eye from front to back, brushing off and moistening the cornea with each blink. The nictitating membrane also serves as a pair of goggles for diving birds, complete with a transparent central lens to help see underwater. Among the few exceptions, owls have thick, opaque nictitating membranes that protect their eyes, and Eurasian Magpies flash a white membrane with bright orange spots when they blink slowly, as in courtship or aggression.

Eye Anatomy

A cross section of the avian eye reveals a small anterior component that houses the **cornea** and **lens** and a larger posterior component that is the main body of the eye (Figure 7–1A). The two sections are separated by a sclerotic ring composed of 12 to 15 small bones, called scleral ossicles. Two striated muscles—Crampton’s muscle and Brucke’s muscle—originate on these bones and insert on the cornea and lens, respectively, and are responsible for focusing on objects. The avian lens is large and conspicuous. The pecten, a distinctive and intriguing feature of the avian eye, projects from the rear surface of the eye near the optic nerve into the large cavity filled with vitreous humor—the clear substance that fills the eye behind the lens.



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(A, C) DATA FROM EVANS 1996. (D) DATA FROM BOWMAKER 2008

Figure 7–1 (A) Cross section of the avian eye. (B) The muscles that focus the lens originate on the scleral ossicles, a ring of tiny bones inside the eye below the iris. (C) The retina is organized with the light-sensitive rods and cones facing away from the path of light so that light is transmitted through the nervous tissue of the retina before being perceived. (D) Avian photoreceptor diversity. Birds have four color cone types, a double cone, and a rod. Light passes through the entire retina and the cone cell oil droplets (circles) before reaching the folded membrane of the cone outer segments (horizontal lines). The cone oil droplets (circles) have high-pass, carotenoid pigment filters that vary with cone type: T = transparent, or no pigment; C = clear, an ultraviolet-absorbing carotenoid; Y = yellow; R = red. The double cone has a pale yellow (P) carotenoid filter. Rods lack oil droplets entirely.

Cornea and Lens

In birds, both the cornea and the lens change their curvature to focus light on the light-sensitive cells of the **retina** at the back of the eye; only the lens does so in mammals. Contraction of Crampton's muscle increases the corneal curvature and thus the cornea's refractive power. Because the cornea bends light very differently in air and in water, aquatic birds need eyes with an exceptionally broad range of focus. Diving birds, such as cormorants, have strongly developed Brucke's muscles to produce large changes in the shape of the soft, flexible lens. As a result, diving birds have a focusing range of 50 diopters, nearly 10 times greater than humans. Plunge divers, such as kingfishers, can even keep a target fish in focus as they dive.

The **pupil** opening is round in all birds except the gull-like skimmers. The skimmer pupil constricts into a catlike, vertical slit to protect the retina from bright (polarized) light; it expands to form a rounded shape in dim light (Zusi and Bridge 1981).

The **iris** is the thin layer of tissue that controls that size and shape of the pupil. Iris colors of birds vary from the common deep brown to bright red, white or bright yellow, green (cormorants), or pale blue (gannets) and may aid species recognition. The diversity of avian iris colors is produced by carotenoid, purine, and pterine pigments as well as structural colors produced by crystal-containing iridophore cells (reviewed in McGraw 2006).

At night, some birds' eyes shine bright red, yellow, or white in the beam of a flashlight or automobile headlights. The "eyeshine" of nightjars is a structural color produced by light scattering from an array of lipid spheres in the last layer of the retina—the retinal pigmented epithelium, which is called a **tapetum lucidum** (Nicol and Arnott 1974). Unlike in mammals, the tapetum lucidum of nightjars is not a permanent tissue but a physiological state of the dark-adapted retinal pigmented epithelium in which the melanosomes are pulled back and the lipid spheres move forward. The function of the tapetum lucidum is to reflect light that has been transmitted through the retina back into the retina, where it may be sensed, thus helping birds to see better at night. Kiwis, thick-knees, the Boat-billed Heron, the flightless Kakapo, many nightjars, owls, oilbirds, and other night birds all produce nocturnal eyeshine indicative of a tapeta lucidum, but the anatomy and physiology of their light scattering structures have not been described.

Retina and Fovea

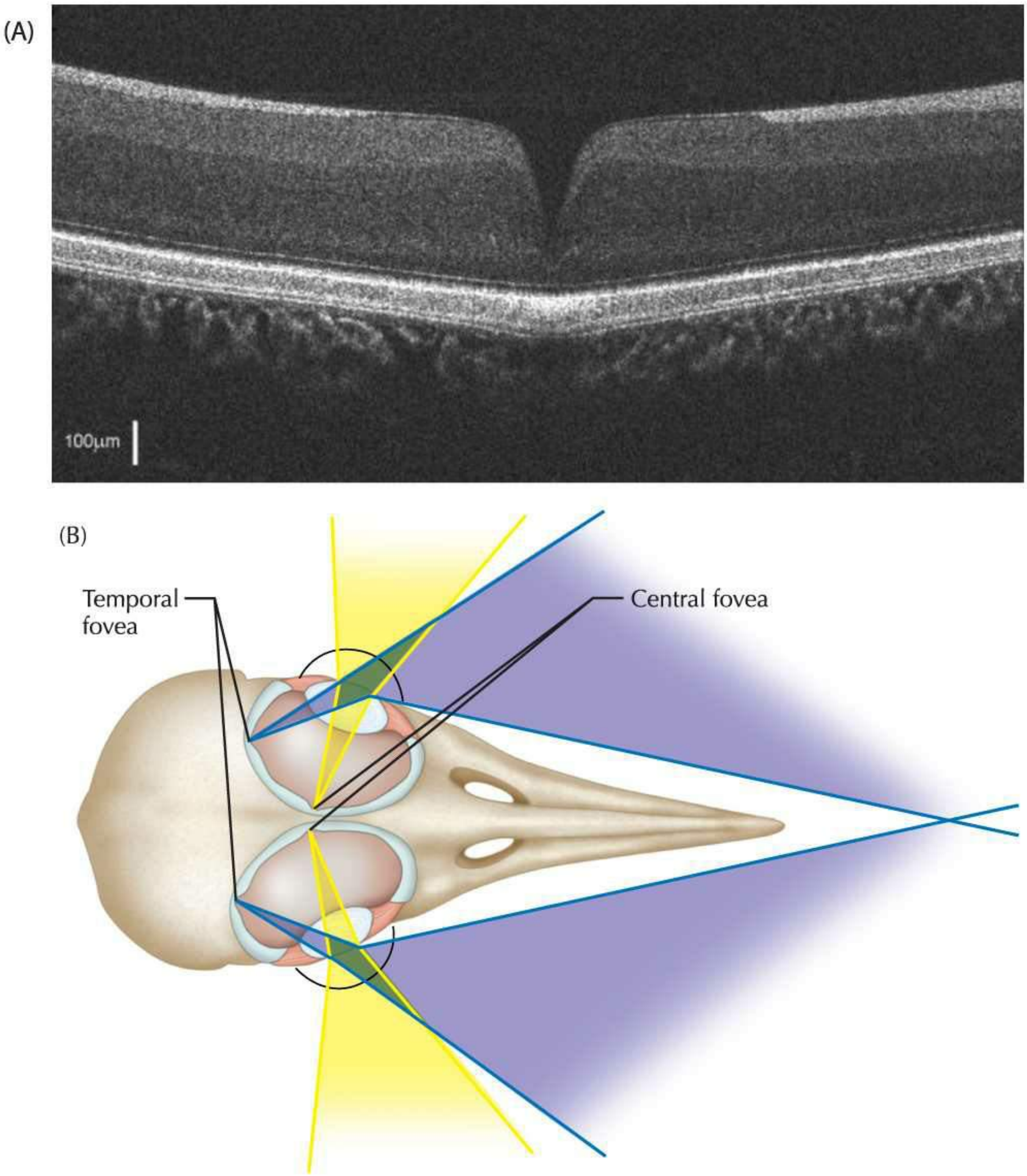
The anatomical organization of retinas in vertebrates is “backwards” with the light receptors pointing away from the iris, beneath layers of visual signal processing neurons and the arteries and veins that supply nutrients and oxygen to the retina (Figure 7–1B). As a result, all vertebrate eyes have a blind spot where the **optic nerve** and retinal blood supply exit the eye orbit. This inferior design is a result of a historical, developmental constraint. The first, primitive light receptors that evolved in early chordates did not function as image-forming eyes, so it did not matter whether the first light receptive cells were covered by other neural tissue. As the vertebrate eye evolved, however, it was not possible to change the initial anatomical arrangement. As we will see, birds have evolved a new structure—the pecten—to partially accommodate for this problem by eliminating retinal blood vessels.

Birds have three general types of light receptor cells (Figure 7–1C). **Rods** are highly sensitive receptors that are used for vision under dark conditions. **Cones** are used for color vision (see below). **Double cones** are an enigmatic light receptor that make up 40 to 50 percent of all retinal receptors and have been hypothesized to provide brightness information (Jones and Osorio 2005).

The high density of light receptors in the avian retina suggests excellent vision. The large number of cones enables birds to form sharp images no matter where light strikes their retina. The number of cones can be as high as 400,000 per square millimeter in House Sparrows and 1 million per square millimeter in the Common Buzzard. In comparison, the human eye has at most 200,000 cones per square millimeter (Walls 1942). Away from the densest concentrations at the foveae, cone concentrations in the human retina drop sharply to only one-tenth of those of birds.

Foveae (sing. fovea) are concave depressions of high cone density (Figure 7–2A), and they are known to be the sites of greatest visual sharpness in humans. Like mammals including humans, most birds have one fovea in each eye located in the center of the retina near the optic nerve. This central fovea images the portions of the visual field on either side of the bird. The central fovea is deeper and more complex in its cellular structure in visually acute passerines, woodpeckers, and raptors than it is in pigeons and domestic chickens.

Some fast-flying birds and aerial or diving predators, including hawks, eagles, terns, hummingbirds, kingfishers, and swallows, have a second temporal fovea (Figure 7–2B). These birds all have forward-directed eyes with good binocular vision. The temporal foveae are positioned to resolve areas of binocular vision. Whether deep foveae enhance avian visual acuity is not yet clear. They may, however, aid in the detection of the movements of small objects.



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(A) Republished with permission of Association for Research in Vision and Ophthalmology, from Ruggeri, Marco et al. “Retinal Structure of Birds of Prey Revealed by Ultra-High Resolution Spectral-Domain Optical Coherence Tomography.” *Investigative Ophthalmology & Visual Science* 51 (11) (2010): 5789–5795. Figure 2. Permission conveyed through Copyright Clearance Center, Inc. (B) Data from Wilson 1980

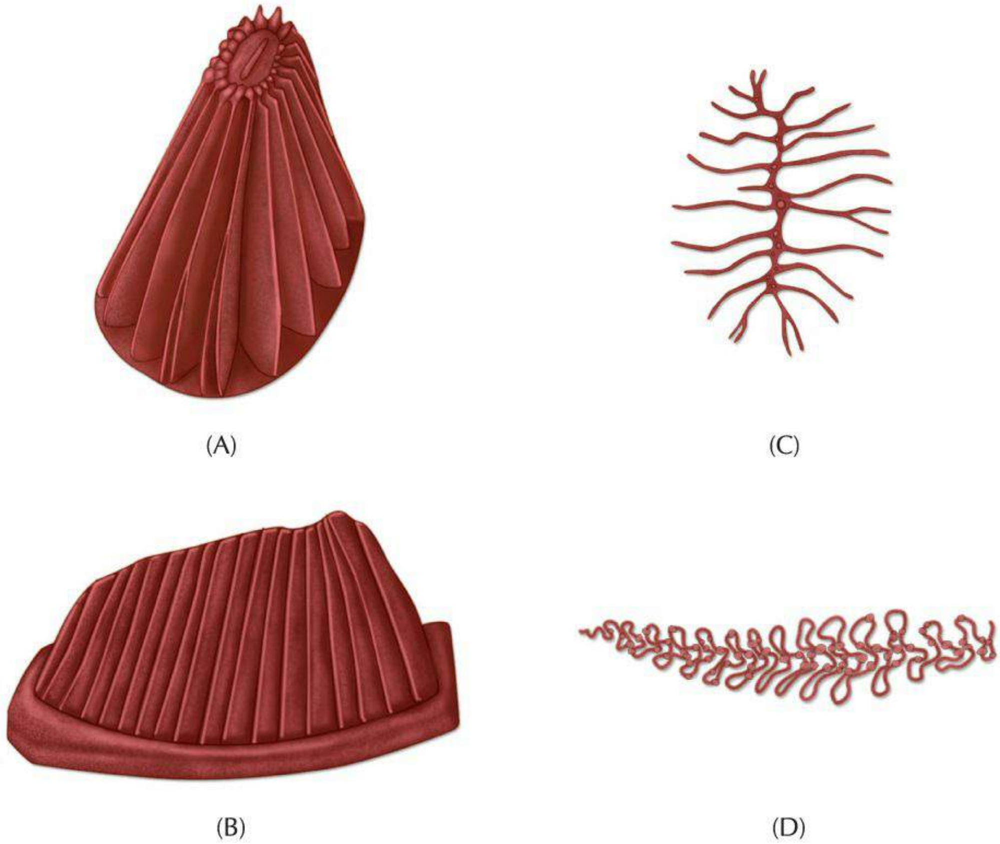
Figure 7–2 (A) Cross section of a Broad-winged Hawk retina showing the visual-cell layer with rods and cones and the deep central fovea. (B) Some birds, such as terns and raptors, have temporal foveae, which enhance forward binocular vision.

Although cones are most abundant in the foveae, high cone densities are also found in horizontal, ribbonlike strips around the retina in albatrosses, grebes, plovers, and other birds. These ribbons apparently increase a bird's ability to perceive the horizon and work in concert with the semicircular canals of the inner ear to achieve proper body orientation.

The complex avian retinal structure confers a high sensitivity to motion and the ability to detect both rapidly moving objects and slowly moving ones (Waldvogel 1990). The human eye cannot resolve movements faster than 60 cycles per second, or 60 hertz, a measure of what is termed flicker-fusion frequency. Birds have higher thresholds of more than 100 hertz. Thus, the 60-hertz oscillation of light in a fluorescent lightbulb appears as a steady light to the human eye but as a series of individual flashes to a bird. The visual motion sensitivity of birds serves them well in all aspects of flight, in prey and predator detection, and in potentially seeing navigation stars actually move through their arcs in the night sky.

The Pecten

The **pecten,** a remarkable feature of the avian eye, is a large, black-pigmented, pleated, and vascularized structure attached to the retina near the optic nerve (see Figure 7–1A). Protruding conspicuously into the vitreous humor and, in some birds, almost touching the lens, the large, elaborate avian pecten is unique among vertebrates. The avian pecten evolved from the smaller conus papillaris of other reptiles. In most birds, the pecten has 20 or more accordion-pleated fins (Figure 7–3). Nocturnal birds have fewer folds. The pectens of owls, nightjars, and the Kakapo have only four to eight folds, and the simple pectens of kiwis have no folds at all—probably representative of an evolutionarily degenerate condition (Sillman 1973).



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DATA FROM WALLS 1942

Figure 7–3 Structure of the pecten of (A) an ostrich and (B) most modern birds. (C) Basal cross section of the structure of part A, including central web and lateral vanes. (D) Dorsal view of the typical pleated structure of avian pectens. The pecten functions as an oxygen and nutrient radiator for the retina.

The avian pecten has fascinated scientists for centuries. At least 30 theories have been proposed to explain its existence. However, the pecten is now known to serve as a source of nutrition and oxygen for the retina (Güntürkün 2000). Like a radiator, the capillary beds of the pecten provide oxygen and nutrients to the retina by diffusion into the vitreous humor. Birds increase diffusion from the pecten by rapidly rotating their eyes by about 10 degrees every 0.5 to 45 seconds (Pettigrew et al. 1990).

Because of the reverse structure of the vertebrate retina, the density of retinal light receptors in most vertebrates, including humans, is highly constrained. Increasing the density of receptor cells would require a greater blood supply, which would require increasing retinal blood vessels, further interfering with visual resolution. However, the evolution of an elaborate pecten and associated eye movements has allowed birds to increase the density of light receptors in the retina while entirely eliminating retinal vasculature. This evolutionary innovation has greatly advanced the visual acuity of birds.

Color Vision

Light perception involves neurons that use visual pigments to absorb light and produce nerve signals. In the rods and cones of the retina, a single molecule of the visual pigment **retinal**—a vitamin A–like molecule that is made by cleaving a dietary carotenoid—is located in the center of a coiled, 7-transmembrane protein, called an **opsin protein** (Figure 7–4). When a retinal pigment absorbs a photon of the appropriate wavelength, it changes shape. The differences in the shapes of their outer segments give the rod and cone cells their names. Enough of these changes will initiate a cascade of molecular events in the receptor cell and produce a nervous impulse. These opsin-retinal complexes are located within the folded membrane of the outer segments of the rod and cone cells.

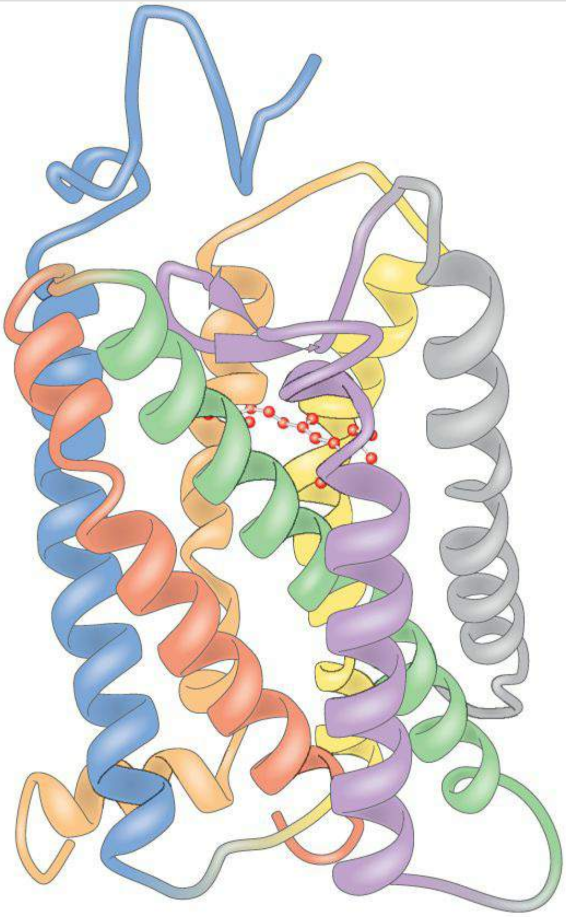

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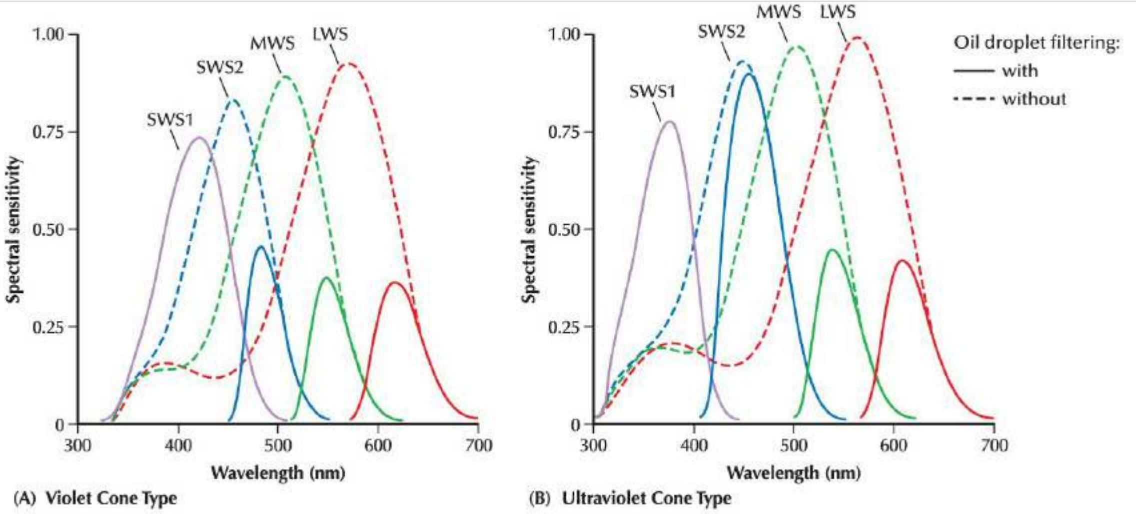
Figure 7–4 The seven coiled helices of the opsin photoreceptor protein hold a single molecule of retinal pigment (red) in its center. The protein sits across the folded membranes of the outer segments the visual receptor cells (see Figure 7–1D). When the retinal molecule absorbs a photon of the appropriate wavelength, the molecule changes shape, contributing to a nervous impulse by the photoreceptor cell. Variations in the specific amino acids that hold on to the retinal molecule within the opsin produce differences in the wavelengths absorbed by the pigment in different photoreceptor cells.

The amino acid sequence of the opsin proteins that hold on to the retinal pigment influences the absorption spectra of the pigment. Avian rod opsins have peak absorption between 500 and 509 nanometers. Birds have four types of color cones, each of which has a different opsin that is tuned to absorb a different portion of the visible spectrum. The four avian cone types are the red (long-wavelength sensitive [LWS]), the green (middle-wavelength sensitive [MWS]), the blue (short-wavelength sensitive [SWS2]), and the ultraviolet or violet cone type (ultraviolet/violet sensitive [SWS1]).

The four-color visual system of birds originally evolved through gene duplication and differentiation from a single, ancestral opsin gene in the common ancestor of bony fishes, amphibians, reptiles, and mammals (Bowmaker 2008). However, most mammals do not see in color because the green (MWS) and blue (SWS2) opsins were lost in the ancestor of placental mammals during a long period of nocturnality in the Mesozoic era. Humans have a simpler, “retrofit” version of color vision because the red opsin gene was duplicated on the X chromosome in the ancestor of Old World monkeys and apes, and the new gene copy diverged in sensitivity to become a new green-sensitive opsin. At the same time, the ultraviolet (SWS1) cone opsin evolved to be sensitive to longer blue wavelengths. As a result, humans have three color cones—red, green, and blue—but in comparison to birds, our color vision is relatively limited both in breadth of sensitivity and in the ability to differentiate colors.

The cones of birds also contain **oil droplets** with carotenoid pigments that filter the incoming light and refine the spectral sensitivities of each cone beyond the variation provided by differences in opsin structure alone (Figure 7–5; see also Figure 7–1C). The carotenoid molecules of the red, green, and blue cones are tuned specifically to match their spectral sensitivities. In contrast, the ultraviolet/violet cone lacks any carotenoid pigment and retains its broad sensitivity into the near ultraviolet.



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Data from Toomey et al. 2016

Figure 7–5 Oil droplet filters refine the spectral sensitivities of the (A) violet-type and (B) ultraviolet-type avian visual systems. The dotted lines depict the absorbance spectra of the opsin molecules within each cone type. The solid lines depict the sensitivity of each type of cone cell after filtration of the incoming light by carotenoid pigments in the cone cell oil droplet (see Figure 7–1D). The SWS1 cone type has no carotenoid filter, so its sensitivity is not changed.

In summary, birds have a greater power to discriminate small differences in color than do humans. However, this discrimination ability comes at a cost of sensitivity under low illumination because the oil droplet carotenoids do absorb light (see Figure 7–5).

Avian Color Space

The variation in spectral sensitivities of the four color cone types in the avian retina produces the information that the bird uses to sense variation in color in its visual environment (see Figure 7–5).

Specifically, the perception of color is a result of differences in the relative stimulation of different color cone types. Red, green, and blue color perceptions result from stimulation of only the red, green, or blue cone types, respectively. The perception of yellow or turquoise colors results from the simultaneous stimulation of red and green cone types or green and blue cone types respectively. Interestingly, purple is a nonspectral color that is the result of simultaneous stimulation of red and blue cone types.

Because humans have only three types of color cones, we are all color blind in comparison to birds. The ultraviolet sensitivity of birds provides them with more than merely expanded spectral sensitivity. It provides them with an entirely new dimension of color discrimination. Psychologists describe the diversity of human color perception using a flat, two-dimensional color area (Figure 7–6A). Because birds have four well-differentiated and integrated color cone types, we need to describe avian color perception using a three-dimensional **tetrahedral color space** (Goldsmith 1990; Stoddard and Prum 2008; Figure 7–6B). In this color space, the origin located at the center of the tetrahedron is a white or gray color. Any avian perceivable color can be described as a point in the color space; the **hue** is described by the angle from the center, and the saturation, or **chroma** (the difference from achromatic white or gray) is described by the distance from the origin.

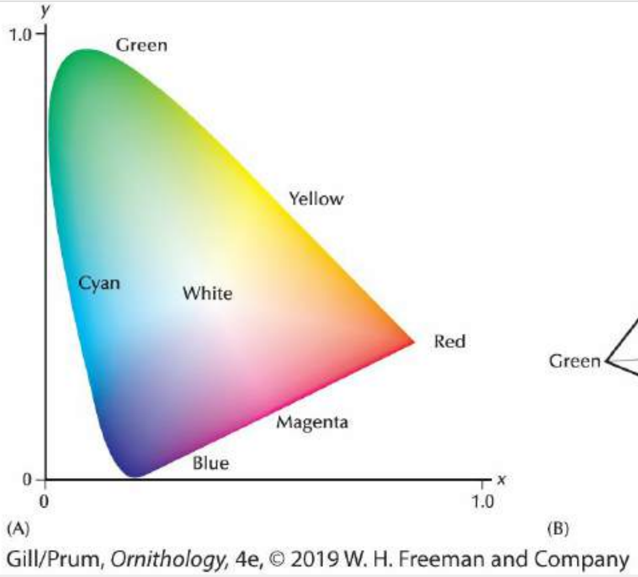
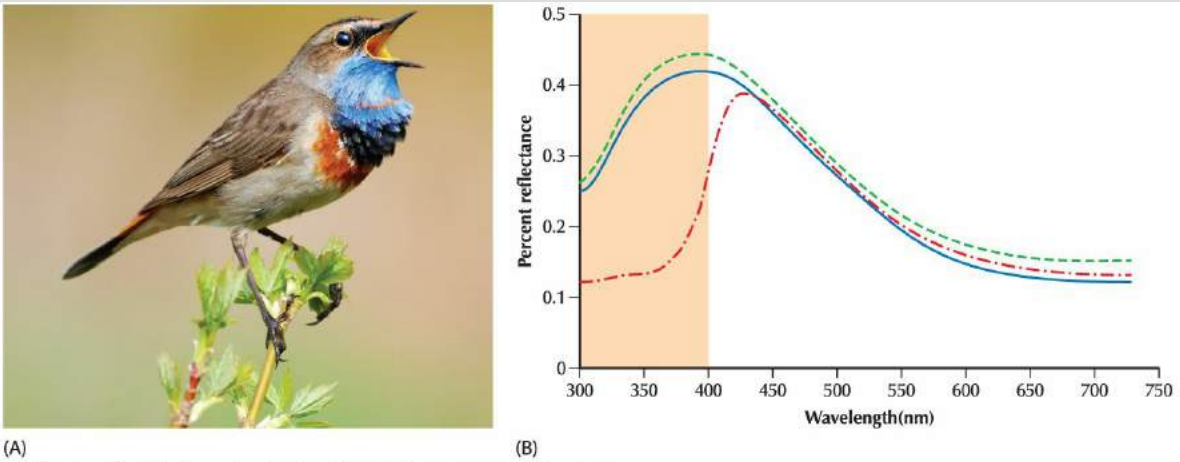


Figure 7–6 Comparison of trichromatic human and tetrachromatic avian color spaces. (A) The standard CIE color space for humans is a two-dimensional surface with white at its center. (B) The tetrachromatic color vision of birds requires a three-dimensional tetrahedral color space with the white, or achromatic, point at the center of the tetrahedron. Points in color space are determined by the relative stimulation of the four color cone types. Each color stimulus is a color vector described by its hue—the angle from the center, θ and ϕ—and its saturation—the distance from the center, *r*. The vertical axis of the tetrahedron defines a whole dimension of colors that are both unperceivable and unimaginable to humans, including ultraviolet, ultraviolet-yellow, and ultraviolet green.

The tetrahedral avian color space allows us to better understand the perception of colors that we cannot see. In addition to pure ultraviolet colors that we are entirely blind to, birds are sensitive to a whole dimension of mixed colors that we cannot imagine, such as ultraviolet-green and ultraviolet-yellow, which are as different from green and yellow as purple is from red (see Figure 7–6B). Although they are unimaginable to us, many birds use these colors in their plumages. For example, the vividly green back of the Painted Bunting has a substantial ultraviolet component and would be perceived very differently by birds and humans (Stoddard and Prum 2008).

Not only can birds perceive ultraviolet colors, but they actually make social and sexual decisions based on their perceptions of ultraviolet signals. For example, the Bluethroat is a small Eurasian thrush with a throat patch of a vivid ultraviolet-blue (Figure 7–7). Male Bluethroats with throats treated with sunblock—an ultraviolet-absorbing pigment—had lower success attracting mates than did control males (Johnsen et al. 1998).



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(A) AlekseyKarpenko/Shutterstock.com. (B) Data from Johnsen et al. 1998

Figure 7–7 Experimental evidence of the function of ultraviolet signaling in wild birds. (A) Male Bluethroat. (B) Reflectance spectra of the male blue throat patches without treatment (dashed green line), after treatment with baby oil (solid blue line), and after treatment with sunblock, an ultraviolet-absorbing pigment (dashed red line). Males that were treated with sunblock had lower success in attracting mates.

Differences in ultraviolet intensity also influence other social and ecological choices. Common Starlings preferentially feed those nestlings having ultraviolet-reflective skin (Jourdie et al. 2004). A thrush, the Redwing of Europe, prefers *Viburnum* berries that reflect ultraviolet light to those that do not (Siitari et al. 1999). Common Kestrels use ultraviolet light to find concentrations of a favorite prey—voles, which (unwittingly) illuminate their meadow trails with urine and feces that shine in the ultraviolet (Viitala et al. 1995).

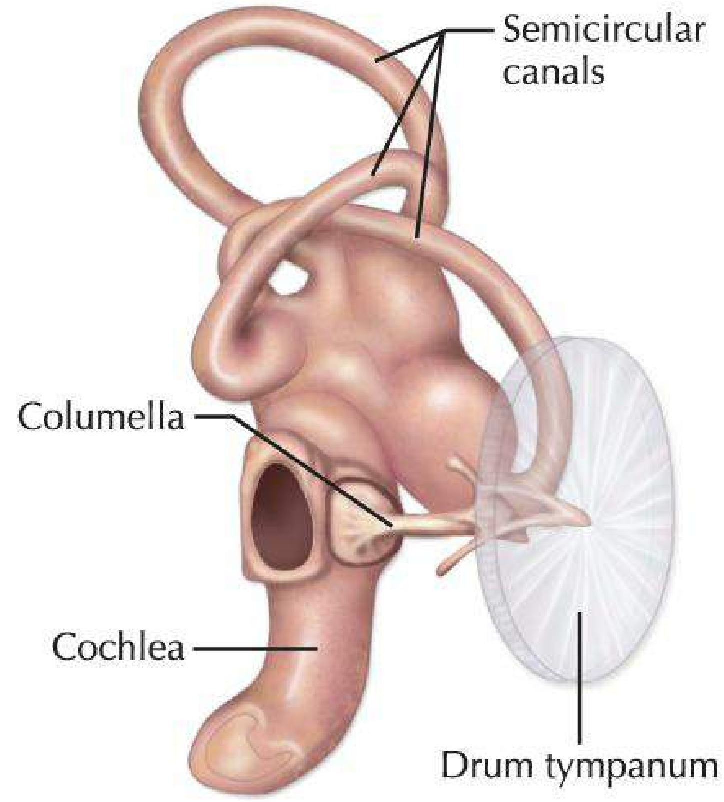
7.2 Hearing

Sounds provide birds with essential information. From territorial defense and mate choice to navigation, birds depend on their hearing for a wide range of activities.

Ear Structure

The three sections of the avian ear are the external ear, the middle ear, and the inner ear. The external ears of birds are inconspicuous structures located behind and slightly below the eye. They lack the elaborate pinnae, or projecting parts, of mammalian ears. Specialized “auricular” feathers on the external ear protect the hearing organs from air turbulence during flight while permitting sound waves to pass inside. Diving birds, such as auks and penguins, have strong, protective feathers covering the external ear openings. These birds protect their middle and inner ears from pressure damage in deep water by closing the enlarged rear rim of the external ear. The entire muscular rim to which the auricular feathers are attached forms an enlarged though inconspicuous ear funnel in some birds, especially passerines, parrots, and raptors. The superb hearing of nocturnal owls is related to their exceptional ear funnels. Large anterior and posterior ear flaps regulate the size of the ear opening and enhance acoustical acuity more than fivefold (Schwartzkopff 1973). In many owls, the external ears and, in some cases, the skull are bilaterally asymmetrical, a condition that aids in the precise location of prey.

In contrast with the three bones in the middle ear of a mammal, the



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DATA FROM PUMPHREY 1961

Figure 7–8 The ear of a chicken. A single bone—the columella, or stapes—transmits sound vibrations from the eardrum, or tympanum, to the fluid-filled cochlea of the inner ear. The three semicircular canals, which are the organs of equilibrium, are located on the top of the inner ear.

middle ear of a bird has only one bone—the **columella,** or stapes—which connects the **eardrum,** or tympanic membrane, to the pressure-sensitive fluid system of the inner ear (Figure 7–8). Located next to the attachment of the columella to the bony cochlea is the flexible round window, which protects the inner ear from pressure damage. The shape of the columella varies with taxon, but most birds have a simple columella similar to that of reptiles (Feduccia 1977).

The external and middle ears funnel sound waves from the environment into the **cochlea**—the fluid-filled, coiled section of the inner ear that is the base of the hearing organ. **Hair cells** in the cochlea are ciliated sensory cells that monitor vibrations transmitted by the fluid and encode them into a temporal sequence of nerve impulses that register in the acoustical centers of the brain.

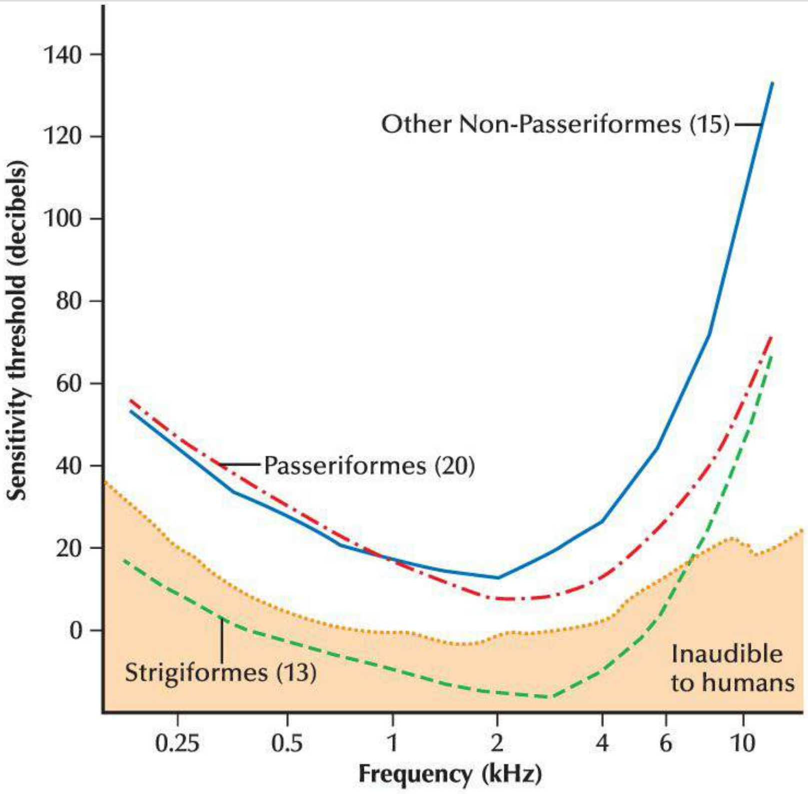
The avian ear is structurally simpler than that of mammals. Compared with those of mammals, avian inner ears have a short basilar membrane, no division between inner and outer hair cells, and a simple system of cochlear nerves. Its acoustical efficiency, however, is the same as that of the mammalian ear.

Acoustical information is processed primarily by auditory nuclei in the hindbrain. The basic plan of the avian auditory central nervous system is the same as that of reptiles, with some derived specializations (Carr 1992). Specialized dark-hunting owls that rely on sound have an extraordinary number of ganglionic cells in the medulla for processing sound and spatial information. The Barn Owl, for example, has about 47,600 ganglionic cells in one-half of the medulla; the Carrion Crow has about 13,600; and the Little Owl, which hunts in the early morning light, has about 11,200 (Winter 1963). Oilbirds, which use sound to navigate in the dark, also have highly developed auditory centers.

Hearing Ability

The substantial amount of experimental data on the hearing abilities of birds supports a surprising conclusion. Most birds do not have extraordinary hearing by standard measures. Humans can hear fainter sounds than most birds at most frequencies. Furthermore, the frequency range of good hearing tends to be wider in mammals than in birds. Some birds, however, can detect low, infrasound frequencies outside the range of human hearing.

The frequencies of sound are measured as cycles per second (**hertz [Hz]**) or, for high-frequency sounds, as thousands of cycles per second (**kilohertz [kHz]**). Birds hear best at frequencies between 1 and 5 kHz. Sensitivity decreases rapidly at both lower and higher frequencies. Owls are an exception; they hear better at these frequencies than humans do and have greater sensitivity than that of humans to low-frequency sounds (Great Horned Owls) and high-frequency sounds (Barn Owls). Pigeons, chickens, and guineafowl, however, hear very low frequencies (infrasound below 20 Hz) extremely well; pigeons can hear much fainter sounds (50 decibels lower) in the 1- to 10-Hz range than humans can hear. The significance of this ability is not yet understood. Oscine songbirds tend to hear high-frequency sounds better and low-frequency sounds less well than do other birds (Figure 7–9).



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DATA FROM DOOLING 1982; DOOLING ET AL. 2000

Figure 7–9 Median hearing threshold curves of birds. Humans cannot hear sounds in the lower shaded area, but owls can. The higher the required intensity, the poorer a bird’s or a person’s hearing. Birds hear well (required intensity less than 40 decibels) over a narrower range of frequencies than do humans.

Unlike bats and some other mammals, birds do not hear ultrasonic sounds—that is, sounds with frequencies higher than those audible to humans. Birds are sensitive to small changes in the frequency and intensity of sound signals but not unusually so. Humans detect frequency changes better than birds at all frequencies. Birds can discriminate temporal variations in sound, such as duration of notes, gaps, and rate of amplitude modulation, as can other vertebrates, including humans. Laboratory tests do not support the idea that birds have exceptional powers of temporal resolution, but these results conflict with the observation that songbirds can learn remarkably fast modulations in the acoustic content of notes that humans cannot resolve with high fidelity (Chapter 8).

Orienting by Sound

Owls can locate prey by sound in complete darkness. The Barn Owl can catch a running mouse in total darkness because it can precisely locate sounds to within one degree in both the vertical and the horizontal planes (Payne 1972). The Barn Owl can also determine the direction and speed of a mouse's movement. Humans can locate sounds in the horizontal plane about as well as a Barn Owl but only one-third as well in the vertical plane.

Birds and humans locate the sources of sounds by **binaural comparison,** comparing the differences in the intensity and time of arrival of sounds at the two ears (Box 7–1). Looking directly at the source equalizes these stimuli. The asymmetrical arrangement of the ears of some owls enhances reception differences and thus the ability to locate prey quickly and accurately. This ability is well developed in the Barn Owl, which locates sounds in the vertical plane by means of its asymmetrical ear openings and the troughs formed by the feathered facial ruff (Figure 7–10). The left ruff faces downward, thereby increasing sensitivity to sounds below the horizontal, and the right ruff faces upward, increasing sensitivity above the horizontal. The owl need only tilt its head up or down to equalize input to the two sides and thus to identify the location of a mouse.

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Figure 7–10 The heart-shaped face of the Barn Owl is not perfectly symmetrical. The left ear, which is higher than the right ear, is most sensitive to sounds from below the horizontal (an imaginary horizontal plane that is parallel to the ground and passes through the owl’s head). Conversely, the lower right ear is most sensitive to sounds from above the horizontal. Enhancing the difference in ear positions are the downward-oriented, feathered ruff on the left side of the face and the upward-oriented ruff on the right side. This asymmetry causes a sound to arrive at each ear at slightly different times, thereby enabling the owl to precisely locate the source of the sound.

BOX 7–1

How Robins Find Worms

The familiar American Robin runs a few steps, cocks its head, and then suddenly seizes on an earthworm and tugs it out of the soil. Capture rates may be as high as 20 worms hiding

Hway Kiong Lim/Shutterstock

An American Robin listening for worms.

in the lawn topsoil in an hour. How does a robin spot an earthworm invisible to human eyes? The cocked-head position could enhance close vision in one eye, or it could focus the robin's hearing toward the ground. An elaborate series of experiments conducted on the campus of Queen's University in Ontario by Bob Montgomerie and Pat Weatherhead (1997) revealed that robins detect hidden worms by listening for the slight sounds made by the worms while moving through the soil. After the robin has detected a worm, the actual strike is likely guided visually. Both sound and sight would be aided by the cock of the head.

A few birds use **echolocation,** or reflected vocalizations, for navigation (Brinkløv et al. 2013). Some swiftlets (*Aerodromus* and *Collocalia*) of Southeast Asia find their way through dark cave corridors by emitting short, probing clicks of one-millisecond duration at normal frequencies (2–10 kHz); they do not employ ultrasound as bats do (Medway and Pye 1977). Echolocation at these normal hearing frequencies is at best only one-tenth as functional as the ultrasound sonar system of bats. For example, the cave-nesting Oilbird, a fruit-eating nightjar of South America, echolocates with sharp clicks from 15 to 20 milliseconds long over a broad frequency spectrum ranging from 1 to 15 kHz (Konishi and Knudsen 1979). It can avoid disks that are 20 millimeters or more in diameter, but it collides with smaller objects.

7.3 Balance and Mechanoreception

Like all vertebrates, birds use the **semicircular canals** of their inner ears and the associated sets of specialized sensory cells as organs of balance and equilibrium. Balance and equilibrium are vitally important for a bird because they provide spatial orientation so essential to skilled flight. Inner ears give birds an excellent sense of balance and body position, enabling them to reorient automatically with respect to gravity, even when blindfolded.

Three semicircular canals, tubes of inner ear fluid, are oriented at right angles to each other like the three sides of a box that meet at one corner (see Figure 7–8). Roughly speaking, one is oriented horizontal, another is vertical facing forward, and the third is vertical facing sideways. Because of the inertia of the inner ear fluid, any change in the relative position of a bird's head will produce a unique combination of fluid flow through the canals (Werner 1958). This fluid flow is detected by hair cells and transmitted as position information to the brain.

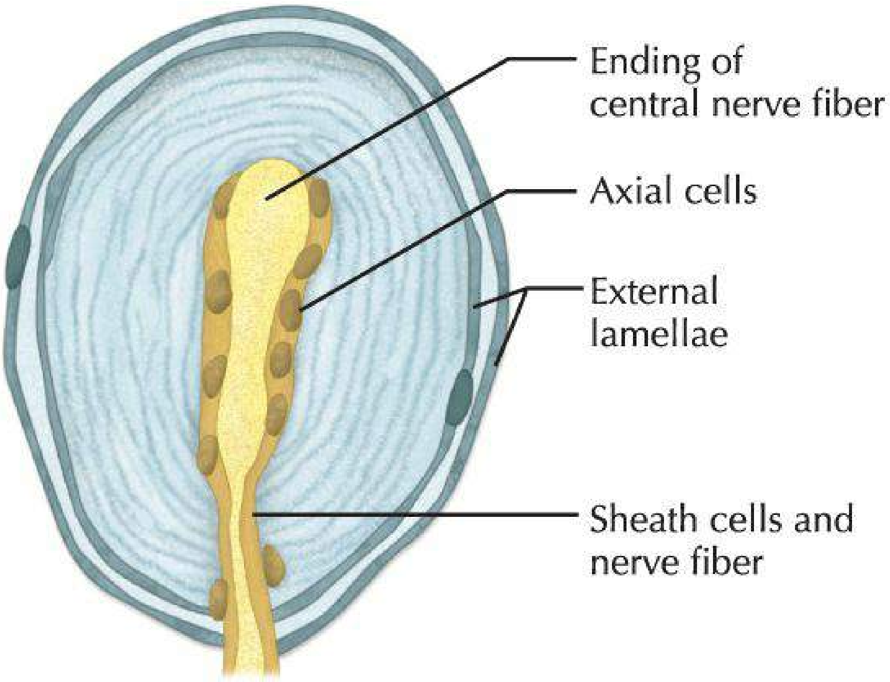
At the bases of the semicircular canals are a distinct pair of inertial movement detectors. Delicate sensory hair cells on the inner ear membranes detect the movements of small crystals of calcium carbonate, or **statoliths,** floating in the fluid. Variations in the pressure of the crystals on the hair cells enable the bird to sense vertical, horizontal, or rotary acceleration.

In birds, the size of the semicircular canals is related to flight performance: pigeons, owls, thrushes, ravens, and raptors have larger canals than those of fowl-like birds and ducks. Among fowl-like birds, the size of the semicircular canal increases with the mobility of a species. So does the size of the cerebellum of the avian midbrain, which is responsible for balanced muscular coordination.

Ornithologists have long known that birds sense an approaching winter storm and feed actively to build their energy reserves. Birds also know how to choose altitudes for migration. These abilities suggest sensitivity to differences in atmospheric or barometric pressure. Homing pigeons are, in fact, extremely sensitive to small changes in air pressure, comparable to differences of only five to 10 meters in altitude (Kreithen and Keeton 1974). Sensitivity to atmospheric pressure is believed to be based in a small sense organ, called the paratympanic organ, in the bird middle ear (von Bartheld 1994).

Birds are extremely sensitive to mechanical stimulation through the senses of **mechanoreception,** the perception of physical forces on the body (Schwartzkopff 1973). Tactile corpuscles, the primary sources of skin sensitivity, monitor changes in muscle tension and provide the bird with **proprioception,** or information about the orientation of the body and its parts within space. These cells, specialized for tactile response, are found at the ends of sheathed nerve fibers.

The ellipsoidal **Herbst corpuscle** is the largest and most elaborate of the tactile corpuscles. It consists of an outer multilayered sheath and an inner core. The onion-like layers of the outer sheath allow elastic



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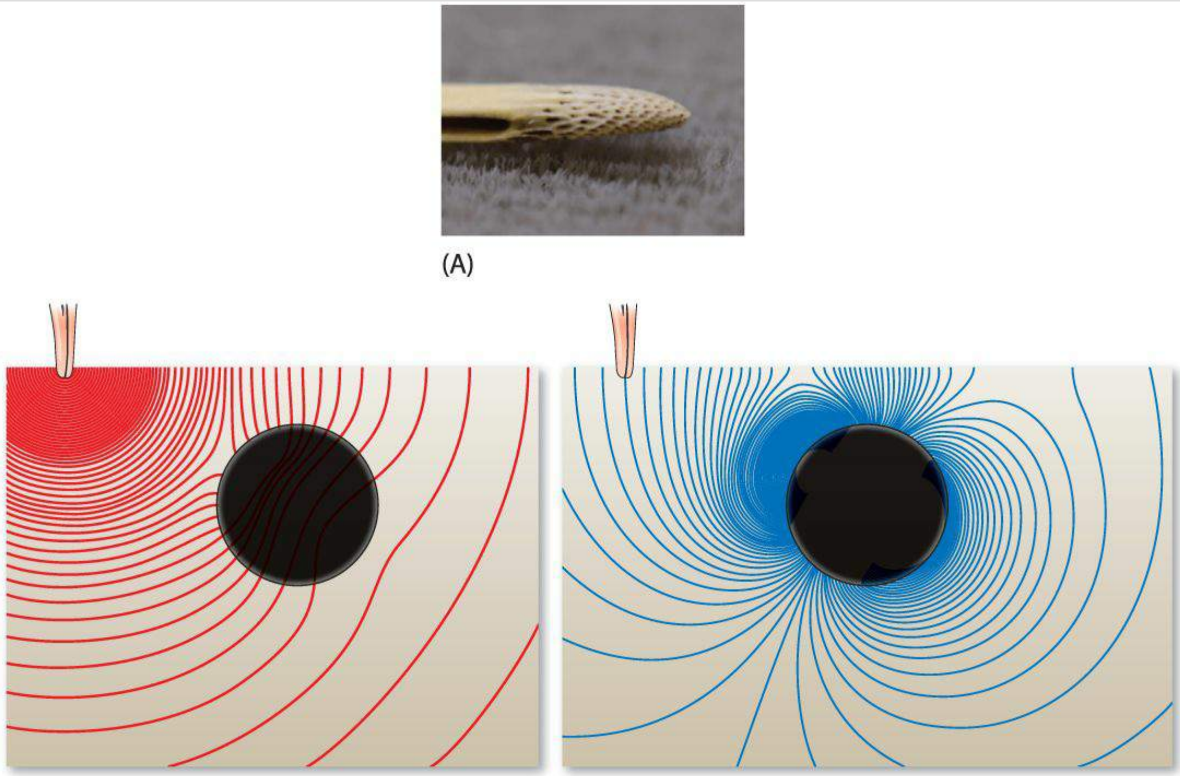
DATA FROM PORTMANN 1961

Figure 7–11 Herbst corpuscle from the bill of a duck. The most elaborate of avian tactile sensors, it consists of as many as 12 onion-like layers of external lamellae that transfer slight pressure changes to the elaborate nerve ending of the receptor axon in the center.

reception and transfer of rapid pressure changes; the inner, cylindrical core is an elaborate sensory nerve fiber (Figure 7–11). Herbst corpuscles are concentrated in feather follicles that have sensory functions, especially those of filoplumes and bristles (see Chapter 4). They are numerous in the wing joints of birds, where they help govern wing positions in flight.

Herbst corpuscles are abundant in the sensitive bill tips and in the tips of woodpecker tongues. Kiwis (Apterygidae), sandpipers

(Scolopacidae), ibises, and spoonbills (Threskiornithidae) have independently evolved concentrated clusters of Herbst corpuscles below the horny rhamphotheca of the beak within pits in the premaxilla and dentary bones of the upper and lower mandible (Cunningham et al. 2013; Figure 7–12). Instead of a hard keratinized rhamphotheca, the beak of waterfowl is covered with a leathery skin that contains novel, mechanosensory bill tip organs. These keratinized papillae protrude through the epidermis and contain dense clusters of pressure-sensitive cells (Schneider et al. 2016). The density of mechanosensory cells in the skin on a duck’s beak is 150 cells/mm^2, matching the density of human finger pads. In contrast, parrots have convergently evolved similar clusters of pressure receptors on the *inside* of the bill, where they apparently provide information used for grasping, manipulation, and extraction of food items in the beak (Demery et al. 2011). To achieve their advanced beak mechnosensitivity, ducks, sandpipers, and parrots have also convergently evolved larger trigeminal nerve sensory nuclei, which receive and process sensory input from the beak (Gutiérrez-Ibáñez et al. 2009).



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(A) COURTESY OF RICHARD O.PRUM.

Figure 7–12 Remote prey detection in wet mud by a probing Red Knot. (A) The tip of the upper mandible has bony pits in which there are clusters of pressure-sensitive Herbst corpuscles. (B) The pressure gradient created in the mud by the insertion of bird’s beak (red) is distorted locally by a solid object, like a mollusk shell. (C) The variation in pressure induced by the shell (blue) is detectable as a difference between the two side of the tip of the beak by the Herbst corpuscles under the ramphotheca. [(B) DATA FROM PIERSMA ET AL. 1998]

Experiments have shown that Red Knots, a shorebird, use an extraordinary physical mechanism to detect bivalves and other invertebrates at distance in water-saturated sand (Piersma et al. 1998). Trained Red Knots can detect bivalves or similarly sized rocks buried five centimeters deep, or beyond the reach of the beaks, in buckets of wet sand. The researchers concluded that by forcing their beaks into the wet sand, Red Knots create a water pressure field that is distorted by the resistance of water flow around an object (see Figure 7–12). This foraging mechanism is consistent with the observations that Red Knot prefer to forage in wet sand and often probe the same area repeatedly before detecting a prey item (de Fouw et al. 2016).

7.4 Chemoreception: Taste and Smell

Birds can taste and smell. The few studies of taste acuity in birds suggest only that they may be equally or less sensitive than mammals with respect to some ingredients (Box 7–2). A few chemosensory cells, or **taste buds,** are located on the rear of the avian tongue and on the floor of the pharynx: about 24 in the chicken, 37 in the pigeon, and 62 in Japanese Quail. Avian taste buds are similar in structure to mammalian taste buds but are negligible in number by comparison. Humans, for example, have roughly 10,000 taste buds on their tongue. The limited number of taste buds of birds, however, guide preferences for basic tastes—sweet, salt, sour, and bitter—as well as such features as lipid and sugar concentration (Clark et al. 2014).

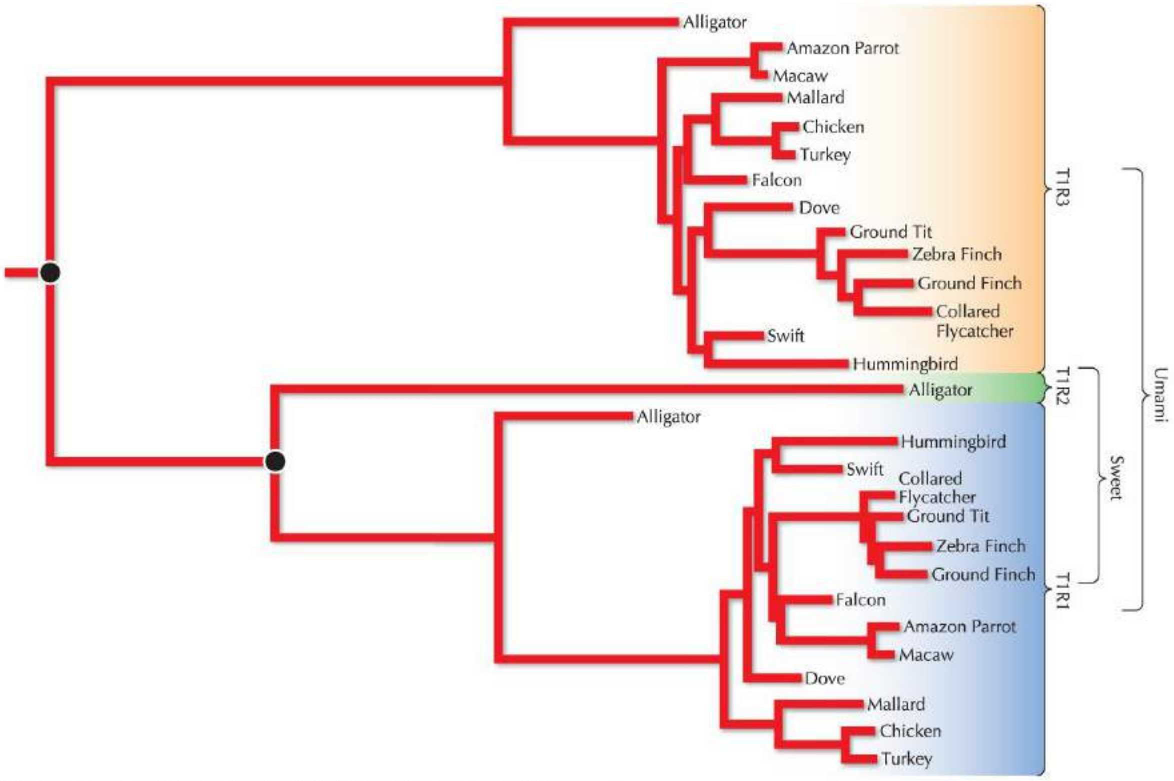
BOX 7–2

Birds Like Chili Peppers

Donald Norman and his colleagues (1992) discovered an ecological link between birds and chili peppers. The active chemical ingredients, called capsaicins, in chili peppers have a familiar, flaming effect on the mammalian oral epithelia and taste buds, mediated by the trigeminal nerve. The normal concentration of these chemicals (1,000 ppm) in wild chilies repels rodents but does not make food distasteful to birds. Indeed, birds are attracted to wild capsicum fruits, called bird peppers, because they are high in vitamins, proteins, and lipids. By monitoring hundreds of wild chili peppers from two species visually and with video cameras in Arizona and Bolivia, Doug Levey and colleagues (2006) showed that all of the pepper fruits were eaten during the day by birds. This result supports the hypothesis that capsaicins provide deterrence directed at mammals and protect the pepper seeds from being consumed by rodents.

Like the diverse opsins that make color vision possible, complex taste perception ability has evolved in vertebrates through gene duplication and differentiation. For example, multiple paralogs of the ***T1R* genes** (which, like opsins, are also 7-transmembrane proteins) provide vertebrates with their sense of sweet and “**umami**”—a word from Japanese that refers to the savory or meaty flavor of proteins. Sweet perception is produced by taste buds using a duplex of *T1R1* and *T1R2* proteins, while umami is sensed by taste buds with a combination of *T1R1* and *T1R3* proteins. Obligately carnivorous mammals, like cats, have evolutionarily lost the *T1R2* gene and can no longer taste sweet flavors.

Recently, it has been shown that all living birds also lack the *T1R2* gene (Baldwin et al. 2014; Figure 7–13). Alligators still have the *T1R2* gene, so the loss of the birds may have occurred in the carnivorous theropod ancestors of birds. However, some birds taste the sweet flavors of the fruits and nectars that they feed on. Hummingbirds have reevolved sweet taste perception by transforming their ancestral umami receptor into a novel sweet receptor. In a series of ingenious experiments, Maude Baldwin and colleagues (2014) demonstrated that hummingbirds have evolved specific amino acid changes to the binding domain of the *T1R3* gene to enable it to bind sugars.

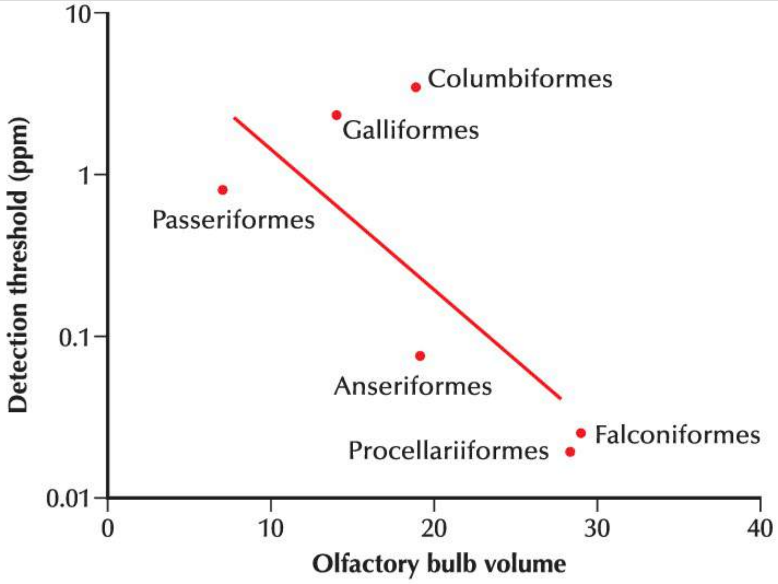


Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
DATA FROM BALDWIN ET AL. 2014

Figure 7–13 A phylogeny of the *T1R* taste receptor gene family in birds and alligator. In most vertebrates, the sweet receptor is composed of a pair of *T1R1* (blue) and *T1R2* (green) proteins, and the umami (or savory) receptor is made of a pair of *T1R1* and *T1R3* (orange) proteins. Birds have lost the *T1R2* gene (green) and have no sweet receptor. Hummingbirds, however, have evolved a novel *T1R3* protein that makes their umami receptor sensitive to both sugar and proteins. The gene duplication events (black circles) occurred before the origin of archosaurs.

Although they have been underestimated in the past, the olfactory abilities of most birds are comparable to those of some mammals (Clark et al. 2014). The avian sense of smell is produced by chemosensory receptors that line the epithelium of the posterior concha of the olfactory cavities (see Chapter 6). Birds use the sense of smell in a variety of activities, ranging from finding food to orientation (Box 7–3). Goslings learn to choose and reject food plants by smell at an early age (Würdinger 1979), and Common Starlings select appropriate nest-construction materials by smell (Chapter 15). In Africa, honeyguides (Indicatoridae) lead animals and people to beehives (see Chapter 6). These relatives of the woodpeckers can find the beehives by their pungent smells. In experiments, honeyguides can find concealed beeswax candles and are attracted to the odor of a burning beeswax candle.

The small size of the olfactory bulbs in most birds (relative to brain size) long fostered the belief that only a few exceptional birds—those with large olfactory bulbs, namely, vultures, kiwis, and petrels—use the sense of smell in their daily activities. Now that view is changing; most birds can probably smell and use odors in their daily routines (Clark et al. 2014). Even passerine songbirds, which have minimal olfactory-bulb sizes (1.5 millimeters) and were assumed to lack a sense of smell, can detect certain odors with the same acuities as rats and rabbits (Clark et al. 1992). Simple and critical olfactory functions can be accommodated by very small amounts of olfactory tissue. Among the orders of birds, however, thresholds for odor detection are correlated with the size of the olfactory bulb relative to the size of the cerebrum (Figure 7–14). Olfactory bulbs are larger in some birds, like kiwi and some New World vultures, which use olfaction in foraging.



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DATA FROM CLARK ET AL. 1992

Figure 7–14 The relation between olfactory acuity, expressed by the detection threshold for a chemical in parts per million (ppm), and the proportion of brain tissue allocated to the olfactory bulb for six orders of birds.

BOX 7–3

New Zealand Kiwis Sniff for Their Food

Unlike mammals, birds rarely sniff. Kiwis—those well-known flightless, chicken-sized birds found only in New Zealand—are an exception (see Figure 5–20B). Active only at night, kiwis probe their long bills into wet soil to find earthworms, which they locate by sniffing through nostrils located at the bill tip. All other living birds have nostrils at the base of the bill.

A series of classic experiments demonstrated that kiwis rely on their highly developed sense of smell to find food (Wenzel 1968, 1971). Screened tubes containing either fragrant food or just dirt (the control) were buried three centimeters deep in a large cage. The captive kiwis quickly found the baited tubes and punctured them to extract the food, but they ignored the control tubes containing only dirt. Parallel laboratory experiments demonstrated increased respiration and brain neural activity with exposure to food odors and conditioned aversion to food containing noxious chemicals.

Odors mediate the daily sexual and foraging behaviors of birds. The sexual activity of male Mallards depends on their ability to smell a female's breeding odors. Experimental cutting of their olfactory nerves inhibits courtship and sexual behavior (Balthazart and Schoffeniels 1979). Female odors apparently come from oil-gland secretions, which change in composition during the breeding season (Box 7–4). Wild flying Turkey Vultures, which find carcasses by smell, are attracted to ethyl mercaptan fumes released into the air to simulate the smell of rotting meat (Smith and Paselk 1986). Engineers have used the remarkable olfactory abilities of vultures to locate leaks in long pipelines by pumping such chemicals through them and then spotting where the vultures gather.

Tube-nosed seabirds (Order Procellariiformes) locate zooplankton on the open seas by the plume of smell they emit at the surface of the ocean. Zooplankton, including the krill consumed by whales and penguins, is a primary food of storm petrels, shearwaters, and other seabirds. The seabirds home in on the scent of dimethyl sulfide, a compound that is released by phytoplankton in response to being eaten by zooplankton (Nevitt 1999). Leach's Storm Petrels are highly attracted to this scent, which they can detect as far as 12 kilometers from the source (Clark and Shah 1992).

Beyond finding meals of krill, such seabirds also use smell to find their nest burrows and to locate their mates. Leach’s Storm Petrels use their well-developed sense of smell to locate their nesting burrows in the dark conifer forests on islands in the Bay of Fundy (Grubb 1974). They reliably chose scents from their own nests in experimental mazes. The Antarctic Prion of the southern oceans distinguishes the smell of its mate from that of other birds and from its own scent (Bonadonna and Nevitt 2004). This ability enables it to find the right nest when returning from sea to relieve its incubating partner and may also play a role in mate choice and kin recognition.

BOX 7–4

Auklets Use Perfume

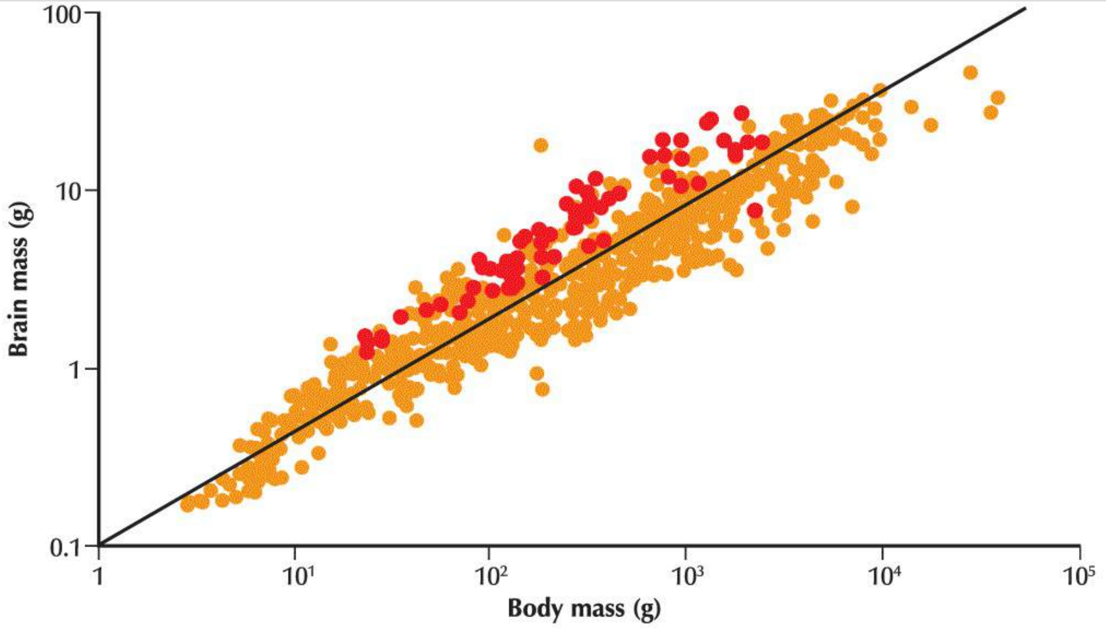

Ian L. Jones

Crested Auklets displaying and sniffing.

Millions of Crested Auklets nest in crowded colonies on the cliffs of the Aleutian Islands in the North Pacific. Clouds of these small buzzy seabirds commute between their nest burrows and rich ocean feeding grounds. On land, the Crested Auklet flaunts its jaunty crest and bright orange bill and practices a striking courtship display that includes “sniffing” its mate’s neck. Ornithologists have long noticed the rich odor of tangerines that hangs in the air over colonies of Crested Auklets. This odor turns out to be a **pheromone,** an olfactory signal that is used in social communication (Hagelin et al. 2004). The auklets are attracted to their distinctive citrus-scented odor in preference to other odors. The auklets produce the chemical compounds responsible for the scent, *cis*-4-decenal and octanal, just during the breeding season. They orient specifically to these chemicals in maze experiments. Finally, the neck ruff that is sniffed during their courtship display is highly scented with these chemicals. Social odors, the avian equivalent of perfumes, are a relatively unexplored and possibly widespread channel for communication and sexual selection.

7.5 Bird Brains

Contrary to common “wisdom,” birds in general and songbirds in particular have big brains relative to their body mass. Indeed, birds have well-developed brains that are six to 11 times as large as those of like-sized reptiles. The brains of most birds and most mammals account for 2 to 9 percent of their total body mass. Parrots, owls, crows, woodpeckers, and hornbills have larger-than-average brains (Ricklefs 2004; Figure 7–15).



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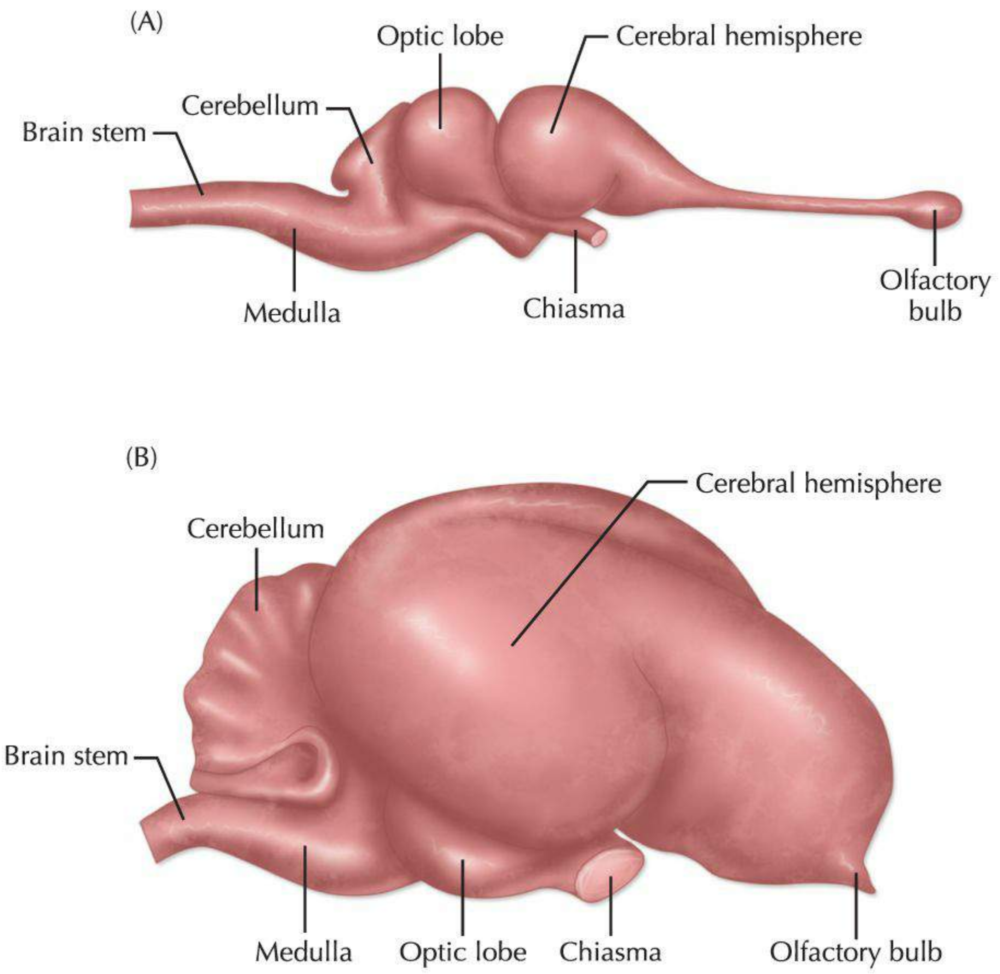
DATA FROM RICKLEFS 2004

Figure 7–15 The relation between brain mass and total body mass in birds, based on data for 837 species. Red circles: Parrots (Psittacidae), owls (Strigidae), crows (Corvidae), woodpeckers (Picidae), and hornbills (Bucerotidae) have relatively large brains. Orange circles: All other species.

Like other vertebrates, the avian brain is composed of the forebrain, midbrain, and hindbrain (Figure 7–16). The **forebrain** is responsible for complex behavioral instincts and instructions, sensory integration, and learned intelligence. It includes the olfactory bulbs and cerebral hemispheres. The **midbrain** regulates vision, muscular coordination and balance, physiological controls, and the secretion of neurohormones that control seasonal reproduction. It includes the optic lobes and chiasmata and the cerebellum. The **hindbrain,** or medulla, links the spinal cord and peripheral nervous system to the major control centers of the brain. Cranial nerves, except those controlling vision and smell, enter the brain through the medulla.



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DATA FROM PORTMANN AND STINGELIN 1961

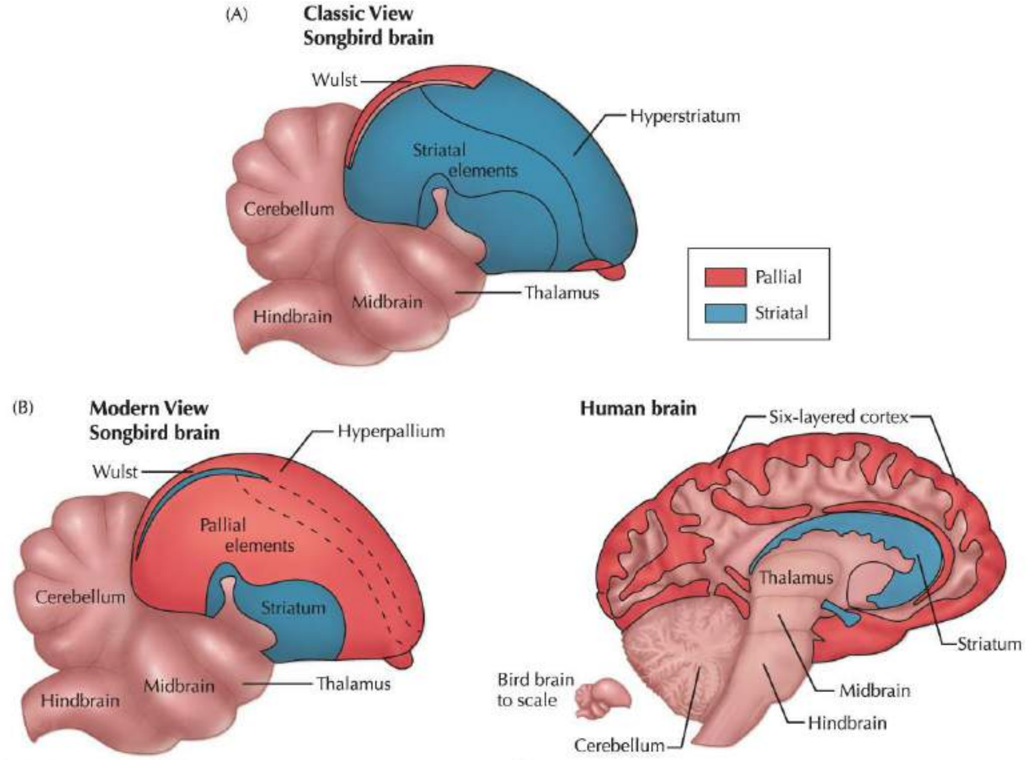
Figure 7–16 The brain of (A) a monitor lizard and (B) a macaw, drawn to the same scale. Note the well-developed cerebral hemisphere and cerebellum in the avian brain.

Peripheral organs receive signals from all the senses—vision, hearing, touch, taste, and smell—and feed them to the brain for processing, integration, and response. Before reaching the main integration centers of the forebrain, sensory signals pass through their respective control centers. Visual information goes to the optic lobes of the midbrain, information on body orientation and localized pressure goes to the cerebellum in the midbrain, acoustical information goes to its related processing centers in the hindbrain, and olfactory information goes to the olfactory bulbs and then to the olfactory lobe in the forebrain.

The midbrain and forebrain, or telencephalon, in both birds and mammals are conspicuously more highly developed than those of reptiles (see Figure 7–16). The optic lobes and the cerebellum dominate the avian midbrain. The two avian optic lobes are huge in relation to the rest of the brain. Together with large eyes, this visual apparatus displaces the rest of the brain from the ventral and lateral parts of the skull, the usual positions in other vertebrates. The cerebellum is involved in motor control, coordination, balance, and spatial orientation. Balance and coordination during flight require extensive input from sensory receptors throughout the body and in the middle ear; the cerebellum is appropriately large to accomplish these important functions.

In mammals, the striatum and basal ganglia of the mammalian forebrain has an architecture that features nuclei, or distributed but interconnected clumps of neurons, and the cortex has a layered, or laminar, organization. Furthermore, the mammalian striatum is involved with instinctive and reflexive behavior, while the deeply fissured cerebral cortex functions in more complex cognitive processing, referred to as pallial functions. In contrast, most of the avian forebrain is organized into distributed nuclei, like the mammalian striatum. The laminar avian cortex—called the Wulst—is limited to a small area in the back of the forebrain. The removal of the Wulst does not impair a bird’s normal motor functions or its ability to make simple choices; however, it does destroy the bird’s ability to learn complex tasks.

Consequently, for 100 years, the avian forebrain was homologized with the primitive, mammalian striatum (Figure 7–17). This hypothesis greatly reinforced the view that birds have limited cognitive capacities. However, this traditional view is incorrect and obsolete (Avian Brain Nomenclature Consortium 2005). Specifically, the majority of the avian forebrain is composed of complex pallial neural cell types with circuits, gene expression, and neurotransmitter composition like the mammalian cortex (Karten 2015). Thus, although the avian forebrain has a different spatial organization from the mammalian cortex, the avian pallial domains are homologous as cell types to the mammalian cortex and responsible for the substantial and even superior cognitive abilities of birds.



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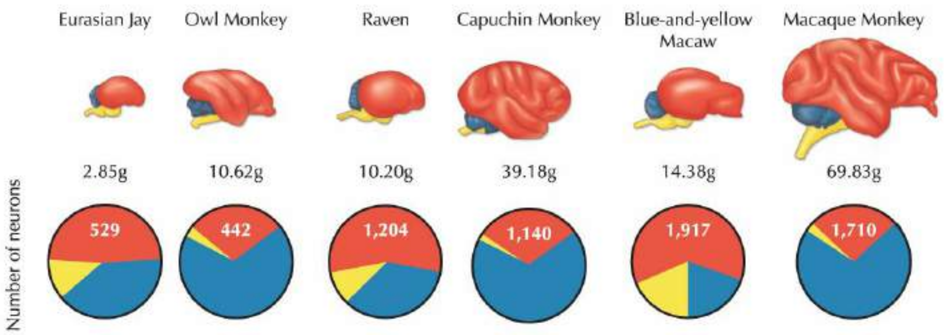
DATA FROM AVIAN BRAIN NOMENCLATURE CONSORTIUM 2005

Figure 7–17 Classical and modern views of the avian brain. (A) The classical view considered most of the avian forebrain (the cerebrum, or telecephalon) to be an expansion of the primitive striatal elements of the vertebrate brain. These elements are limited in extent in the human forebrain, which is dominated instead by the expanded, highly folded cortex that enabled higher intelligence. (B) The modern view considers most of the avian forebrain to be made of pallial neurons homologous to those in the mammalian cerebrum, constructed differently but still enabling higher cognitive abilities.

In mammals, the cerebral cortex is the principal feature of the forebrain. It overgrows the small corpus striatum and reaches its largest and most deeply fissured state in higher primates, such as chimpanzees and humans. In birds, the **hyperpallium** is the center of learning and intelligence. The hyperpallium is unique to birds and is best developed in intelligent birds, such as crows, parrots, and other passerines. Domestic chickens, Japanese Quail, and Feral Pigeons, which do not perform as well in laboratory intelligence tests, have smaller hyperpallia. Damage to the hyperpallium severely impairs a bird’s behavior.

Some birds exhibit cognitive capacities equivalent some primates (see below). However, most birds have much smaller brains than mammals with equivalent cognitive abilities. Recent data have established that avian brains have considerably higher density of neurons than primate brains (Olkowicz et al. 2016; Figure 7–18). Furthermore, parrots and corvids (crows, jays, and relatives) have more pallial neurons than much larger primates. Thus, avian brains have greater “cognitive power” per gram than mammal brains do (Olkowicz et al. 2016).



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Data from Olkowicz et al. 2016

Figure 7–18 Comparisons of the size, mass, and the number of neurons in forebrain (red), midbrain (blue), and hindbrain (yellow) of a jay, a raven, and a macaw to three species of primates. Pie diagrams show the relative numbers of neurons in each portion of the brain. These intelligent bird species have more pallial neurons in their forebrains (red) than do primates with brains that are over three times more massive.

Like primate brains, bird brains exhibit functional lateralization, and the left hemisphere is dominant. In general, the left cerebral hemisphere controls complex integration and learning processes and suppresses sexual and attack behavior. The right cerebral hemisphere monitors the environment and selects novel stimuli for further processing, which may entail memory by the left side.

In humans, right-handedness relates to dominance of the left hemisphere of the brain. Some birds also may be righties or lefties. Crossbills (*Loxia*) are either left-billed or right-billed, and they approach pine cones counterclockwise or clockwise accordingly (Knox 1983). Individual Red-necked Phalaropes spin consistently left or right while feeding (Rubega et al. 2000). Dark-eyed Juncos favor the right eye (which feeds visual information to the dominant left hemisphere) to scan for predators, as predicted (Franklin and Lima 2001). And parrot lovers have known for centuries that captive parrots are either left-footed or right-footed when they hold food. Perhaps the strongest case for true primatelike handedness in birds is that of New Caledonian crows, now well known for their skilled toolmaking (section 7.6). Most of these crows use the right eye and left part of the brain to make tools, just as most humans do.

Birdsong is normally controlled by the left hemisphere of the forebrain, specifically with learning and innovation in vocal repertoires (Nottebohm 1980). The right cerebral hemisphere assumes control of the functions of the left hemisphere only if the left hemisphere is damaged. The impairment of a young Atlantic Canary’s song-control centers in the left hemisphere leads to the formation of an alternative set in the right hemisphere and the acquisition of a new song repertoire.

Such functional lateralization of the brain was once thought to be an exclusively human attribute, associated with extraordinary language abilities.

Spatial Memory and the Hippocampus

The hippocampal complex of the avian brain is a primary target of analysis of the relation between brain evolution and social behavior in birds. Homologous in structure and function to the structures in mammals, the avian hippocampal complex includes the hippocampus and the associated parahippocampus of the forebrain. The **hippocampal complex** is a well-delineated, paired anatomical structure that lies adjacent to the midline of the dorsal forebrain. The hippocampi of birds and mammals are functionally equivalent with respect to controlling certain memory tasks, including spatial orientation and cognitive memory. Spatial memory processed in the hippocampus controls the daily behavior of highly mobile animals, such as birds that accurately revisit feeding places, nests, and remote wintering grounds. For example, lesions in the hippocampi of homing pigeons—a specialized, domesticated breed of Feral Pigeon—disrupt their ability to learn a navigational map (Bingman 1988).

The extraordinary spatial memory of seed-caching birds is processed by an enlarged hippocampus. Members of three families of passerine birds—Corvidae (crows, jays, and nutcrackers), Sittidae (nuthatches), and Paridae (titmice and chickadees)—cache thousands of seeds as a means of exploiting temporary food surpluses and providing reserves for future use. These three families have significantly larger hippocampal volumes than do other passerine birds. Experimental studies of chickadees and nutcrackers have demonstrated that spatial memory for seed recovery is indeed based in the hippocampus. Chickadees with experimental lesions to the hippocampus continue to hide seeds in normal fashion but cannot find them again, except by chance.

TIM ZUROWSKI/AGE FOTOSTOCK

Figure 7–19 Clark’s Nutcracker, a seed-caching bird with extraordinary spatial memory.

The spatial memories of seed-caching birds are prodigious. Each autumn, individual titmice may stock more than 50,000 caches of one spruce seed each (Haftorn 1959). They recover seeds as many as 28 days later (Hitchcock and Sherry 1990). Crows, jays, and nutcrackers are especially diligent hoarders. The development of spatial memory varies among species in relation to their dependence on cached seeds (Balda et al. 1996). Probably the most extraordinary is the Clark’s Nutcracker (Figure 7–19), which hides between 22,000 and 33,000 individual pine seeds in more than 2,000 unique cache sites to survive the winter and early spring. The ability to accurately find these caches as many as nine months later is evidence of a phenomenal spatial memory and cognitive function.

Obligate brood parasites that lay their eggs in the nests of other bird species (Chapter 13) must search for those nests and keep track of the growth of their clutches so that they lay their egg in the nest on some day between the first and last egg added to the clutch. Interestingly, brood-parasitic cowbirds have larger hippocampi than do related blackbirds (Reboreda et al. 1996). In cowbird species where the females search alone, only females have large hippocampi. In the two species where females search along with their mates, both males and females have large hippocampi. Finally, an experimental study has shown that depriving female Brown-headed Cowbirds of opportunities to search for nests prevents the enlargement of their hippocampi (Day et al. 2008). Thus, comparative differences in hippocampus size among birds appear to be the result of neural plasticity and cell growth (see below) driven by behavior rather than by genetics.

New Neurons

Research on neural pathways that control song and spatial memory in birds led to a major discovery: the fine structure of the adult brain is dynamic, not static. New connections, called synapses, form in the spring when some birds, such as Atlantic Canaries, learn new songs; these connections disintegrate in the fall when the birds stop singing (Alvarez-Buylla and Kim 1998). Chickadees cache seeds in the autumn for use later in the winter. They increase their capacity for remembering where they put the seeds by adding new cells to the hippocampus, which expands in volume by almost 30 percent and then shrinks in size the following spring when fresh insect food is available (Saldanha et al. 2004). Thus, adult songbirds can form new neurons, replace old ones, and reallocate brain space appropriately to seasonal efforts. This process, called **neurogenesis,** is now an established fact (Nottebohm 2002).

At least in a few specific circuits, the transient brain cells have limited life spans—in some cases, only several weeks or months. They are culled and replaced on a regular as well as a seasonal basis in brain circuits controlling behaviors as varied as singing, food caching, and even social interactions. Such dynamics call for new theories of long-term memory (Nottebohm 2002). One of the advantages proposed is that the replacement of some old neurons by new ones enables the rejuvenation of key brain circuits and continued ability to learn new information or skills. Long-term memory resides in other neurons that are retained.

The study of the replacement of neurons in songbird brains helps to inform medical research concerned with treating damaged brains and spinal cords. When he tried to isolate the neural growth factor in Zebra Finches, for example, Mark Gurney (1988) found a large protein molecule that he named neuroleukin. Analysis of the functional structure of neuroleukin led Gurney and his colleagues to the part of the AIDS retrovirus that destroys neurons in the human brain, thereby causing dementia.

Sleep

It is well understood that sleep evolved as a way of restoring brain function, but exactly what is being restored is difficult to understand. Many explanations of the advantages of sleep reduce to the observation that sleep cures sleepiness.

Most vertebrates sleep in one way or another; sleepless bullfrogs, sea turtles, alligators, and some fishes are the exception. Sleep is so important to mammals that hibernating animals must come out of torpor occasionally in order to sleep. Without sleep, the synapses are less reactive, leading, among other things, to short-term loss of memory. No similar data exist on birds in torpor.

The convergent evolution of the large brains and advanced endothermic metabolisms of birds and mammals has been accompanied by the convergent evolution of complex sleep patterns in the two groups. Unlike other reptiles, birds exhibit **slow-wave sleep (SWS)** and **rapid-eye-movement (REM) sleep,** each of which is also present in mammals. Physiological data demonstrate that SWS and REM restore brain function in both birds and mammals (Rattenborg et al. 2009).

Birds are capable of SWS with one side of the brain at a time (Kavanau 1996; Rattenborg et al. 1999). This so-called unihemispheric sleep has been observed in over 29 bird species belonging to 13 orders. Birds typically close their eyes when they sleep, but they close just one eye at a time for unihemispheric sleep. Unihemispheric sleep enables continued vigilance. For example, Mallard ducks on the edge of a group engage in unihemispheric sleep more frequently than their flock mates in more secure, central positions. As expected, unihemispherically sleeping ducks keep open the eye that is facing outward toward potential dangers. Because the visual input from each eye is processed by the opposite side of the brain, these ducks are sleeping with the outward-facing side of the brain.

REM sleep takes place with both sides of the brain simultaneously and both eyes closed. Very short and frequent bouts of REM sleep are a feature of sleep in birds (Ayala-Guerrero et al. 2003). Electroencephalograms of brain activity during REM sleep suggest that birds dream. In one study, Zebra Finches were shown to “practice” new song patterns in their dreams (Dave and Margoliash 2000; Spinney 2003). We will discuss the role of dreaming in avian song learning further in Chapter 8.

Despite the homeostatic functions of avian sleep, some birds can function well with limited sleep during certain times of the year. For an intensive three-week period on their Arctic breeding grounds, male Pectoral Sandpipers are so busy defending territories and attracting mates that they may sleep as little as 5 percent of the time (Lesku et al. 2012). Those individuals that sleep the least have the greatest reproductive success.

Studies using advanced tracking and physiological monitoring devices on Great Frigatebirds, Sooty Terns, and Common Swifts have established that birds can engage in SWS and REM sleep during long flights (Rattenborg 2017). Great Frigatebirds use more unihemispherical SWS in flight; when rising in thermals, they keep open the eye that is facing into the turn. Frigatebirds use REM when gliding downward. Although they can function on long flights with less than 45 minutes of sleep per day, they return to sleeping around 12 hours a day when they return to the nesting colonies.

Most frequently, birds sleep in a distinctive posture with their bills on the backs or tucked underneath the scapular feathers of the wing (Figure 7–20). This posture allows them to conceal their bill and to open one eye at any time. Interestingly, an extraordinary fossil of a tiny, Chinese, toothed troodontid dinosaur indicates that this distinctive sleeping posture evolved in theropod dinosaurs before the origin of birds and before the origin of the beak itself (Xu and Norell 2004; see Figure 7–20E, F).

(A) Nick Dale/AGE Fotostock. (B) Pamela Bogle/Shutterstock. (C) Paul Reeves Photography/Shutterstock. (D) Ramona Edwards/Shutterstock.com. (E, F) Mick Ellison

Figure 7–20 Birds sleep in a distinctive posture with the head on their back or tucked under the scapular feathers of the wing. (A) Penguin. (B) Flamingo. (C) Duck. (D) Passerine. (E, F) The type specimen of the troodontid dinosaur *Mei long* was fossilized in a posture identical to sleeping modern birds, indicating that this sleeping behavior evolved in dinosaurs before the origin of birds.

7.6 Cognition and Intelligence

Behavior in its broadest sense mediates a bird’s relations to the environment, both social and ecological. Central to daily behavior are the acquisition and processing of information from the environment, or **cognition.** More formally defined, cognition “includes perception, learning, memory, and decision making, in short, all ways in which animals take in information about the world through the senses, process, retain, and decide to act on it” (Shettleworth 2001). Of greatest interest are flexible and novel behaviors that solve problems adaptively or with apparent intelligence. Complex social interactions and innovative foraging behavior are evident in many bird species. For example, birds routinely assess the relative abundance and economic values of alternative foods to make foraging decisions.

Bird species vary greatly in their cognition skills in ways that affect an individual bird’s survival and reproduction. Superior cognitive abilities are evident in many crows, jays, and parrots (Table 7–1), which can remember what happened not only where but also when. The benefits and costs of cognition are tied to the evolution of life-history traits that characterize species and major groups of birds (Ricklefs 2004). Larger brain sizes, for example, require longer incubation periods to mature as well as greater investment of metabolic and cellular resources. Foraging skills, cooperative breeding, parental care, long life span, and play behavior are correlates of the brain sizes and cognitive abilities of birds.

Table 7–1 ***Cognitive Capacities of Parrots and Corvids***

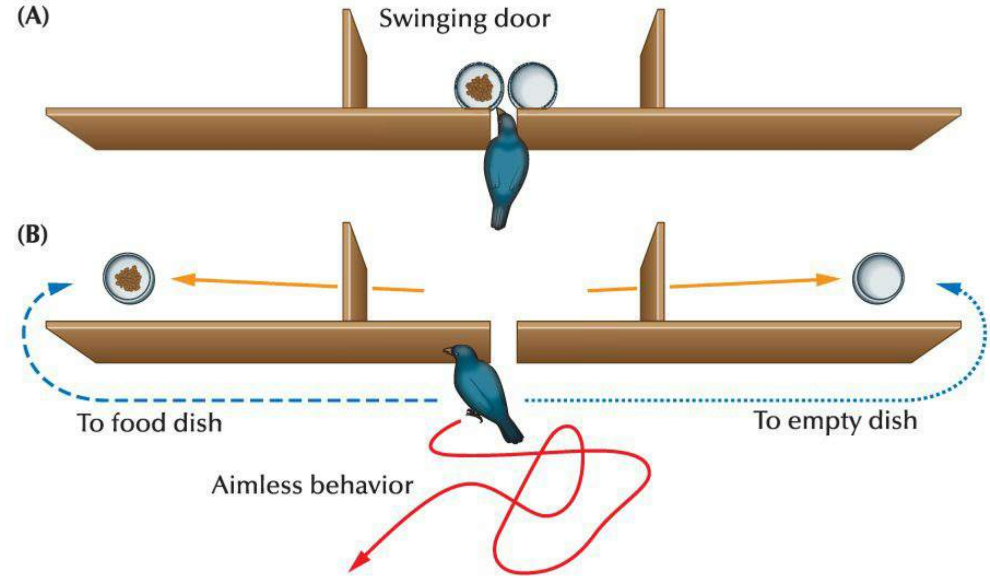
Object Permanence: Memory of objects that are out of view	Most crows and parrots can infer where an object that has moved out of view has gone. Gray Parrots and Tanimbar Corellas can track a food item hidden under one of multiple cups through rotations or transpositions of the cups or translocations of the bird relative to the cups.
Delay of Gratification: Ability to delay a reward in order to receive a bigger reward; impulse control	Gray Parrots will wait only a few seconds. Crows and ravens will wait up to five minutes to improve reward quality, not at all to improve reward quantity.
Mental Time Travel: Memory of past episodes and planning ahead	Jays and magpies remember the what, where, and when about cached food items. Western Scrub Jays remember the perishability of cached food items and retrieve them accordingly. Western Scrub Jays remember episodes of hunger and cache more food in places where they have experienced hunger.

Reasoning: Inferring correct solutions from partial information	*By Exclusion:* Corvids can infer the correct solution by excluding the alternatives. Gray Parrots can reason by exclusion in both visual and acoustic domains. *By Transitivity:* Several corvids can infer information about two objects by each of them to a third object. *By Analogy:* Gray Parrots can apply same/different categories to objects in response to verbal requests.
Metacognition: Awareness about your own knowledge	Large-billed Crows can evaluate how well they remember a past visual stimulus.
Mirror Self-Recognition: Awareness of your own body	Magpies and Jackdaws show self-referential behavior to a mirror; two of five magpies recognize a mark placed on their plumage in a mirror. New Caledonian Crows and Gray Parrots can use a mirror to locate otherwise hidden food, but they do not engage in self-exploration in front of a mirror.
Theory of	Some corvids follow the gaze of others into

Mind: Inferring the mental states of others	the distance. Jackdaws are sensitive to the direction of human attention. Ravens and Western Scrub Jays differentiate between conspecifics that know or are ignorant about cached food items. Western Scrub Jays with prior experience stealing the food caches by others will move items they cache if they are seen hiding it by another individual; individuals without prior experience of stealing food do not. They can attribute their own behavioral motivations to others.
Vocal Learning: Sound production learning	See details in Chapter 8.
Source: Data from Güntürkün and Bugnyar (2016).	

Avian cognitive abilities have evolved in parallel with the expansion of their pallial forebrains, and the performances of the best birds and mammals rival those of nonhuman primates (Güntürkün and Bugnyar 2016). Many corvids and parrots are capable of startling cognitive sophistication (see Table 7–1). Various corvids and parrots can delay gratification, plan for the future, reason from examples, evaluate the quality of their own memories, recognize themselves in the mirror, and infer the mental states of others. Our understanding of the sophisticated cognitive abilities of birds increases every year, as will be apparent in each of the subsequent chapters of this book. As a prelude, here are some highlights of avian cognition and intelligence.

Birds master complex problems in the laboratory, outperforming many mammals in advanced learning experiments (Kamil 1985, 1988). Crows and magpies do especially well in laboratory experiments that test higher faculties. In one such experiment, the **Krushinsky problem,** the bird looks through a slit in a wall at two food dishes, one empty and one full, that move out of sight in opposite directions (Figure 7–21). The bird must then decide which way to go around the intervening wall to get to the dish that contains food. Cats, rabbits, and chickens do poorly in this test, but dogs and crows solve the problem immediately.



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DATA FROM STETTNER ANA MATYNIAK 1968

Figure 7–21 Crows and dogs performed best in the Krushinsky problem experiment, in which food dishes (A), viewed by the subject through a slit in a wall, move out of sight behind swinging doors. (B) The subject must then choose to proceed left or right to find the food dish.

Learning to count is a formidable problem for most mammals. Monkeys require a long training ordeal of 21,000 trials to learn to distinguish between sound series with two or three different tones; rats never learn to make this distinction. Birds, however, more easily master complex counting problems (Davis and Pérusse 1988). Ravens and parakeets, for example, can learn to count to seven and can learn to identify a box containing food by counting the number of small objects in front of it (Koehler 1951). In the wild, female coots can count their own eggs in a nest, ignoring eggs laid by other brood-parasitic females, and decide how many more to lay (Lyon 2003; Chapter 13).

One of the most advanced forms of learning, **insight learning**—that is, learning by the observation and imitation of others—may be routine among birds. Blue Jays, for example, can learn the difference between edible and inedible butterflies by watching the feeding behavior of jays in another cage (Brower et al. 1970). The spread of the milk bottle feeding habit among English titmice is attributed to learning by imitation (see below). Novel tool use, such as throwing stones at ostrich eggs by Egyptian Vultures, also probably spreads through imitation of individual innovative birds.

Parrots are capable of complex reasoning and communication (Box 7–5). Feral Pigeons, amazingly, can converse without any assistance from humans (Epstein et al. 1980). In this experiment, modeled after the demonstration of communication through symbols by chimpanzees, two pigeons named Jack and Jill learned to ask about different colors coded by symbols and to find them. In the ultimate conversation, Jack asked Jill "What was a hidden color?" by using a symbol. Jill peeked at the color and told Jack which color it was by depressing a key with the symbol for that color. Jack responded by pecking the "Thank you" key, which rewarded Jill with food. The conversation continued for other colors and their symbols. The transmission of novel behavioral traits from one individual bird to another, a kind of culture, can thus be important in the evolution of behavior in birds.

BOX 7–5

Conversations with a Parrot Explore Avian Intelligence

A Gray Parrot named Alex has been a source of deep insights into the intellectual abilities of some birds. Irene Pepperberg (2000) first taught Alex a vocabulary of English vocalizations to identify, request, refuse, or comment on more than 80 objects of different colors, shapes, and materials. Alex's comprehension of categories and labels was illustrated by his performance in a series of trials. Alex was presented with an array of objects—purple truck, yellow key, green wood, orange paper, gray peg wood, and red box—and was then asked, "What object is green?" Alex replied, "Wood." He responded with an accuracy of 81 percent over 48 such trials. The ability for two-way communication between Irene and Alex increased, enabling increasingly complex tests of Alex's abilities. He could provide additional information about an object that was uniquely defined by the conjunction of two other categories. For example, to the question "What color is the three-corner [shape] key [object]?," Alex would answer, "Yellow."

In general, birds quickly learn to recognize the odd object, not only in a set of familiar objects but also in sets of unfamiliar objects; monkeys master this task with difficulty. Alex went a step further; he learned to report on the absence or presence of similarity and difference between two objects (Pepperberg 1988). When asked either "What's same?" or "What's different?," he responded, "None," if the two objects were, respectively, totally dissimilar or identical. The required concepts of nonexistence or absence are related to advanced cognitive (and linguistic) abilities to deal with discrepancies between the expected and the actual state of affairs.

Sadly, Alex died in September 2007 of natural causes. He is likely to be the only bird to have received an obituary in the *New York Times* (Carey 2007).

RICK FRIEDMAN/GETTY IMAGES

Alex, a Gray Parrot that has changed our understanding of avian intelligence, and his companion, Irene Pepperberg, discuss the different objects between them.

Pigeons are especially good at learning visual patterns. They can be trained to memorize as many as 725 different visual patterns, to separate human-made from natural objects, to discriminate different styles (cubism versus impressionism) of painting, to communicate by using visual symbols, and even to “lie” (Avian Brain Nomenclature Consortium 2005, p. 156).

Smart Feeding

Birds tend to choose food of high energetic profit. A classic example is that of White Wagtails, which prefer medium-sized flies, even though large flies with greater energy content are more common (Davies

1977). Medium-sized flies yield comparatively more energy per second of foraging time because large flies take too long to subdue and swallow relative to their higher energy content.

Many birds, from gulls to raptors, drop hard-shelled prey from the air to crack them open. Crows (*Corvus*) break open hard-shelled food items in a variety of clever ways. In Japan, Carrion Crows now use cars as big tools to crack their walnuts. Since 1990, newly urbanized crows have learned to wait for a red traffic light, then place the nuts on the crosswalk in front of stopped cars and return on the next red light to pick up meat from the crushed nuts (Attenborough 1998).

Birds also use time adaptively when they harvest renewable resources by returning regularly to productive foraging sites, such as backyard bird feeders. Hummingbirds, for example, repeatedly return to flowers to harvest nectar produced by the flowers since their last visit. Some hummingbirds cycle among widely scattered flowers, just as fur trappers check their circuit of widely scattered traps, called a trapline. In one field study, traplining hummingbirds of the rain forest learned to time their returns to coincide with the interval of experimental refill, a form of operant conditioning (Gill 1988). Counteracting the advantages of waiting, however, was the prospect of losing the nectar to a competitor. When that happened, the hummingbirds returned frequently to harvest small amounts of nectar, keeping flowers almost empty and unattractive to competing birds.

Western Scrub Jays apply the concepts of past, present, and future in ways similar to what is called “episodic memory” or “memory time travel" in humans. They remember where and when they hid what kinds of food (Clayton et al. 2003). The jays also adjust their efforts and plan for future needs. Briefly, in a series of elegant experiments, the jays hid two types of food—perishable insects and nonperishable nuts—for later recovery and eating. They quickly learned to recover the insects before they spoiled. If too much time had elapsed, causing likely decay, they switched to their hidden nuts without checking on the status of the hidden insects. When known thieving colleagues were allowed to watch a jay hide its food, the jay would move the food to a new site at its first private opportunity.

Innovation and the Use of Tools

Foraging behavior is a rich source of **behavioral innovation.** Forty years ago, a few Great Tits in the British Isles learned to rip open milk bottle caps to drink the cream. Apparently, it was a novel application of normal bark-tearing behavior (Morse 1980). The skill passed rapidly to other titmice, forcing milk companies to replace the cardboard caps with sturdier aluminum ones. The tits learned to open the aluminum caps, too.

Behavioral innovation is not equally distributed across all birds. Innovation increases with forebrain size across a variety of bird species (Lefebvre et al. 2001).

Some birds use tools in feeding. There are many observations of different species of herons placing objects on the surface of water as bait to attract fish. Similarly, Burrowing Owls use mammal dung to attract one of their main prey: dung beetles. Burrowing Owls routinely gather dung and place it around the entrance to their nest burrows as bait. Doug Levey and his colleagues (2004) found that owls consumed 10 times as many dung beetles and six times as many dung-beetle species when dung was present than when it was absent (Figure 7–22).

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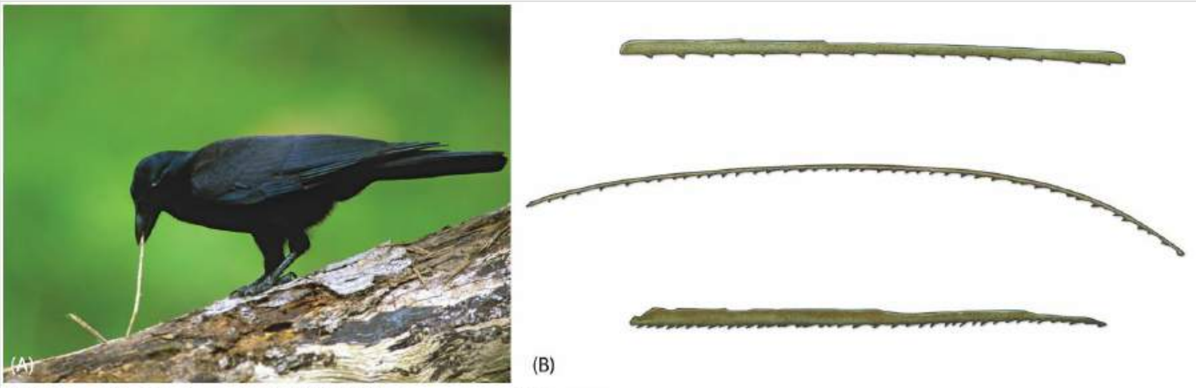
DATA FROM LEVEY ET AL. 2004. PHOTO: MAURICIO S. FERREIRA/SHUTTERSTOCK.COM

Figure 7–22 Number of dung beetles eaten by Burrowing Owls in the presence (blue) and the absence (orange) of cow dung positioned at their burrows.

Like chimpanzees, the long-well-known Woodpecker Finch of the Galápagos pries grubs from crevices with a stick or a cactus spine held in its bill. Other instances of probing and prying have since been recorded, but the making of tools by New Caledonian Crows is the premier example of advanced toolmaking by birds (Hunt 1996; Hunt and Gray 2003; Figure 7–23). These crows “craft” a variety of hooked tools by first selecting the raw material, then trimming it, and finally sculpting it into a hook. In the laboratory, one female crow named Betty figured out how to make the hooks that she needed to get food from inside a tube by crafting them from metal wire. Beyond her use of a novel material, Betty also chose, from a large assortment of wires in a toolbox, the wire of the correct length and diameter to make a functional tool (Weir et al. 2002). New Caledonian Crows craft a particular tool from the leaves of a screw pine (*Pandanus*) by alternating angled cuts with horizontal rips. They use the tools for extracting insect prey from crevices. The fundamentals required—standardization, discrete tool types with deliberate sculpting, and the creation of hooks—are not known in any free-living nonhuman organisms. Further, the design of the leaf tools has diversified with the passage of time throughout the island of New Caledonia, reflecting a cumulative cultural technology. The crow has developed the cultural capacity to evolve its tools in ways that resemble the feats of the early ancestors of modern humans.



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(A) Auscape International Pty Ltd/Alamy

Figure 7–23 (A) New Caledonian Crow probing for insect food with the use of a self-fashioned tool. (B) Selection of tools crafted by New Caledonian Crows.

REVIEW KEY CONCEPTS

7.1 Vision

Birds have a highly advanced visual system. Their large eyes have a high density of rods and cones, and they focus by changing the shape of both the lens and the cornea. Many aerial foraging birds have two retinal foveae to achieve extra visual acuity when looking forward and to the sides. The pecten functions as an oxygen and nutrient radiator into the vitreous and allows birds to reduce visual interference from retinal blood vessels.

Birds have four different color-sensitive cone types in the retina: red, green, blue, and ultraviolet or violet cones. Thus, birds have four-color vision. Avian cones are more finely tuned than human cones. In addition, the avian red, green, and blue cones have oil droplets with carotenoid pigments that refine the sensitivities of these cones. Consequently, birds can distinguish much finer gradations in hue than humans can. Humans are “color blind” with respect to birds, but we can analyze avian color perception using a tetrahedral color space.

Key Terms: ultraviolet, nictitating membrane, cornea, lens, retina, pupil, iris, tapetum lucidum, optic nerve, rods, cones, double cones, fovea/foveae, pecten, retinal, opsin protein, oil droplets, tetrahedral color space, hue, chroma

7.2 Hearing

Birds have a typical reptilian ear with an eardrum, a single middle ear bone (the columella) and a cochlea, or inner ear. Airborne vibrations of the eardrum are transmitted to the cochlea by the columella. Ciliated hair cells sense vibrations in the fluid-filled cochlea, and nerves transmit these impulses to the brain. Owls are extremely sensitive to low-volume sound. Surprisingly, however, most birds are more limited in acoustic sensitivity—in both breadth of frequency and volume sensitivity—than humans. Birds use binaural comparison to locate sounds. A few lineages of cave-dwelling swiftlets and the oilbird have evolved the capacity to echolocate using clicking calls.

Key Terms: columella, eardrum, cochlea, hair cells, hertz (Hz), kilohertz (kHz), binaural comparison, echolocation

7.3 Balance and Mechanoreception

Balance, equilibrium, and spatial orientation are essential to flight and are thus vitally important for birds. The semicircular canals and the statoliths of the inner ear provide birds with information about their orientation and movement, respectively, in three dimensions. Mechanoreceptors in their muscles give birds information about their position in space. Mechanoreceptors in their bills provide birds with tactile information that is used in foraging as well.

Key Terms: semicircular canals, statoliths, mechanoreception, proprioception, Herbst corpuscle

7.4 Chemoreception: Taste and Smell

Long ignored by most researchers, the taste and olfactory receptors of birds are receiving renewed research attention. Birds have lost one taste receptor protein that reptiles and mammals use in the sweet receptor, but hummingbirds have evolved a receptor that is highly sensitive to sweet from their umami taste receptor protein. Although the olfactory bulbs in their brains are small, many birds have acute senses of smell, which can be useful in foraging, as in kiwis and New World vultures, or in social communication, as in Parakeet Auklets.

Key Terms: taste buds, *T1R* genes, umami, pheromone

7.5 Bird Brains

Birds have complex, compact, and highly efficient brains. Many birds rival primates in intelligence using many fewer brain cells. The center of avian intelligence and learning—the hyperpallium—is similar to the mammalian cortex in complex cellular function but completely distinct in its layered, anatomical organization. Many birds achieve prodigious tasks of spatial learning—like food storage and brood parasitism—with an enlarged hippocampus. The growth of new brain cells, or neurogenesis, is broadly distributed in vertebrates but was first discovered in the song-learning systems of canaries. Birds and mammals have convergently evolved the capacity for slow-wave and rapid-eye-movement sleep, which help restore brain function. Birds can sleep with one-half of their brain at a time, and some birds sleep during long flights.

Key Terms: forebrain, midbrain, hindbrain, hyperpallium, hippocampal complex, neurogenesis, slow-wave (SWS) sleep, rapid-eye-movement (REM) sleep

7.6 Cognition and Intelligence

Birds are capable of many advanced cognitive tasks, including understanding object permanence, delay of gratification, planning for the future, counting, and transitivity—inferring information about objects by comparing them to another object. Tool use has evolved multiple times in perching and nonpasserine birds. Many social birds are capable of behavioral innovation and insight learning from observation and imitation of others. Birds often apply their intelligence in strategic and efficient foraging.

Key Terms: cognition, Krushinsky problem, insight learning, behavioral innovation

APPLY YOUR KNOWLEDGE

1. Describe the anatomy of the avian brain, the locations of functional regions, and the roles they serve.
2. Evaluate the derogatory term “bird brain” in light of new discoveries suggesting that bird brains exceed those of many mammals. What new or improved skills would you have if you had a bird brain?
3. Describe the features of a bird’s retina that enable high-resolution vision and broad color perception and color space.
4. Explain how sound entering the avian ear is transmitted through the ear and transduced to nerve impulses that arrive in the auditory center of the brain.
5. How can Barn Owls locate and catch moving prey in total darkness?
6. Compare and contrast the structures and functions of the cerebral cortex of mammals and the hyperpallium of birds. How are they similar? How are they different?

7. Explain how functional lateralization of the bird brain affects behavior and can enhance different modes of sleep under different conditions.
8. Describe experiments that support the observations of birds’ powers of memory, cognition, and intelligence.

CHAPTER 8 *Vocalizations*

Michal Pesata/Shutterstock.com

The avian vocal organ—the syrinx—is incredibly efficient. The tiny 10-gram male Winter Wren can produce a loud and brilliantly dynamic cascade of song with a syrinx that is only a few millimeters across in size.

8.9 Female Song and Duets

8.10 Songs and Mates

> Birds have the greatest sound-producing capabilities of all vertebrates, and their vocal repertoires are among the richest and most varied in the animal kingdom. [MARLER AND HAMILTON 1966]

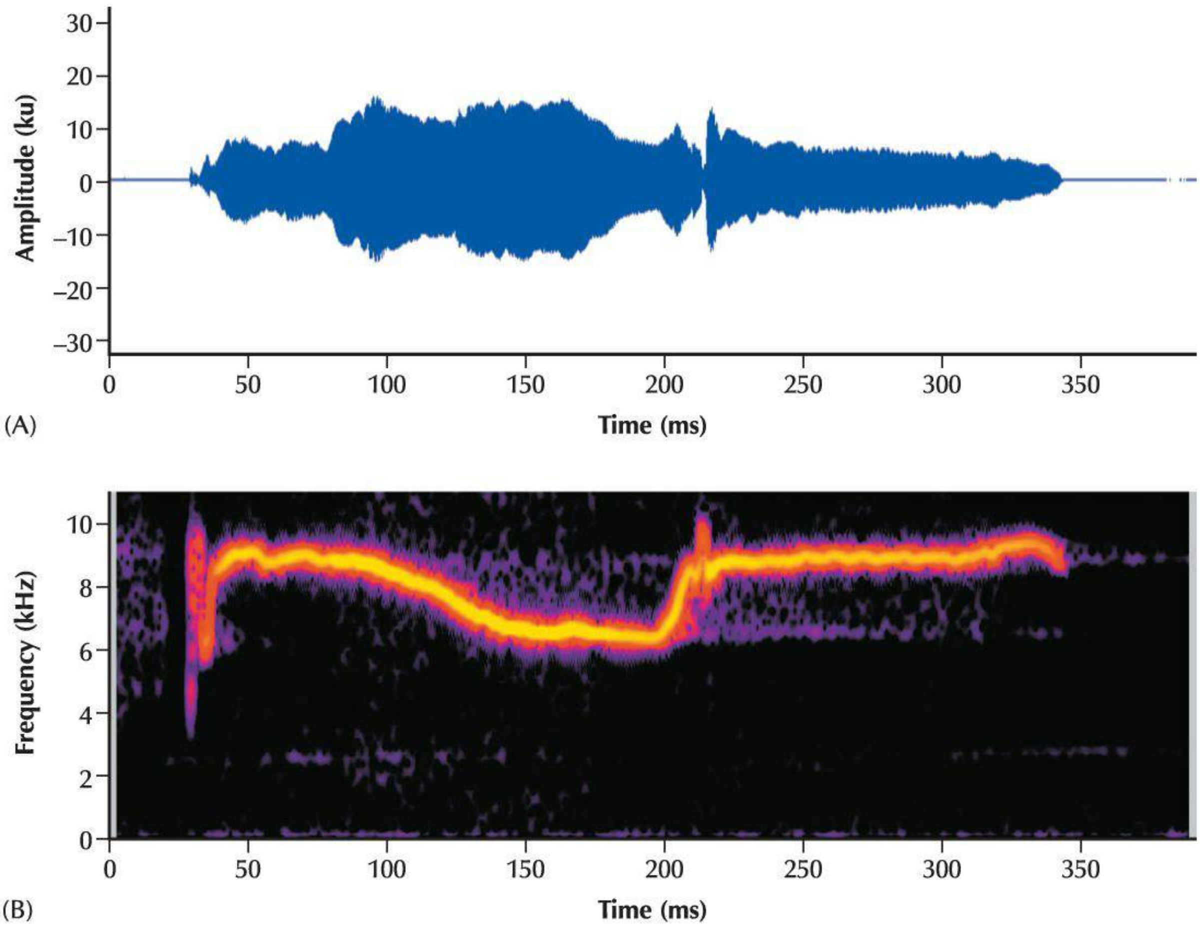
The vocalizations of birds are among the most diverse, complex, and even beautiful aspects of the biology of birds. From the fluty songs of the Wood Thrush to the stream of imitations of the Northern Mockingbird, birds produce some of the most striking social signals of all animals. Avian vocalizations also include the simple begging calls of baby chicks in the nest and the predator warning calls of flocking birds. Vocalizations provide species-specific social and sexual signals and function in many aspects of the lives of birds. For cryptically colored species, like nightjars and tyrant flycatchers, vocalizations can be more distinctive than their plumages. Interestingly, the diversity and complexity of avian vocalizations are made possible by the unique avian vocal organ—the syrinx—which provides them with vocal capabilities that no other organisms can rival. Some birds can even produce two different, simultaneous sounds at the same time with different sides of their syrinx—a vocal capacity unknown in other vertebrates.

This chapter begins with the physical characteristics of bird vocalizations and examines how the syrinx and the brain interact to produce these sounds. Then follows the process of how some groups of birds learn their songs, including the development of specific neural pathways in the brain and the resulting formation of regional dialects or “accents” within a species. Vocal repertoires and displays are central to reproductive success and subject to sexual selection, just as are plumage ornaments and visual displays. The final section of this chapter explores the roles of song repertoires and vocal displays in species recognition, the choice of superior mates, and the maintenance of pair bonds.

8.1 Physical Attributes

Bird vocalizations range from the short clicks of swifts; to the quavering whistles of the tropical tinamous; to the long, tinkling melodies of wrens; and to the seemingly endless imitations of other birds by mockingbirds and lyrebirds. They range in pitch from deep infrasounds to high pitches inaudible to older human ears. Some bird species are virtually silent; others are garrulous. At one extreme, Mute Swans, Turkey Vultures, and Greater Rheas merely hiss and grunt occasionally. At the other extreme are the seemingly unlimited repertoires of mynas, parrots, mockingbirds, and skylarks.

Sound is composed of pressure waves that propagate through the environment. Birds can communicate with sound because sound waves that are made by one individual travel through the air to where they can be heard by another individual. The variety of birdsongs is the result of variations in **frequency** (pitch) and **amplitude** (energy or loudness) of the sound waves. Birds have a unique capacity to modulate, or control, frequency and amplitude compositions of their vocalizations (Box 8–1). Ornithologists can describe and analyze the complex composition of avian vocalizations by examining the **waveform**—a picture of the sound pressure waves—and the **sonogram**—a picture of the different frequency components of the sound (Figure 8–1).



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HANS BILGER. DATA FROM STOKES, D.W., THE NEW STOKES FIELD GUIDE TO BIRDS: EASTERN REGION (LITTLE, BROWN AND COMPANY, 2013)

Figure 8–1 Complex modulations of frequency and amplitude characterize the song of the Brown-headed Cowbird. (A) Waveform of the *glee* phrase, in which the rapid cycles of the sinusoidal waveform cannot be individually distinguished. (B) A summary of the succession of frequencies composing the phrase. Note the rapid frequency modulations at 35 and 200 milliseconds.

BOX 8–1

A Vocabulary for Sounds and Vocalizations

Discussions of bird vocalizations require a small, specialized working vocabulary of terms from acoustics (the physics of sound) and music.

Amplitude Loudness, volume, or maximum energy content of a sound.

Amplitude is measured in decibels (dB) or pascals (Pa).

Filtering The elimination or diminution of some frequency components of a sound by reverberation off of surfaces. Filtering by the airway can eliminate harmonics during post-source modulation.

Frequency Number of complete cycles per unit time completed by an oscillating sound waveform; usually expressed in hertz or kilohertz. Variation in frequency is perceived as pitch; high and low frequencies are perceived as high and low pitches.

Fundamental frequency (see **Harmonic**).

Glissando A blending of one tone into the next in a scalelike passage.

Harmonic A series of pitches naturally produced simultaneously with a fundamental frequency. The frequencies of a harmonic series of tones are consecutive multiples of the fundamental frequency.

Hertz (Hz) Unit of frequency equal to one cycle per second. The high frequencies of birdsong are often reported in kilohertz (kHz), or thousands of cycles per second.

Modulation Control of the form of a sound by variation of either frequency or amplitude (or both).

Overtone (see **Harmonic**).

Pitch Relative position of a tone in a scale, as determined by its frequency.

Post-source modulation Control of the composition of a sound after the syrinx by filtering and resonance of the airway.

Resonance The intensification or prolongation of a sound, especially of a musical tone, produced by reverberation off of, or sympathetic vibration by, surfaces. A constructive mechanism of post-source modulation.

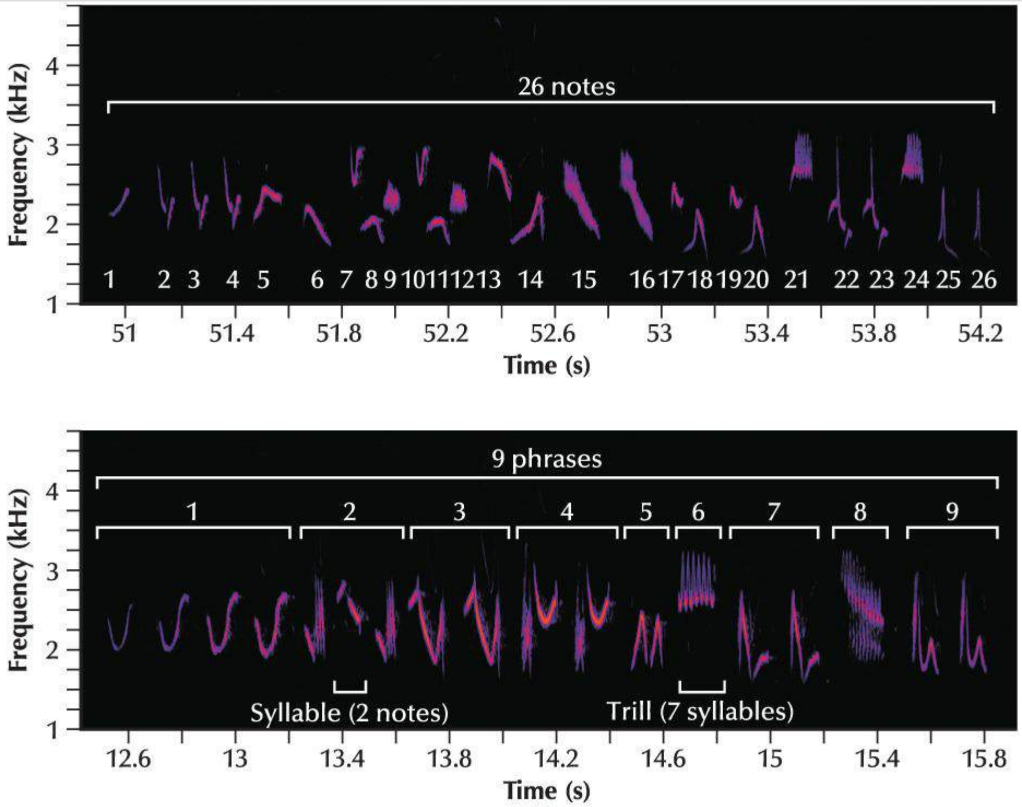
Sonogram Visual display of the frequency content of a sound distributed in relation to time. The *y*-axis depicts the frequency or pitch content of the sound, and the *x*-axis depicts the change in frequency composition over time. Darkness and color scale indicates amplitude or volume.

Tone A sound of distinct pitch and quality; in music, the interval of a major second.

Waveform The physical energy of a sound wave depicted as a graph of the air pressure (in decibels or pascals) over time. The height, or amplitude, of the waveform is a measure of volume. A sonogram is the decomposition of the frequency components of a complex waveform.

Simple pure tones, such as the notes of a White-throated Sparrow, contain little modulation, whereas the variable songs of a Song Sparrow and the brief notes of a Tree Swallow contain complex, rapid frequency modulations. Even short phrases within songs may include rapid frequency and amplitude modulations. The brief *glug glug glee* song of the Brown-headed Cowbird spans a four-octave interval from 700 to 11,000 **hertz,** or cycles per second, which is the greatest frequency range known in a single birdsong. In one four-millisecond fraction of the *glee*, the signal rises continuously from five to eight kilohertz, an amazingly rapid glissando (see Figure 8–1). Female cowbirds select males on the basis of their abilities to perform such vocal gymnastics.

A traditional distinction has been made between “songs” and “calls,” but the two categories remain difficult to define strictly. The term **song** usually refers primarily to the loud, often long vocal displays of territorial or courting male birds. Specific, repeated patterns are often pleasing to the human ear. The primary components of a birdsong are notes, syllables, phrases, and trills (Figure 8–2). The term **call** often connotes a short and simple vocalization, usually given by either sex. Various calls include distress calls, flight calls, warning calls, feeding calls, nest calls, flock calls, and nocturnal migration calls. There is, however, no strict dichotomy between songs and calls in their acoustical structure, delivery, physiology, development, function, and taxonomy, all of which have served as criteria for different definitions of "song" in birds (Spector 1994; Baker 2001). Despite the lack of a single accepted definition, we continue to use the term *song* because it is so entrenched, and because we lack better alternatives.



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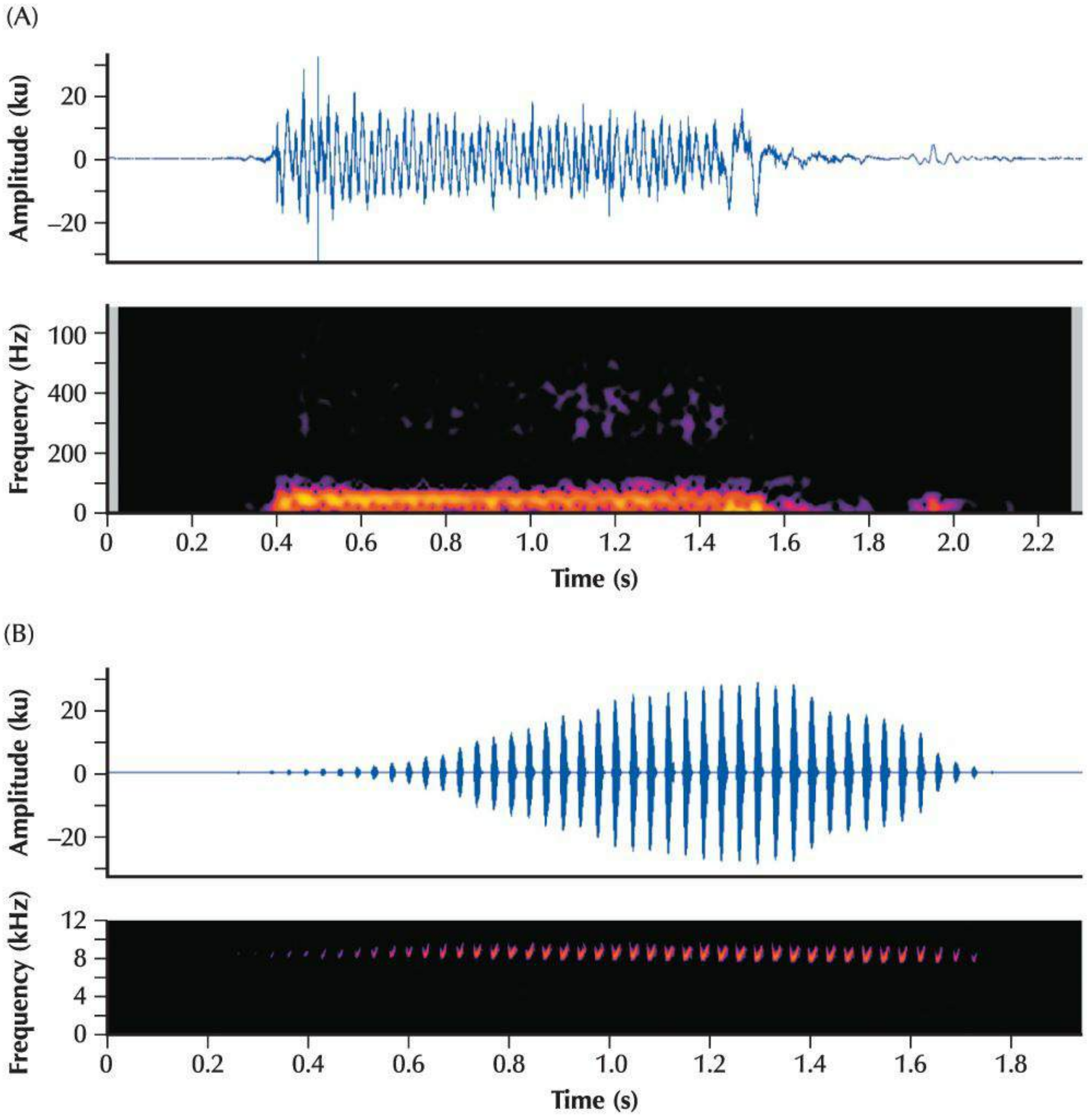
Hans Bilger. Data from Stokes, D.W., L. Stokes and L. Elliott, The Stokes Field Guide to Birds: Eastern Region (Little, Brown and Company, 2013)

Figure 8–2 Components of a birdsong, as illustrated by two songs of (*Top*) Indigo Bunting (*Passerina cyanea*) and (*Bottom*) Lazuli Bunting (*Passerina amoena*). Notes and syllables are the principal basic units. They may appear as a single continuous trace on a sonogram or as a set of two or more different notes that occur together and are separated from other such groups of notes. Phrases are groups of repeated syllables. Trills are rapid repetitions of three or more (simple-note) syllables.

A fundamental dichotomy, unlinked to the function of songs versus calls, defines the acoustical structure of bird vocalizations: pure-tone whistled songs versus harmonic songs (Greenewalt 1968). Whistled songs consist of nearly pure sinusoidal waveforms—the higher the pitch, the more frequent the oscillations of the sound waves. Both the basso profundo (80–90 hertz) of a Spruce Grouse and the high, thin notes (9,000 hertz) of a Blackpoll Warbler are, technically speaking, whistled songs (Figure 8–3).



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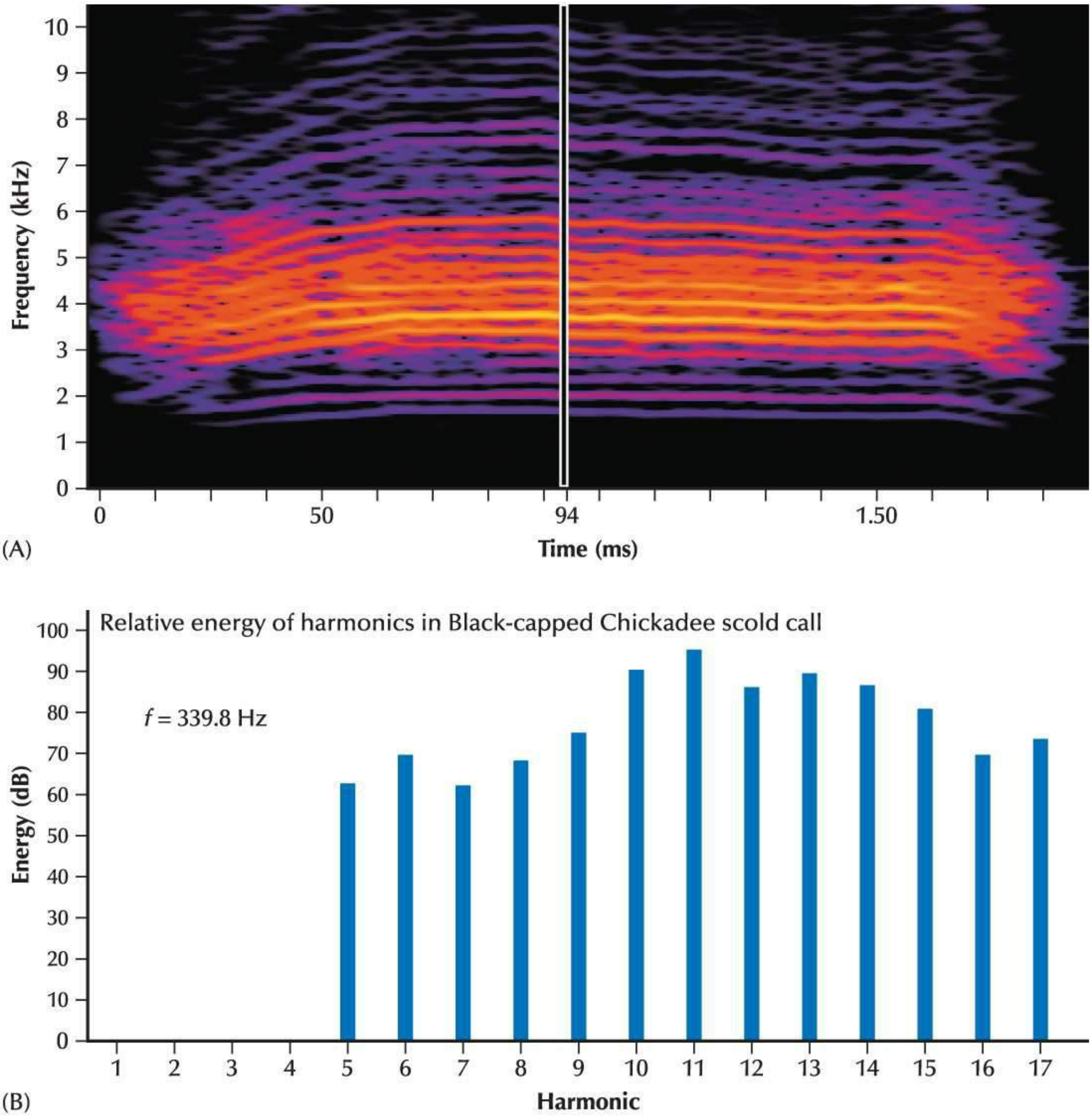
Hans Bilger. Data from Tayler Brooks, XC59161. Accessible at http://www.xenocato.org/59161

Figure 8–3 Birds can produce a striking diversity of sounds. (A) The Spruce Grouse produces very low frequency bass notes (90 cycles per second = 90 hertz). (B) The whistled song of a Blackpoll Warbler includes high, thin notes (9 kilocycles per second = 9 kilohertz). The waveforms (upper graphs) display the amplitude, or the change in air pressure by the sound, as the vertical deflection (above and below the midpoint) of the waveform. The sonograms (lower graphs) display the distribution of energy of the sound into its frequency components. Frequency is the number of complete cycles in a song with respect to time per second (1 kilocycle per second = 1 kilohertz).

Harmonic songs include overtones with **harmonic frequencies** that are multiples of the **fundamental frequency.** The number of harmonics and their relative amplitudes determine the timbre, or general tonal quality, of the notes of birdsongs, in the same way that they produce the distinctive sounds of musical instruments playing the same note. Qualities such as clarity, brilliance, and shrillness, as well as nasal, hollow, and hornlike tones, are due to various combinations of harmonics and their emphases (Figure 8–4). For example, the distinctive sounds of a clarinet and a Hermit Thrush result from an emphasis on the odd-numbered (3, 5, 7, etc.) harmonics (Marler 1969).



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Hans Bilger. Data from Kroodsma, D., The Singing Life of Birds: The Art and Science of Listening to Birdsong (New York:Houghton Mifflin Harcourt, 2015)

Figure 8–4 The *dee-dee-dee-dee* scold call of a Black-capped Chickadee consists of a series of notes with complex harmonic content. (A) Sonogram of one *dee* phrase. Each horizontal line is a harmonic, or integer multiple, of the fundamental frequency. Chickadees increase the number of these phrases in relation to the threat of predation (see Box 8–2). (B) The frequencies and relative amplitudes of the tones of the harmonic series. (Should be viewed as a section along the black vertical line in the sonogram in A, with the amplitude, or darkness, depicted on the *y*-axis.) The fundamental frequency, *f*, is 339.8 hertz. Numbers on the *x*-axis represent the frequencies of the harmonics as multiples of the fundamental (1; *f* at 339.8 hertz). The loudest tone is the eleventh harmonic, which is assigned an amplitude of 100 percent. The amplitudes of the other tones are calculated relative to that value.

Birdsong has much in common with human music and speech, having similar sounds, tones, and tempos. Furthermore, birdsong is produced by a series of rapid and complex motor activities, much like those controlling the tongue of a person speaking or the fingers of a skilled violinist playing an intricate passage (Marler 1981; Suthers et al. 1999). Some of the pure high-pitched whistles of birds are quite like the notes from a human-made flute. However, the avian vocal system is a new instrument (Smyth and Smith 2002).

The acoustic structure of a sound affects the ease with which a listener—either a predator or a neighbor—can locate its source. Birds locate a sound source by binaural comparison, comparing the difference in arrival time of the sound waves to their two ears (see Chapter 7). As a result, sounds with abrupt “edges” and lots of simultaneous frequencies, like a finger snap, will be easier to locate than pure-tone sounds that change slowly in amplitude. As predicted, the calls that birds use to locate or attract one another or warn against a terrestrial predator, like a snake, are made up of short notes with broad frequency ranges that provide more information about direction and distance. In contrast, alarm calls that warn against aerial predators like hawks (which can attack the caller if its position is revealed) are faint, thin (narrow frequency range), high-pitched calls of long duration and limited amplitude modulation that conceal the sender’s whereabouts.

The physical structure of a particular sound also affects the distance that it will travel and how much distortion, called attenuation, that it will sustain before reaching the listener. Interference, absorption, and scattering of the sound waves by vegetation, the ground, and the air itself progressively distort sounds as they travel. Low-frequency sounds, such as the calls of grouse, bustards, cuckoos, doves, and large owls, are the most effective for long-distance communication; they are less subject to attenuation and interference than are high-frequency sounds. Reverberations off forest vegetation can mask or degrade the fine temporal structure of birdsongs. Forest-dwelling birds, therefore, tend to produce simpler sounds. Conversely, broadband songs rich in temporal structure (with complex frequency modulations) are advantageous in open habitats because simple, sustained tones tend to be distorted by strong temperature gradients and air turbulence. Thus, the complex buzzy songs of open-field birds, such as Grasshopper Sparrows, contrast with the simpler clear whistles of forest birds, such as Rose-breasted Grosbeaks.

Birds evolve or adjust their singing behavior in relation to their sound environment. Even hummingbirds sing louder in the presence of increased background noise, such as that of a nearby creek (Pytte et al. 2003). Urban noise, in particular, now affects the ability of birds to communicate with one another. Just as we humans have a hard time hearing birds singing at a distance because of the intense background noise of traffic and so forth, so do birds. Low-frequency sounds prevail in urban noise. To communicate more effectively in an urban environment, male Great Tits in Leiden, Holland, now sing at higher frequencies above the background noise than do male Great Tits in quieter places (Slabbekoorn and Peet 2003).

Some birds can hear low-frequency sound called **infrasound,** which is below the range of human hearing (see section 7.2 in Chapter 7). Elephants and some whales talk to other members of their species over long distances by using infrasound below 20 hertz. Birds were not known to do so until one recent discovery. Cassowaries—large flightless, solitary birds of the dense rain forests of New Guinea—produce low, pulsed booms of infrasound as low as 23 to 32 hertz that are felt as strange vibrations by humans (Mack and Jones 2003). These low-frequency sounds are ideal for communication between cassowaries over long distances through thick forests, just as they are for elephants that keep track of one another in the dense forests of West Africa. Exactly how a cassowary produces the low, booming notes is not known, but it may involve resonance through the distinctive casque on the top of their skull.

8.2 Repertoire Size and Communication

Most birds have from five to 14 distinct vocalizations of varied acoustical structures and overlapping functions that form the vocal **repertoire** of the individual. The Chaffinch of Europe, the subject of pioneering studies of birdsong, renders 12 adult sounds, seven of which are used only in the breeding season—six by the male and one by the female (Table 8–1). The functions of these calls include proclamation of territorial ownership, attraction of mates, broadcast of personal characteristics (species, age, sex, and competence), warning of potential dangers, and maintenance of social contact. Most birds also have calls that are used only occasionally for special purposes. Alarm calls, which signal danger and advise escape flight, can even tell flock mates which predator is threatening (Box 8–2). Precopulatory trills and postcopulatory grunts integral to mating ceremonies are heard at no other time.

Table 8–1 ***Repertoire of the Common Chaffinch***

Vocalization	Transcription	Context
Flight call	*tupe* or *tsup*	Flight or flight preparation
Social call	*chink* or *spink*	Seeking companion of unknown whereabouts
Injury call	*seeee*	Injured in flight
Aggressive call	*zzzzzz* or *zh-zh-zh*	Fighting (captive males only)
Alarm calls	*tew*	Danger, used especially by

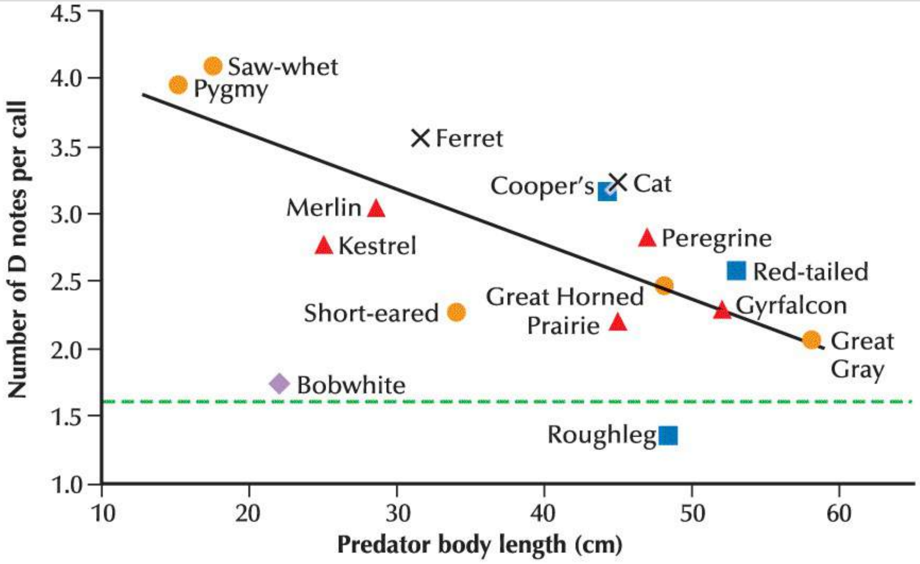
		young birds
	seee	Escaping a real threat, just after copulation (breeding males only)
	huit	Moderate danger or after real danger (breeding males only)
Courtship calls	*kseep*	Active courtship (breeding males only)
	tchirp	Ambivalence toward approach and copulation with female (breeding males only)
	seep	Ready for copulation (females only)
Subsong		Practice of real song
Song		Territoriality, identification, and courtship; average is two or three per male, as many as six

DATA FROM MARLER (1956).

BOX 8–2

Chickadees Tell Flock Mates Which Predator Is Lurking

When alarmed, Black-capped Chickadees typically start to scold with their familiar *chick-a-dee dee dee* call. In fact, one of the best ways to find an owl is to seek what chickadees are scolding. Studies of the scolding behavior of chickadees in Montana have revealed that chickadees rank predators according to their size and potential threat (Templeton et al. 2005). A chickadee tells its flock mates which type of predator it has spotted and the degree of threat posed by the predator. The chickadee increases the number of *dee* syllables as the potential threat increases. Small owls (with short wings) are more likely than big owls to catch a chickadee, so small owls elicit the most *dee*’s.



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DATA FROM TEMPLETON ET AL. 2005

Chickadees react to predator body size and potential threat by increasing the average number of *dee* syllables. Big predators that pose minimal threat elicit only two *dee*’s; little owls elicit four dee’s. Different symbols indicate each taxonomic group of raptors: circle, owl; triangle, falcon; square, hawk; X, mammal.

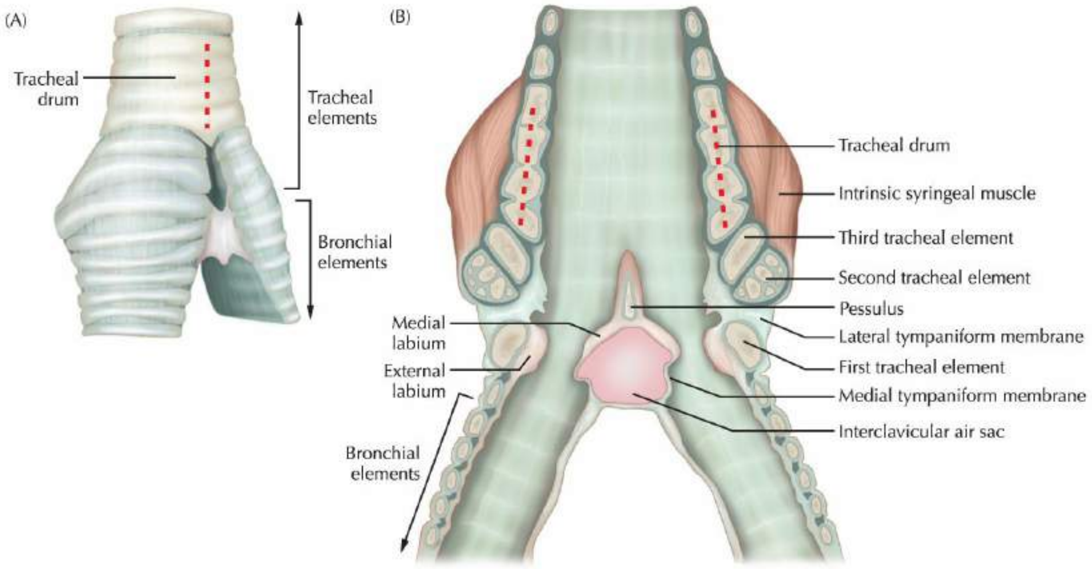
Among different species of songbirds, the repertoires of territorial songs alone vary from the single song type of the White-throated Sparrow and the two distinct territorial songs of many species of North American wood warblers to the hundreds of songs used by some wrens and mockingbirds. Among wrens, Canyon Wrens have but three simple songs per individual bird, whereas individual Sedge Wrens have more than 100 songs (Kroodsma 1999). Repertoire size can also vary among populations. Marsh Wrens in eastern North America have repertoires of around 40 songs, whereas western Marsh Wrens have repertoires of over 100 distinct songs (Kroodsma and Canady 1985). Even though Pacific Wrens in Oregon have a relatively small repertoire of roughly 30 songs per individual bird, each of these songs is extraordinary and variable. Lasting a full eight seconds, their songs are composed of organized sets of syllables, each consisting of 50 notes selected from a pool of 100 (Kroodsma 1980).

In addition to species identity, bird vocalizations can also communicate individual identity and sex, with implications for social status, pair bonds, and family relationships. Details of song pitch, phrase structure, **syntax** (the ordering of notes and phrases), and composition serve as individual signatures that enable birds to identify offspring, parents, mates, and neighbors. White-throated Sparrows, for example, use variations in pitch to this end. Ovenbirds use variations in the structure of the phrase that can be verbalized as *téa-cher*, and Indigo Buntings use groups of repeated syllables as individual signatures. Discrimination of individual vocalizations enables mates to recognize each other. The choppy, accelerating trills of Sedge Wrens are composed of an individually unique note repeated in a rapid, species-specific sequence (Kroodsma et al. 1999). Colonial seabirds—penguins in particular—use unique vocalizations to distinguish their partners from the hordes of potentially antagonistic neighbors (Jouventin and Aubin 2002). Individual vocal differences also enable birds to distinguish neighbors from strangers and to respond accordingly. Territorial males concentrate their defense efforts against strangers and accommodate neighbors as long as they stay where they belong—in their own territories.

8.3 Sound Production by the Syrinx

The scientific literature on bird vocalizations began almost 400 years ago with the observation by Ulyssis Aldrovandi that ducks and chickens could call even after their heads were chopped off; the source of the vocalizations was apparently located in the body and not the head. The source of avian vocal abilities is, in fact, a unique organ—called the **syrinx**—that operates with nearly 100 percent physical efficiency to create loud, complex sounds and, in many birds, can produce two independent songs simultaneously.

From frogs to humans, most vertebrates vocalize with the larynx and hyoid apparatus, which are located at the top of the trachea at the back of the oral cavity. However, the avian hyoid has become the bony tongue of birds, and the larynx functions only to open and close the glottis, and thereby keep food and water out of the respiratory tract. Thus, at some point since common ancestry with alligators and crocodiles, the ancestors of modern birds were evolutionarily silenced. In order to reacquire the capacity to vocalize, birds evolved a novel vocal organ: the syrinx. This complex, anatomically diverse organ is located deep in the body cavity behind the heart near the junction of the trachea and the two primary bronchi (Figure 8–5A). It resembles a Y-shaped vacuum cleaner hose; it is composed of the thin **syringeal membranes** of the airway, cartilaginous or bony **syringeal supporting elements** that keep the trachea and bronchi from collapsing, syringeal muscles that attach to the supporting elements and membranes, and **syringeal nerves** that control the contractions of the muscles. The syrinx itself may include portions of both the trachea and the bronchi, the trachea alone, or the bronchi only. Critically, the syrinx is located *inside* of the air-filled interclavicular air sac.



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DATA FROM HÄCKER 1900

Figure 8–5 (A) Bird vocalizations are produced by the syrinx, an elaboration of airway that is typically located at the junction of the trachea and the two bronchi. The syrinx is made of tracheal elements (Neotropical woodcreepers, antbirds), bronchial elements (cuckoos, nightjars, owls), or both tracheal and bronchial tissues (most birds including the syrinx of the oscine perching bird shown here). (B) The elements of the syrinx are its vibrating membranes, supporting cartilages, the muscles that control tension in the membranes, and the nerves that innervate those muscles.

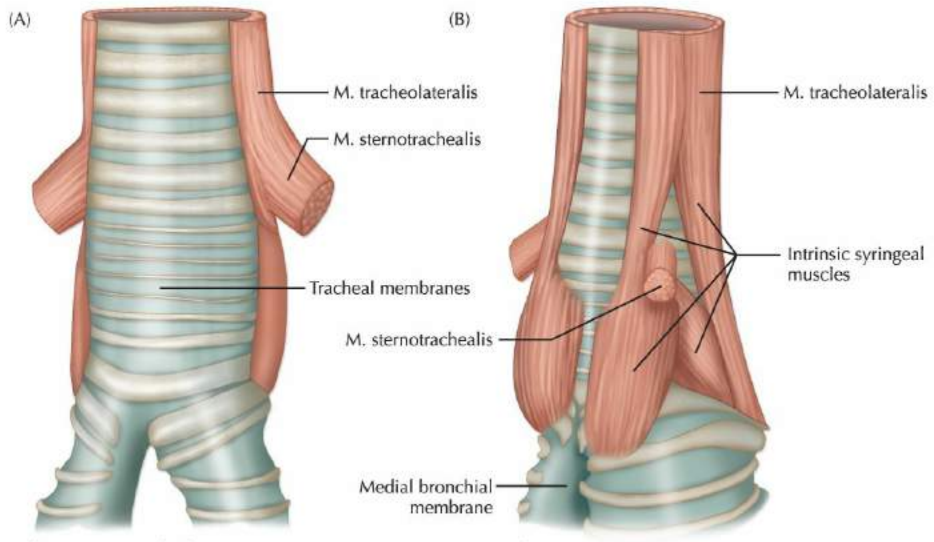
The efficiency of sound production by the syrinx is extraordinary; nearly 100 percent of the air passing through it is used to make sound, compared with only 2 percent in the human larynx. Consequently, birds can produce some of the loudest vocalizations of all terrestrial animals. The Neotropical bellbirds, in the cotinga family, produce startlingly loud songs that can be heard more than a kilometer away.

Even the tiny, 10- to 12-gram male Winter Wren produces its lively, complex, and dynamically modulated cascade of song with a syrinx that is only a few millimeters in diameter. The vocal capacity of birds is truly stunning.

Sound is caused by the compression of the air column as it passes through the syrinx. All syringes produce sounds as a result of the Bernoulli effect, which you may recall from avian flight (see Chapter 5). Air traveling through the syringeal passageway will result in lower static pressure against the syringeal membranes. Because the syrinx lies in the airspace inside of the interclavicular air sac, this causes a difference in air pressure on the two sides of the syringeal membranes, which causes them to oscillate into the airway like a flag flapping in the wind. A needle puncture of the interclavicular air sac prevents buildup of the pressures needed to move the tympaniform membranes, thereby rendering a bird voiceless. However, the morphology of the syrinx is so variable that different syringes accomplish use of this mechanism to produce sound in different ways.

In oscine passerine songbirds, doves, and parrots, sound is produced as thickenings of the syringeal membranes, called the internal and external labia, constrict the narrow syringeal passageways (Figure 8–5B). The vibrations of the labia into the passageway compress the air flowing through the syrinx to produce sound (Suthers and Margoliash 2002).

The syringes of many birds, including the suboscine perching birds, lack syringeal labia and must produce their sounds through the vibrations of lateral or medial bronchial membranes (Figure 8–6). The tracheophone suboscines, including Neotropical antbirds, ovenbirds, and their relatives, have a unique tracheal syrinx with novel sound-producing membranes on the dorsal and ventral surfaces of the trachea. The nocturnal, frugivorous Oilbird has an unusual bronchial syrinx with two separate sound sources in each bronchus, but its function has not been investigated.



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DATA FROM VAN TYNE AND BERGER 1976

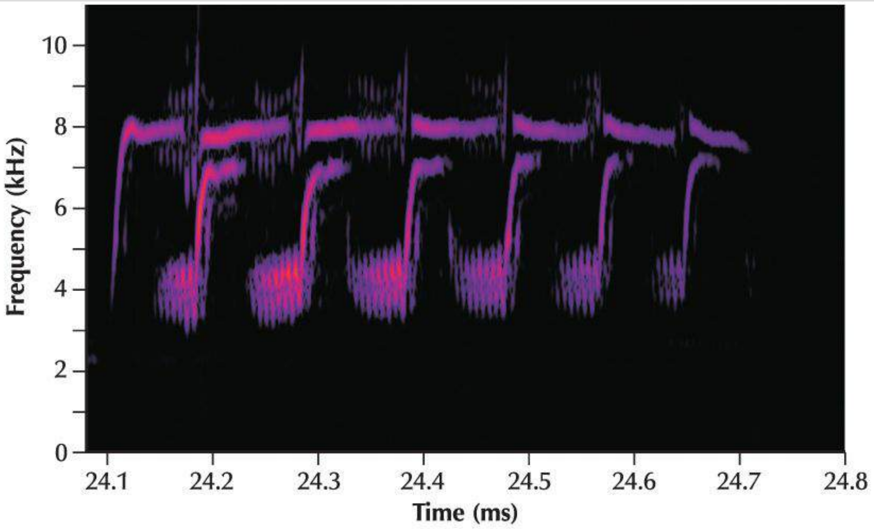
Figure 8–6 Simple and complex syringes (ventrolateral views). (A) The tracheal syrinx of the Hooded Gnateater, a suboscine passerine bird of South America, has only two pairs of extrinsic syringeal muscles. Tracheal syringes produce sound with vibration of dorsal and ventral tracheal membranes. (B) The elaborate tracheobronchial syrinx of the American Crow, an oscine songbird, has the same two pairs of extrinsic muscles and four pairs of intrinsic syringeal muscles that originate and insert on the surfaces on the syrinx.

In many species of birds, the left and right sides of the syrinx can produce different simultaneous and independently modulated songs (Box 8–3). Stunningly, many birds can sing two-part harmony with themselves.

BOX 8–3

Many Birds Have Two Independent Voices

The tracheobronchial syrinx consists of two left and right halves that many birds can control independently to produce two different, complex sounds alternatively or simultaneously (see Suthers et al. 1999; see also Figure 8–5). In addition to having different frequency content, the notes produced by the dual voices can be modulated independently of one another in frequency and volume. The two sources can also be coupled to produce a single, complex sound with unusual acoustic quality (Nowicki and Capranica 1986). The phenomenon of two independent voices has since been reported for many diverse birds, including grebes, bitterns, ducks, sandpipers, bellbirds (Cotingidae), and songbirds (Miller 1977). In most birds, the left side of the syrinx is larger in size than the right and generally produces lower sound frequencies. For example, in Northern Cardinals, the left side of the syrinx produces fundamental frequencies below 3.5 kilohertz, whereas the right side produces fundamental frequencies above 4.0 kilohertz. Depending on the frequency composition of the song, one side of the syrinx can produce most of the songs of a species. For example, in canaries, the left side produces 90 percent of the songs. In other species, such as the thrasher, the two sides contribute equally to song production. The left and right sides switch to produce successive notes of the complex song of the Brown-headed Cowbird.



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Hans Bilger. Data from Kroodsma, D., The Singing Life of Birds: The Art and Science of Listening to Birdsong (New York: Houghton Mifflin Harcourt, 2015)

The Wood Thrush can sing a “duet” with itself by using two separate voices. Shown here is a sonogram of the final double phrase of the song. The right side of the syrinx sings a series of notes on a single high frequency, while the left side of the syrinx sings a repeated trilled phrase with rapid frequency modulations. at a lower frequency.

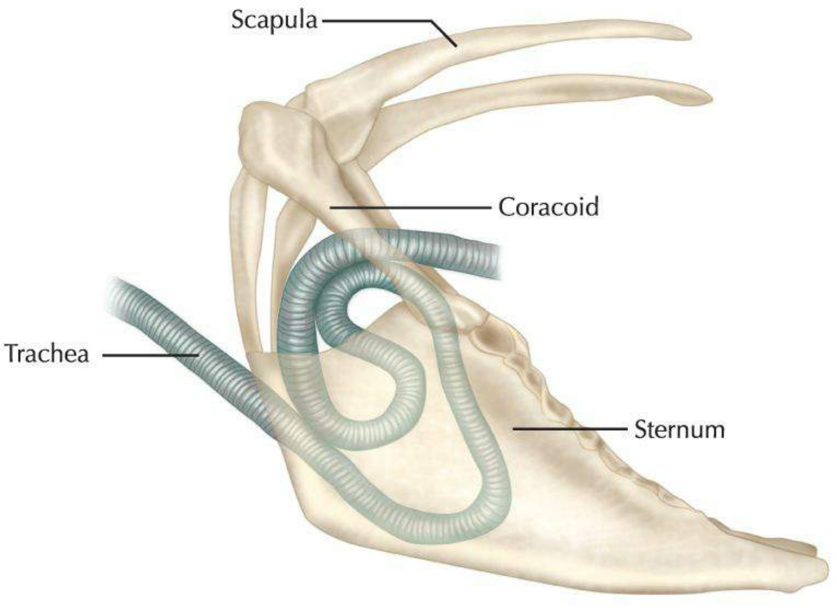
Syringeal muscles control the tension of the syringeal membranes during song production. Species that lack functional syringeal muscles, such as some ratites, storks, and New World vultures, can only grunt, hiss, or make similar, simple noises, as noted previously. Most nonpasserine birds have two pairs of narrow muscles on the sides of the trachea above the syrinx, which are called **extrinsic syringeal muscles** because they originate outside the syrinx. Many groups of birds have evolved more elaborate muscles called **intrinsic syringeal muscles** because they originate and insert within the syrinx itself. The oscine songbirds have the most complex syringes of all, with six pairs of intrinsic syringeal muscles. Even with their elaborate syringeal muscles, the vocalizations of oscines are not predictably more complex than those of birds with simpler syringeal muscles because some oscines, like crows and House Sparrows, sing simple songs with very complex vocal organs.

The syrinx is a complex organ, but the production of vocalizations is even more so. Song production requires intricate coordination among the vocal centers and neural pathways of the brain (section 8.6), the thoracic and abdominal respiratory muscles, the diameter and length of the trachea, the mouth and bill, and the two sides of the syrinx itself. The tone and pitch of a sound depends on the precise tensions and vibrations of the vocal membranes (Suthers et al. 1999).

For many years, the central nervous system was assumed to control most of the intricate details of birdsong. However, the intrinsic mechanical properties of the syrinx, combined with regulation of airflow by the respiratory muscles, also contribute strongly to the structure of birdsongs (Fee et al. 1998; Goller 1998). Contractions of thoracic and abdominal muscles force air from the main air sacs through the bronchi to the syrinx. Rapid-fire control of airflow by the respiratory system determines the temporal pattern of a vocalization. Syllables of expired air are spaced by short pauses of inspiration. Birds with long, sustained songs, such as the Common Grasshopper Warbler, breathe and sing simultaneously by using a rapid series of shallow **minibreaths** (Brackenbury 1982). Fast series of syllables can result from fast pulses of expiration without breaks for inspiration. For example, rapid vibrations of the abdominal muscles (as many as 50 cycles per second) produce the trilled whistles of young chicks (Phillips and Youngren 1981).

8.4 Post-Source Modulation

So far, we have described the modulation mechanisms that occur at the syringeal sound source. But the sounds produced by the syrinx can be modulated by filtering after the source through changes in the length, diameter, and shape of the trachea and mouth cavity (Nowicki 1987). This mechanism is called **post-source modulation.** Vocal **filtering** works by eliminating or enhancing particular source frequencies through resonance in the vocal cavity. The loud, rich, resonating, trumpetlike calls of swans, cranes, some curassows, guineafowl, and manucodes are due in part to an unusually long trachea that is coiled in the body cavity or in the bony sternum itself (Figure 8–7).



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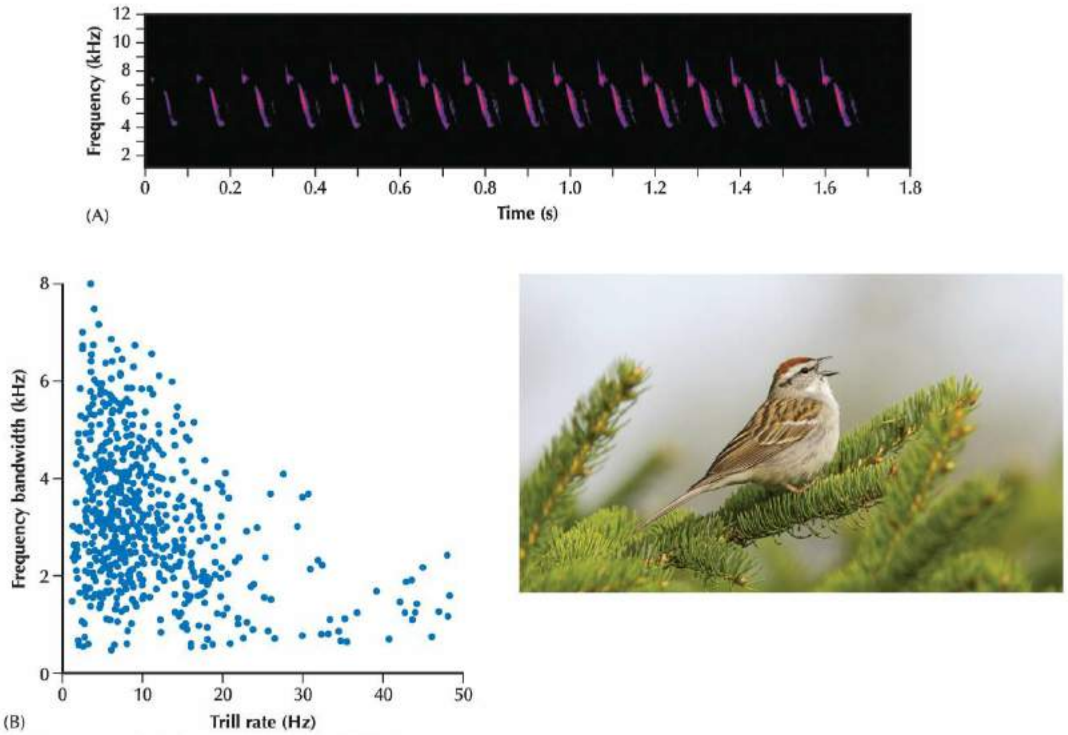
Data from Grassé 1950

Figure 8–7 A crane’s elongated trachea is coiled inside the keel of the sternum. Like a trombone, the long trachea provides a resonance chamber to enhance the volume of low-frequency contents of the sound produced by the syrinx.

Whether the trachea modulates sounds produced by the syrinx was once in dispute. Critical experiments with the use of a helium–oxygen atmosphere proved that it did. Birdsong, like human speech, is the result of rapid, coordinated output of two or more motor systems acting in concert (Nowicki 1987). These clever experiments were based on the fact the lower density of helium will influence post-source filtering without changing sound modulation at the source. (Human voices shift to a higher pitch after inhaling helium because human speech involves post-source modulation.) The helium experiments revealed that a bird's vocal tract filters the harmonic spectrum produced by the syrinx and concentrates the energy at particular frequencies.

Furthermore, a bird can actively control the filtering process by varying tracheal length, by constricting the larynx, and by opening or closing its beak. The rapid beak and throat movements of singing birds help filter out harmonics to produce pure-tone notes (Suthers et al. 1999). In other words, most sounds made by the syrinx are harmonically complex, and specific movements of the trachea and beak are required to filter out harmonics and produce pure-tone notes.

Post-source filtering creates a motor challenge for birds that sing pure-tone trills because singing a repeated series of pure tones requires the singer to move its trachea and beak as rapidly as the frequency of each pure note changes, like an acrobatic trombonist. Jeffrey Podos (1997) has shown that there is a trade-off between **trill rate**—the number of notes repeated per second—and the frequency range of each pure-tone note, called the **frequency bandwidth** (Figure 8–8). Birds can sing slow trills with large frequency bandwidths, or rapid trills with small frequency bandwidths, but they cannot sing fast trills with large frequency bandwidths. Furthermore, beak shape and feeding ecology can also constrain a bird’s ability to perform rapid post-source frequency modulation. Large, conical beaks provide lots of force for cracking open seeds, but they move less rapidly than thinner beaks. Thus, thin-billed, insect-eating warblers are able to sing complex, rapidly modulated pure-tone songs, whereas the aptly named Rose-breasted Grosbeak sings a harmonically richer, more slowly modulated song. Ecology and beak shape strongly affect the performance capabilities of different species (Box 8–4). In summary, birds with robust beaks find it impossible to wrap their beaks around songs that require rapid post-source modulations.



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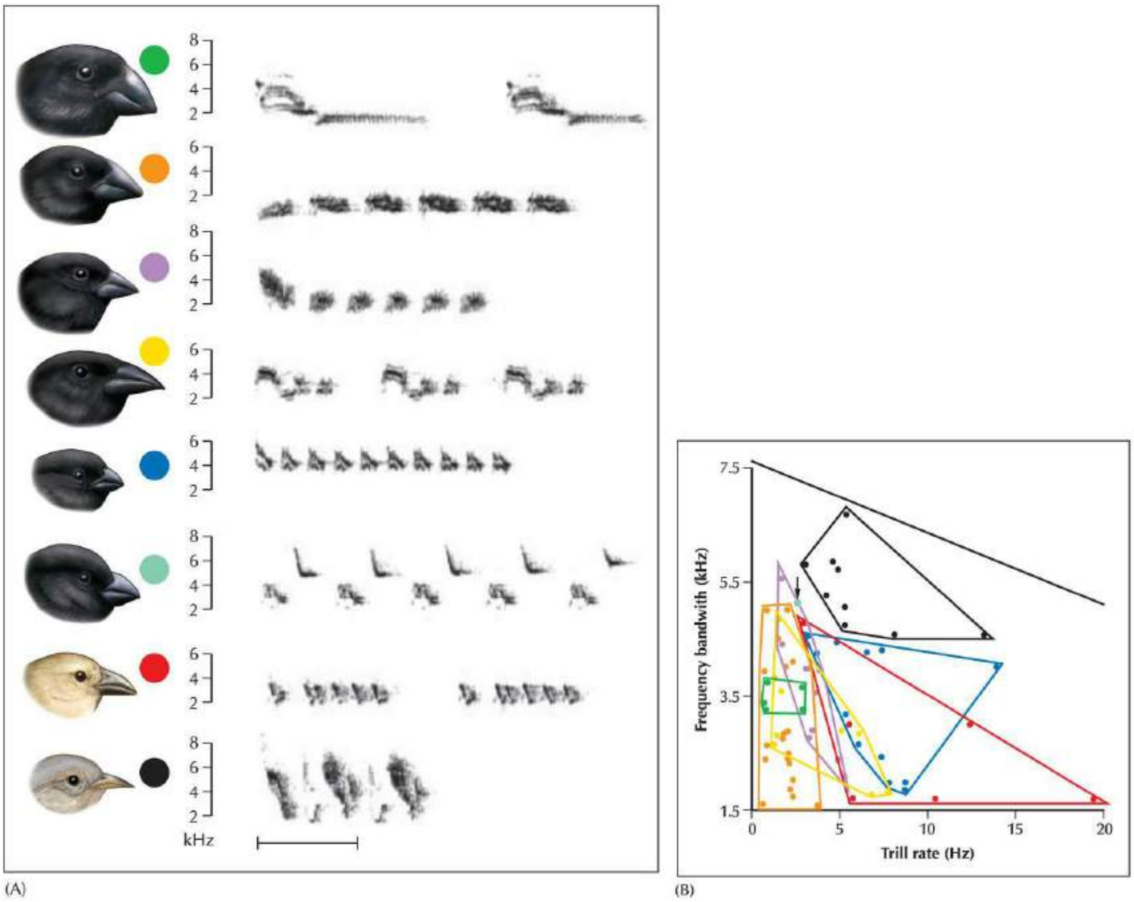
(A) Hans Bilger. Data from Kroodsma, D., The Singing Life of Birds: The Art and Science of Listening to Birdsong (New York: Houghton Mifflin Harcourt, 2015). (B) Data from Podos 1997. Photo: (Chipping Sparrow) Trevor Jones/Shutterstock.com

Figure 8–8 (A) A pure-tone trill, like this Chipping Sparrow song, is composed of a rapid series of notes that requires the bird to move its trachea and beak to filter out harmonics. Trills can be characterized by a trill rate (notes per second) and a frequency bandwidth (the difference in frequency between the beginning and end of each note in kilohertz). (B) Songs of New World sparrows (Emberizidae) demonstrate the trade-off between trill rate and frequency bandwidth. High-rate, pure-tone trills with large-frequency bandwidths (upper right) are impossible for birds to sing because they require the bird to move its beak faster than is physically possible.

BOX 8–4

Foraging Ecology Can Constrain the Evolution of Song

The Galápagos Finches are well known as an adaptive radiation in beak shape for different diets. But research by Jeffrey Podos (2001) has demonstrated that beak shape variation among species of Galápagos Finches constrains their capacity for post-source vocal modulation. Birds with bigger, more powerful beaks that are specialized for feeding on larger, harder seeds cannot move fast enough to perform the beak movements required to filter out harmonics to sing pure-tone trills. Finch species with finer, less powerful, but more adroit beaks can perform faster beak movements required to perform more complex post-source modulation. This research documents the powerful influence of ecology on avian vocal capacity and evolution.



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REPRINTED WITH PERMISSION FROM MACMILLAN PUBLISHERS LTD: FROM PODOS, J. 2001. CORRELATED EVOLUTION OF MORPHOLOGY AND VOCAL SIGNAL STRUCTURE IN DARWIN'S FINCHES. NATURE 409: 185–188, FIGURE 1. PERMISSION CONVEYED THROUGH COPYRIGHT CLEARANCE CENTER, INC.

(A) The diversity of beak shapes in Galápagos Finches is associated with variation in song complexity. (B) Because beak shape limits how rapidly a bird can move its beak and filter out harmonics as it sings, the adaptive radiation in Galápagos Finch beak shape has resulted in strong differences among species in vocal performance capacity. Finch species with bigger beaks (green, orange, purple, yellow) have more limited vocal performance abilities than do species with smaller, thinner beaks (blue, light green, red, black).

8.5 Learning to Sing

Only birds and a few mammals—whales, humans, and some bats—have **vocal learning** ability. Vocal learning is the process by which an individual develops a song with acoustic structure that is determined, at least in part, by the songs of other individuals in its social environment. Among birds, learning guides vocal development in four known groups: oscine songbirds, parrots, hummingbirds, and Neotropical suboscine bellbirds (*Procnias*) (Saranathan et al. 2007; Kroodsma et al. 2013). The vocalizations of other birds—chickens and doves, for example, as well as flycatchers and other suboscine passerines—are genetically inherited. When these birds are raised in acoustical isolation or are deafened before they hear their fellow birds sing, they nonetheless sing normal songs as adults. In contrast, songbirds listen to the songs of other individual birds, practice them, and incorporate the specific features of the songs they have heard into their own vocal repertoire. Song development has been well studied in oscine songbirds (Box 8–5). The stages can be grouped into two phases: (1) the sensory acquisition phase, in which hearing song models is paramount, and (2) the sensorimotor phase, in which practice is paramount (Figure 8–9).

BOX 8–5

Birds with Fixed Repertoires Learn Songs in Four Stages

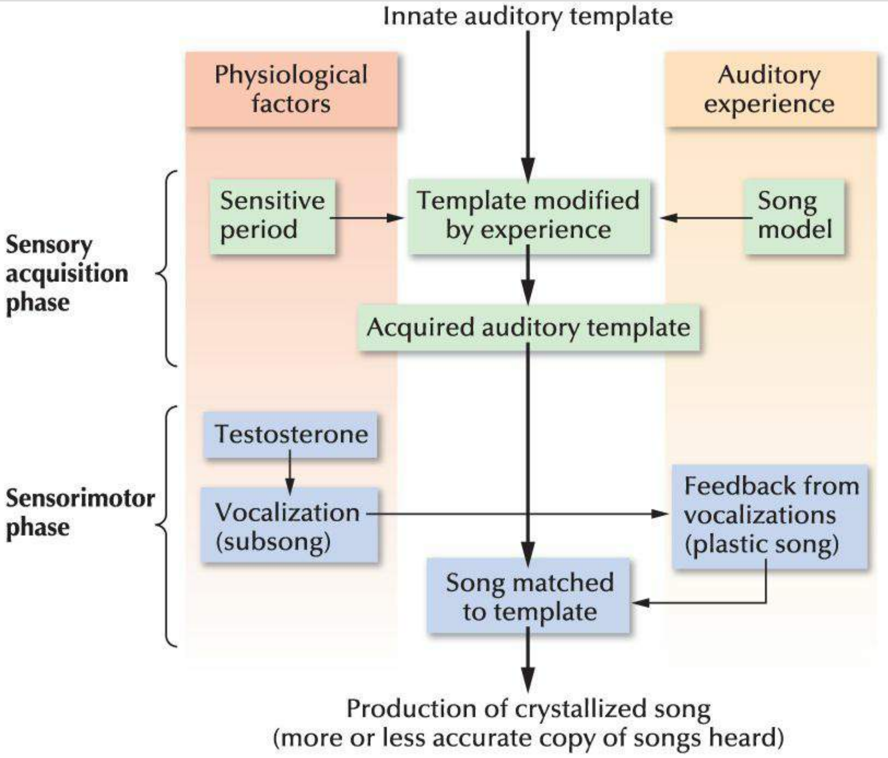
Observations of the development of the singing behavior of hand-reared baby birds, as well as experiments on it, have revealed four key periods that influence adult songs.

1. Critical learning period The early period during which information is stored for use in later stages of learning. In most species, the critical learning stage lasts less than a year—sometimes much less.

2. Silent period The long period (as long as eight months) in which syllables learned during the early critical learning period are stored without practice or rehearsal.

3. Subsong period This practice period is analogous to infant babbling. It apparently bridges the gap between the perceptual and sensorimotor stages of vocal learning. The subsong period is a period of practice without communication; perhaps subsong is a form of vocal play. (See text for a discussion of subsong.)

4. Song crystallization The next practice period during which the young bird transforms plastic song into real song by selecting a few syllables from its unstructured repertoire, perfecting them, and then organizing them into correct patterns and timing. (See text for a discussion of plastic song.)



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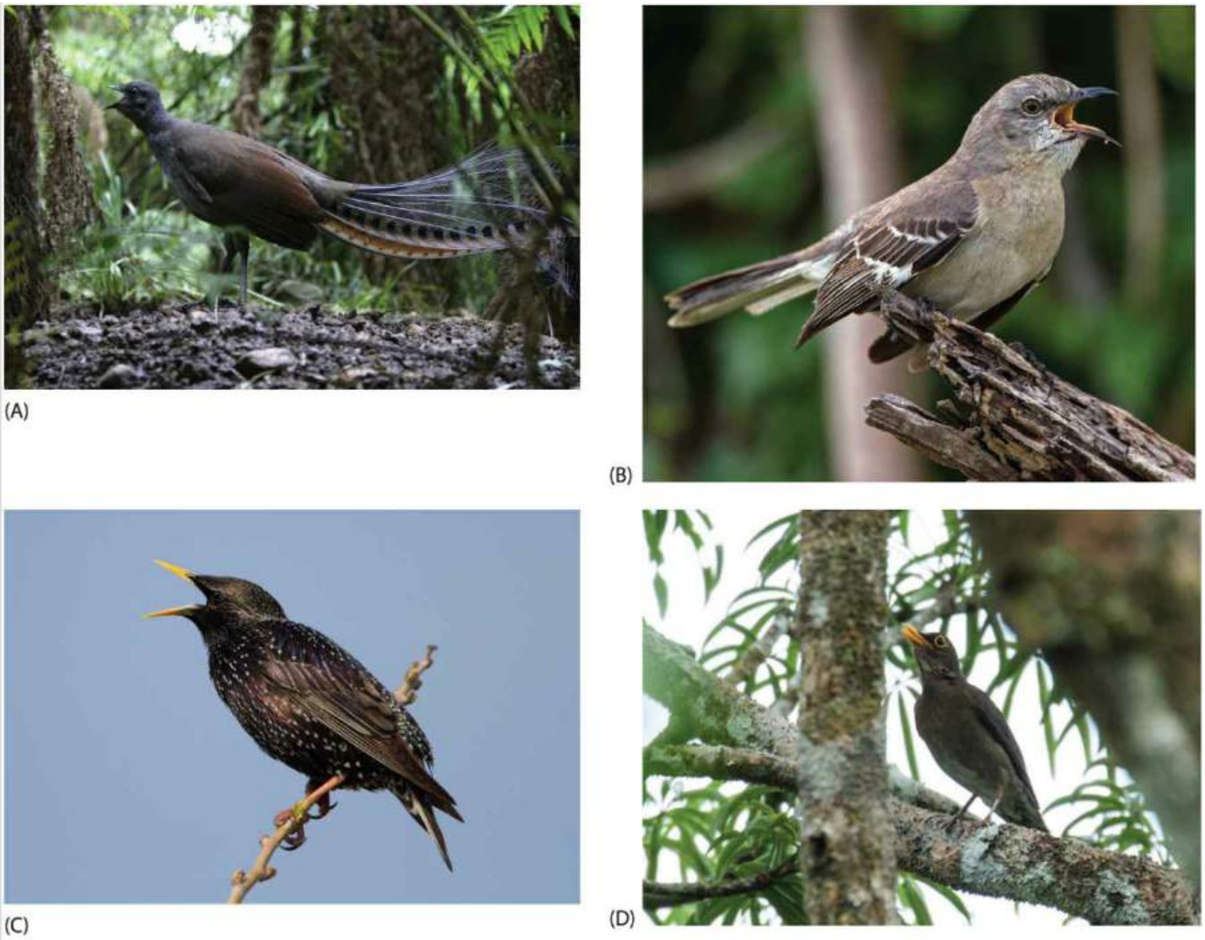
Data from Slater 1989

Figure 8–9 Stages of song acquisition by an oscine songbird. In the initial sensory acquisition phase, auditory experiences with external models or tutors refine the innate template during a physiologically based sensitive period. In the second, sensorimotor phase, practice and feedback mold initial subsong elements into plastic song, which is then refined into crystallized song by matching components to the template produced in the first phase.

The development of birdsong provides one of the best working models in any animal of how a complex, learned motor skill develops (Brenowitz and Kroodsma 1999). Specifically, neurobiologists can track how specific parts of the brain's song system participate in the process of song development (see below).

Some virtuoso birds, such as Northern Mockingbirds (Figure 8–10), add new vocalizations to their repertoires throughout their lives. These "open-ended" learners often mimic other species' songs (section 8.8).

At the other extreme are “age-limited” learners, which acquire their songs mainly during a restricted critical learning, or sensitive, period at early ages. Age-limited species differ in the timing and duration of their critical learning periods. For example, White-crowned Sparrows memorize song phrases that they hear when they are from 10 to 50 days old, whereas Chaffinches are receptive to song models for 10 to 12 months into the first breeding season, at which time first-year males have a chance to learn songs from more experienced males. Termination of the critical learning period of the Chaffinch corresponds to the rise of its testosterone level in the spring.



[(A) JÃ¶rg Hauke/Getty Images; (B) Liz Miller/Shuttestock.com; (C) skapuka/Shutterstock.com; (D) Courtesy of Nick Athanas

Figure 8–10 Vocal mimicry is found across a wide diversity of song-learning bird species, including (A) Superb Lyrebird, (B) Northern Mockingbird, (C) Common Starling, and (D) Lawrence’s Thrush.

Isolation from the model songs during the **critical learning period** permanently handicaps a young bird’s future singing ability; it will never develop a normal song. Although individual birds isolated at an early age still sing, their songs resemble “babbling” subsongs (see Box 8–5). They are less complex, have fewer notes per syllable, and have less frequency modulation than normal songs. Nevertheless, the innate songs of isolated birds may resemble the normal songs of their species in the form, rhythm, and rough tonal quality of syllables.

During the second stage of song development—the silent period—the young bird stores syllables that it memorized during the critical learning period. Swamp Sparrows store memorized song syllables for 240 days (Marler and Peters 1981). When this period has elapsed, young sparrows start practicing by listening to themselves and matching some of their vocalizations to previously memorized syllables. Thus, the initial, sensitive perceptual phase of song learning is well separated from the later motor phase by a period of silence. For temperate region songbirds, this phase takes place during the nonbreeding season, and it may not be the same for tropical birds with less distinct seasonality.

The practice stages begin with **subsong,** a long, soft, unstructured series of syllables and ill-formed sounds. Distinctly formed sounds begin to emerge, some of them recognizable as syllables heard during the sensitive period. Within a month or so, depending on the species, subsong develops into the first attempts to produce mature song. This so-called **plastic song** contains only rudiments of the final structure. In a matter of weeks, during what is called “song crystallization,” the young bird transforms plastic song into final form. Not all syllables learned or practiced are included in the final performance. In their **final songs,** young male Swamp Sparrows use only one-fourth of the syllables that they learned and practiced in the earlier phases of song development (Marler and Peters 1982).

Auditory feedback is essential for song learning. No oscine songbird produces a normal song if it has been deafened before song crystallization begins. In the deaf bird, recognizable structural entities seldom appear, and, when they do, they deteriorate quickly. Frequency modulation of syllables also is poor in deaf birds; they do not repeat sounds accurately. Experimental deafening of male White-crowned Sparrows during their silent period (70–100 days of age) erases their original song memory or interferes with a necessary matching process. Songs of such males do not differ from those of males that have been deafened before they hear model songs. Deafening after song is crystallized, however, has little effect.

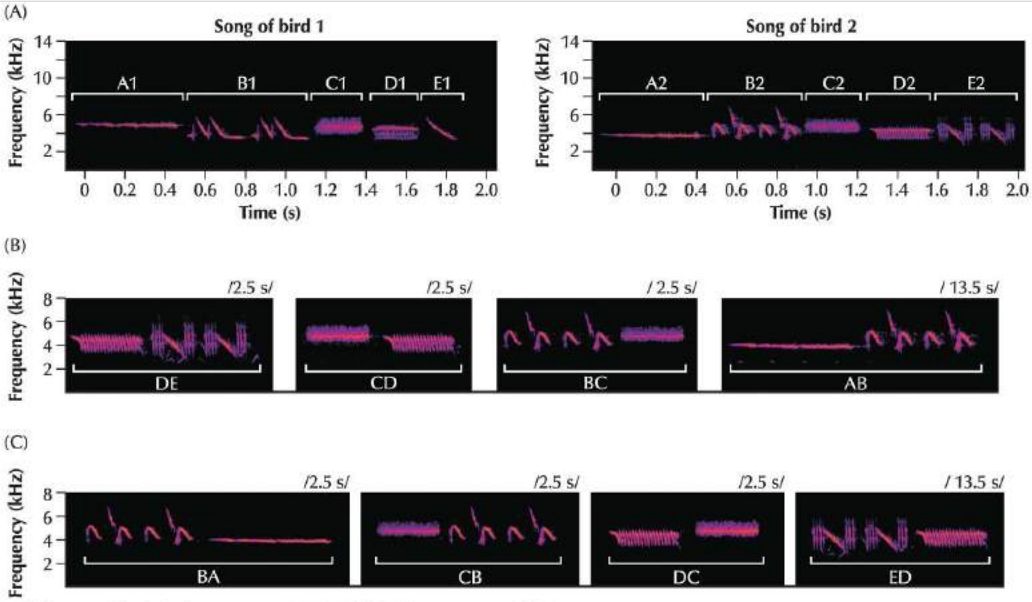
A young bird must select appropriate song models with precision from a rich sound environment. Song learning is mediated and constrained by an innate **auditory template**—a genetically inherited cognitive bias to learn sounds with particular species-typical features.

The auditory template allows the individual to screen out irrelevant sounds, such as those made by insects, frogs, waterfalls, and trains, and respond to appropriate song models. Even more exacting, the hearts of young Song Sparrows actually beat faster the first time that they hear the song of their species but not when they hear the song of another kind of sparrow.

Comparisons of song development in Swamp Sparrows and Song Sparrows illustrate this aspect of song learning. A Swamp Sparrow's song is a repetitious trill of a single syllable, whereas a Song Sparrow's song uses a pattern of many complex syllables. To discover how the young of these species learn their own songs, despite the fact that they grow up hearing both songs, Peter Marler and Susan Peters (1989) isolated nestling sparrows and then exposed them to taped songs during the critical learning period. Syllable structure is the key to song learning for young Song Sparrows, whereas temporal pattern is the key for young Swamp Sparrows. Swamp Sparrows do not learn the Song Sparrow song because they cannot learn its syllables. Song Sparrows do not learn the Swamp Sparrow song because they cannot learn its temporal pattern.

Learning and imitation are not the only elements of song acquisition. Individuality is important, too. Young birds transform and improvise as they develop individual signatures in their songs. They systematically transform memorized themes or mix syllables from several models to create novel combinations. A single song of the Swamp Sparrow, for example, may contain invented, improvised, and imitated elements. However, the creative sparrow rarely breaks up a series of notes that constitute a syllable. The syllable itself may be a natural perceptual unit, designed to map readily onto a template of acceptable patterns of sound production (Marler 1981; Baptista 1999).

We don’t know exactly how the auditory template works or even where it resides in the song system of the brain. Studies of how young White-crowned Sparrows assemble their songs in the proper sequence, however, have been sources of an important insight (Margoliash 2004; Rose et al. 2004). The process of song development in White-crowned Sparrows is one of the best known, in part because this species produces song dialects that differ strikingly among local populations in California (see below). Like other age-limited species, the fledgling White-crowned Sparrow memorizes songs when it is between 20 and 70 days old. The basic song of all populations consists of an initial whistle followed by four or five distinct phrases (Figure 8–11). Phrase-sequence information, it turns out, is a key part of the template for song development. Young sparrows can assemble a complete song when tutored with just pairs of phrases—that is, without ever hearing a full normal song. When they hear the phrase pairs AB, BC, CD, and DE in that order, they construct a final song rendered correctly as A-BCDE, where A is the standard initial whistle. Conversely, if they hear the phrase pairs BA, CB, DC, and ED in that order, their final song inverts to EDCB-A.



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Hans Bilger. Data from Rose, G.J., F. Goller, H.J. Gritton, S.L. Plamondon, A.T. Baugh, and B.G. Cooper. 2004. Species-typical songs in White-crowned Sparrows tutored with only phrase pairs. Nature 432:753.

Figure 8–11 Sound spectrograms of (A) the full songs of two White-crowned Sparrows and (B and C) the tutor models of syllable combinations. In these experiments, the young sparrows assembled a full song from only the paired syllable combinations used for tutoring. Note the long introductory whistle are designated by A1 or A2.

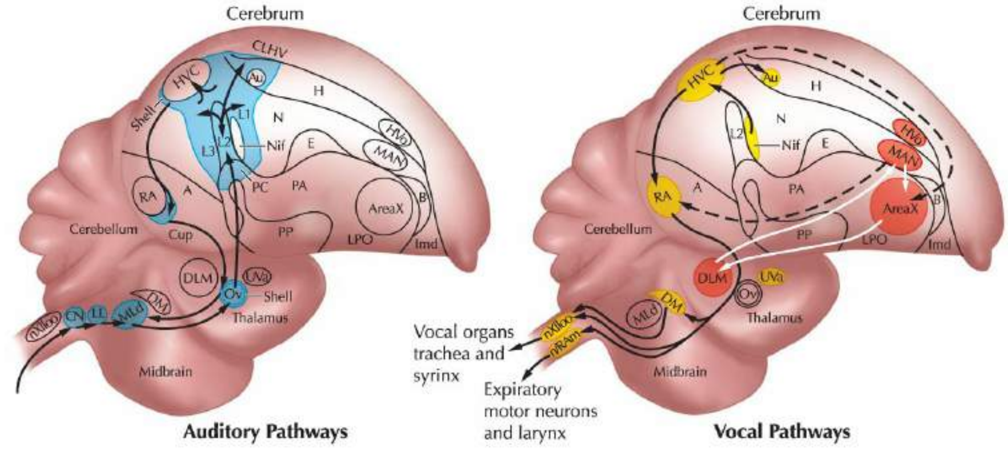
The Common Nightingale of Europe is renowned for its vocal virtuosity and its long solo singing bouts often late at night. Each male has roughly 200 distinct and discrete song types. It sings them in long continuous strings of successively different songs (Todt and Hultsch 1999). Which sequence packages it sings depend on social context—for example, daytime group singing versus nighttime solo singing—and which other males countersing. They learn most of their songs from 15 to 90 days of age. Individual songs are the unit of learning, which the young nightingale assembles early on as packages that are probably limited in length to constraints of its short-term memory. Interactions between males are defined by exchanges of appropriate packages. Similarly, sentences of human language are constrained by short-term memory to interactive packages of reasonable length.

Most of the classical studies of song learning by young birds explored responses to recorded song by birds raised in isolation. One study revealed that White-crowned Sparrows learned their songs better from other White-crowned Sparrows—that is, live tutors—than from tapes (Baptista and Petrinovich 1984). Through field studies, young birds were then discovered to prefer to learn songs shared by several male tutors. The process of song acquisition by young, free-living Song Sparrows, for example, follows three main rules: (1) sample the repertoires of at least three or four adult neighbor tutors, (2) preserve the identity of the song tutor and its song type, and (3) learn with priority the song types shared among tutors (Beecher 1999). These rules lead naturally to the formation of local song dialects (see section 8.7).

8.6 The Central Nervous System and Song Learning

In order to learn songs, birds must hear the songs of conspecifics, distinguish appropriate acoustic inputs from other sounds using their innate template, remember the appropriate songs, produce their own vocal song, listen to their own vocalizations and compare them to the remembered songs, and then repeat the process until they develop a species-typical vocalization. Vocal learning requires more than mere development. Although we often say that a child “learns to walk,” the development of the ability to walk is not a form of learning because it does not involve the acquisition of information from examples in the social environment. Avian vocal learning is true learning in this sense.

The neural pathways in the brain that control the complex process of song learning, memory, and vocal production have been mapped in great detail for oscine songbirds. Birdsong learning results from the coordinated interactions of three primary neural pathways that connect key parts (nuclei) of the brain and, in turn, the syrinx (Figure 8–12).



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Data from Jarvis et al. 2002

Figure 8–12 Vocal learning involves three distinct neural pathways. As in other amniotes, the auditory pathway (blue) projects auditory input from the ears, via the auditory nerve and the brain stem, to the cerebrum. The anterior and posterior cerebral pathways are unique to vocal learners. The posterior vocal pathway (yellow) connects various cerebral vocal control centers (HVC, RA, etc.) to the brain stem and manages the motor control of vocalization. The anterior vocal pathway (red) forms a loop of nonvocal forebrain regions and includes cerebral nuclei (LMAN [the lateral magnocellular nucleus of the anterior nidopallium], Area X, etc.) that are responsible for analysis auditory input and acoustic output involved in song learning, social context, vocal syntax, and maintenance of song structure.

First, the **auditory input pathway** brings acoustic information from the ears into the brain stem via the auditory nerves (see Figure 8–12, blue). These signals are projected up into the forebrain, or cerebrum, to interact with the posterior forebrain pathway.

Second, the **posterior pathway** is the main, descending motor pathway that regulates song production; it produces the nerve impulses that control the syringeal muscles, larynx, and respiration (see Figure 8–12, yellow). This pathway includes the well-studied HVC (or high vocal center) and the RA (or robust archopallial nucleus). Stimulation of the motor neurons in the posterior motor pathway contracts the syringeal muscles that control the tensions and the dimensions of the vocal tract. Likewise, experimental lesions in these regions either completely abolish or disrupt singing behavior. Information from the HVC also projects to Area X in the anterior forebrain pathway.

The **anterior pathway** in the forebrain plays a central role in comparing the bird’s own vocal output to the remembered conspecific songs (see Figure 8–12, red). This pathway creates critical feedback loops from the motor control centers in the posterior pathway to the anterior auditory analysis centers (Area X, LMAN). It may also play a secondary role in the actual control of song production (Kao et al. 2005). Young birds with lesions in LMAN continue to sing, but their songs crystallize prematurely with a poor match to the tutor songs. These findings indicate that the anterior pathway enables the bird to improve the fit of its songs to the learned model songs.

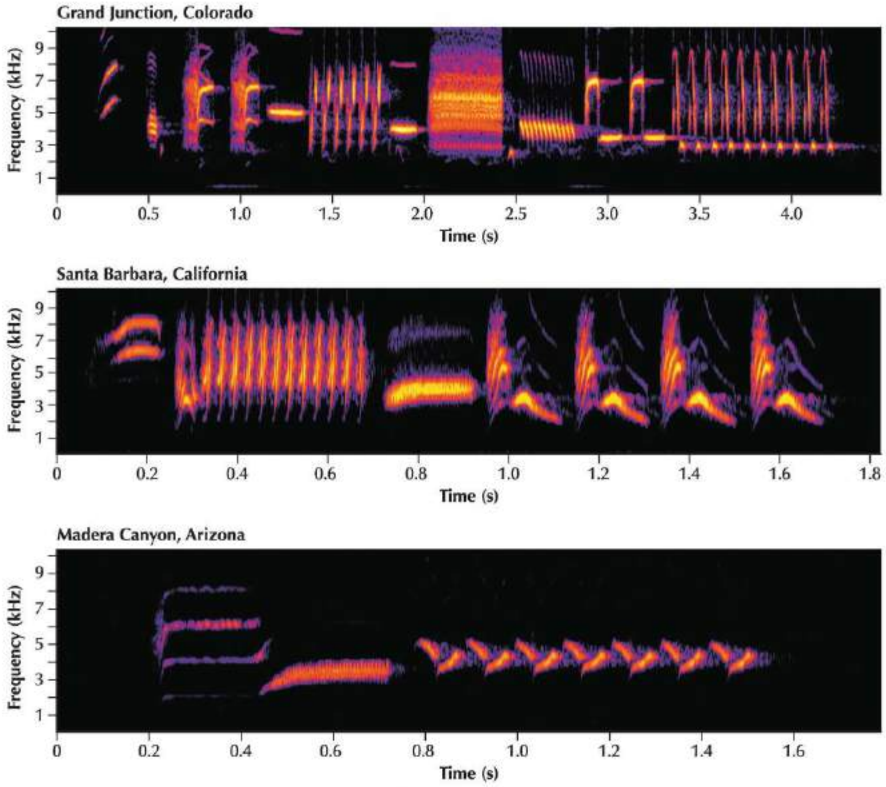
Functional lateralization of the brain was once thought to be an exclusively human attribute, associated with extraordinary language abilities. Bird brains, as well as the syrinx, also are lateralized (see section 7.5 in Chapter 7). The left hemisphere of the forebrain controls birdsong—specifically, learning and innovation in vocal repertoires. The right cerebral hemisphere assumes control of the functions of the left hemisphere only if the left hemisphere is damaged. The impairment of a young Atlantic Canary’s song-control centers in the left hemisphere leads to the formation of an alternative set in the right hemisphere and the acquisition of a new song repertoire.

The amount of brain space that controls song is flexible. In particular, the development of brain tissue controlling song increases with the size of individual song repertoires (Brenowitz and Kroodsma 1999). Male canaries with large repertoires have larger song-control nuclei than do male canaries with small song repertoires. Populations of Marsh Wrens that differ in song-repertoire size also differ in the amount of brain space allocated to the high vocal song-control center (Brenowitz et al. 1994). Marsh Wrens in California learn three times as many songs as do Marsh Wrens in New York, and have 40 percent larger volumes of the song-control nuclei. This difference in brain space and song-learning ability appears to be genetically controlled and related to the competition among males for mates—competition that is more intense in the West than in the East.

8.7 Dialects

Male Olive-sided Flycatchers sing their distinctive *hic-THREE BEERS* song in the coniferous forests across North America, and the song is acoustically uniform from California and Alaska to northern New England and the Canadian maritime provinces. This tyrant flycatcher has an innate, genetically determined song that limits its geographic variation.

Birds that learn their songs often exhibit much greater geographic variations in song, which are called **dialects.** Species of bird that learn their songs can vary from one hilltop to the next or from one region of the country to another. Learning vocalizations from conspecific neighbors with some frequency of error or innovation leads naturally to regional dialects—local variations in syllable structure or delivery patterns, quite like the local accents of humans. Carolina Wrens in Ohio, for example, sing faster than those in Florida. Bewick’s Wrens in California, Arizona, and Colorado each have very distinct song patterns (Figure 8–13). Some of the local dialects of the handsome White-crowned Sparrows on the central California coast are restricted to areas of only a few square kilometers. Dialects may be stable and long lived. The song themes in one well-known dialect of White-crowned Sparrows in California, the Berkeley dialect, have persisted for at least 60 years (Payne 1999).



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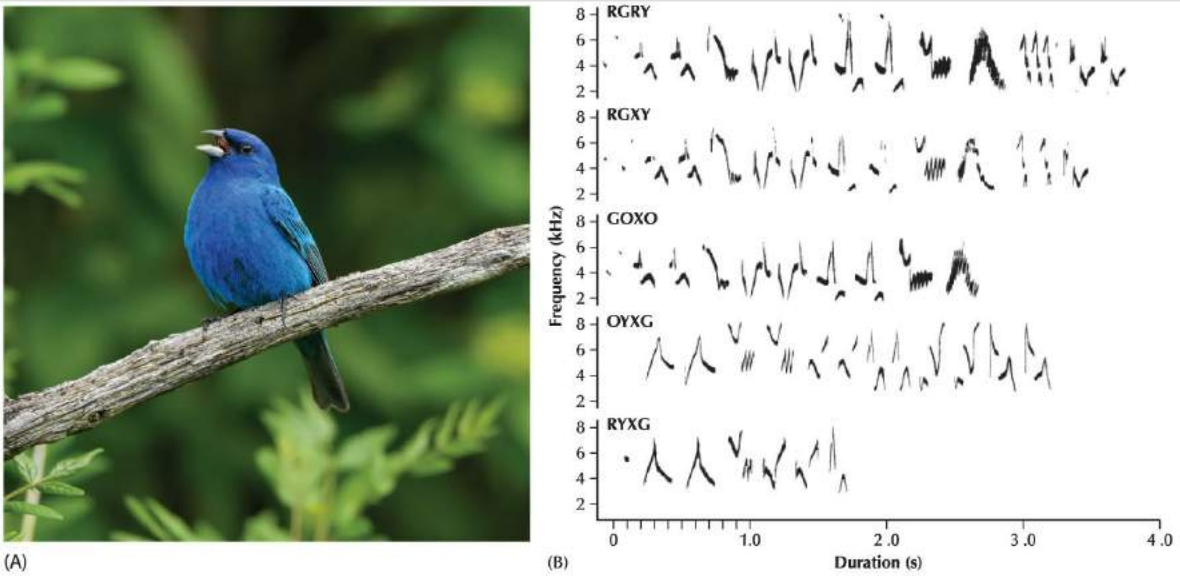
HANS BILGER. DATA FROM DONALD KROODSMA

Figure 8–13 Song dialects: Bewick's Wrens sing strikingly different songs in Colorado, California, and Arizona.

Patterns of geographical song variation may simply reflect recent history of dispersal and isolation. New song traditions arise when young birds colonize new areas and start a local culture of song forms. For example, populations of the Saddleback, an endangered oscine, introduced to small offshore islands around New Zealand, have rapidly acquired striking distinctions in acoustic structure and lower population song diversity as a result of translocation (Parker et al. 2012). Such "bottlenecks" or "founder effects" are likely to affect learned behaviors more strongly than the genetic composition of populations.

Dialects arise because young males do not learn from their older neighbors with perfect fidelity. In southern Michigan, first-year male

Indigo Buntings learn their song syllables from established neighbors, but they may combine those syllables in novel ways (Payne 1999; Figure 8–14). A male's innovative song may be learned by another male in a later year. Thus, Indigo Bunting song types live longer than the individual birds that invent them. Songs persist in the population three times as long as a male bunting does. The half-life expectancy of a copied song over a 15-year period was 4.23 years compared with 1.33 years for the average individual male bunting (Payne 1999).



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
(A) FotoRequest/Shutterstock.com. (B) Payne, R.B., L.L. Payne, and S.M. Doehlert. 1988. Biological and cultural success of song memes in Indigo Buntings. Ecology 69: 104–117

Figure 8–14 The songs of (A) male Indigo Buntings include pairs of repeated phrases. Each male learns its song from other males but can combine learned phrases in innovative ways. (B) The "North Gate song tradition" persisted in the E. S. George Reserve for more than 10 years. This microcultural birdsong variation lived longer than the original male that created it.

These temporal and geographic changes in learned birdsongs are a form of **cultural evolution,** in which vocal traits passed from one generation to the next by learning, with parallels to human language and other cultural traits (Lynch 1999). The units of cultural inheritance have been called **memes,** in parallel to genes. Learning errors or other individual innovations in song are the equivalent of cultural mutations. The differential survival of these variations gives rise to a pattern of cultural change over time and geography.

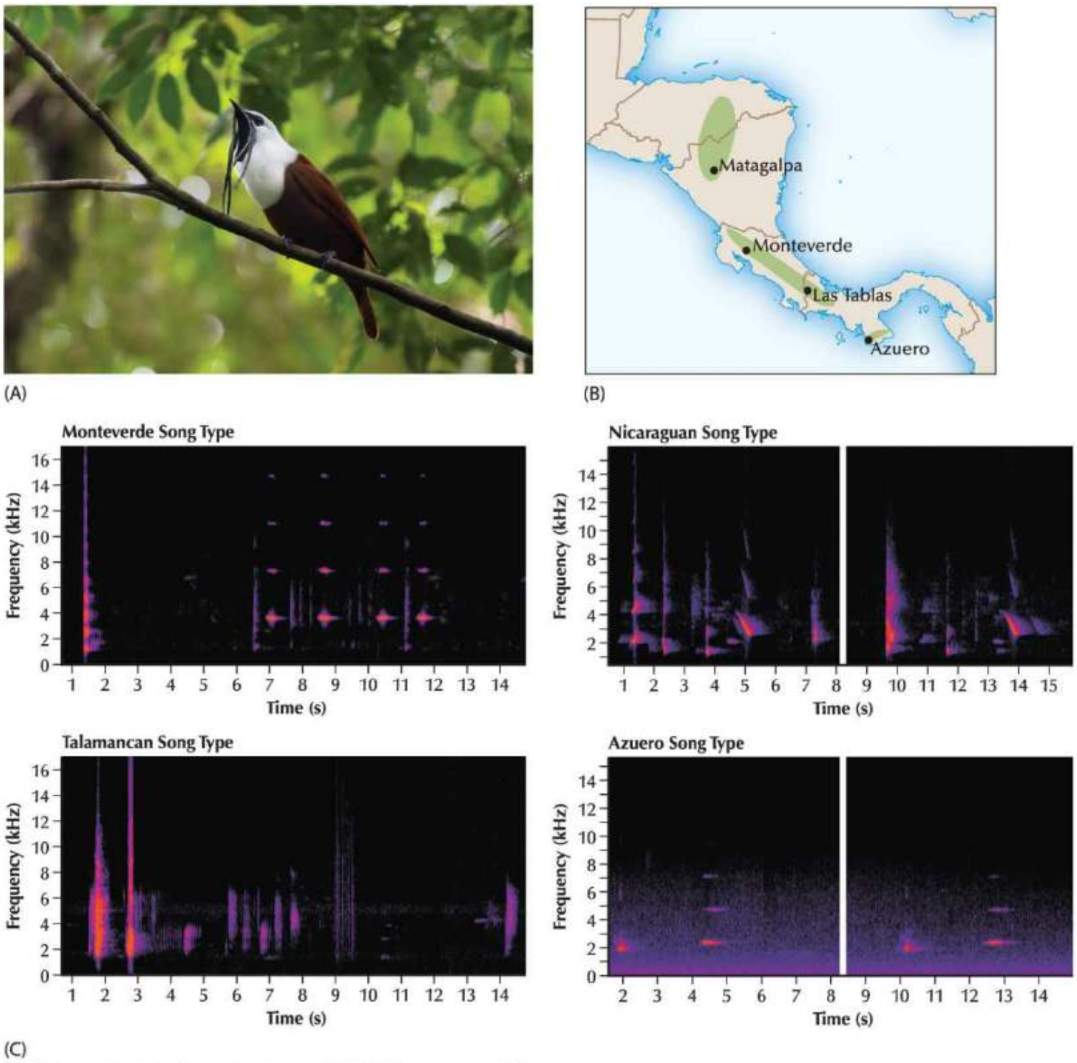
Dialects are so closely associated with vocal learning that fine-scale geographic variation in song has provided the first evidence of vocal learning in hummingbirds (Snow 1968) and bellbirds (Kroodsma et al. 2013). David Snow's observation of vocal convergence among male Long-billed Hermits that display in the same arena provided the first evidence of vocal learning in hummingbirds. Donald Kroodsma's observations of vocal dialects in Three-wattled Bellbirds in Central America provided the first indication of vocal learning in this genus of cotinga (Box 8–6).

BOX 8–6

Song Learning in the Neotropical Bellbirds (Cotingidae)

Although most suboscine passerines do not exhibit local learning and lack the cerebral nuclei that make it possible (Nottebohm 1980; Kroodsma 1984), observations of vocal dialects in the absence of genetic differentiation among populations of the Three-wattled Bellbird, *Procnias tricarunculata,* a cotinga from Central America, provide evidence of a unique, fourth origin of vocal learning in birds among the suboscines (Saranathan et al. 2007; Kroodsma et al. 2013). Individuals from the different dialects exhibit too little genetic differentiation for these vocal differences to be attributed to genetic evolution.

Experimental deprivation studies are impractical, but a captive Bare-throated Bellbird has learned the song of a Chopi Blackbird with which it was housed. Male Three-wattled Bellbirds continue to learn new songs throughout their lives (Kroodsma et al. 2013). These bellbirds (*Procnias*) are the only suboscines that are known to have vocal learning. Observations of rapid vocal variation over geography can provide evidence of vocal dialects and song learning when experimental evidence of learning is unavailable.



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(A) Lee Dalton/Alamy stockphoto. (C) Hans Bilger. Data from Saranathan, V., D. Hamilton, G.V. Powell, D.E. Kroodsma, and R. O. Prum. 2007. Genetic evidence supports song learning in the Three-wattled Bellbird Procnias tricarunculata (Cotingidae). Molecular Ecology 16: 3689–3702.

(A) A male Three-wattled Bellbird. (B) The four vocal dialects of the Three-wattled Bellbird in Central America. (C) Sonograms of the four highly distinct, learning vocal dialects of the Three-wattle Bellbird.

Cultural traits, including birdsongs, can be passed vertically from parents to offspring, horizontally between unrelated individual birds or populations of the same generation, or obliquely between unrelated individual birds of successive generations. All three modes of transmission are found for songbirds, but oblique transmission, as is the case from unrelated neighbor to yearling Indigo Buntings, is the most common mode in songbirds.

Medium Ground Finches are among the few birds in which song learning and transmission are vertical from parent to offspring. Young male Medium Ground Finches, found in the Galápagos Islands, learn their single, structurally simple song from their fathers (Grant and Grant 1995). They pass it in turn to their sons as a strictly cultural trait that drives species recognition and mate choice. Females are faithful to the songs of their species. On rare occasions, a male may mistakenly learn the very different song of the Cactus Finch, in which case it will be picked as a mate by a female Cactus Finch and produce hybrid offspring. These rare mistakes document the importance of song in mate choice and definition of the species.

Brood-parasitic indigobirds lay their eggs in the nests of other finch species (section 14.4 in Chapter 14). Both males and females imprint on the song of the host species, so when they mature, they can find each other and choose appropriate mates. However, multiple species of indigobirds have evolved explosively because brood parasites that are raised by a new finch host species will learn new songs and vocal preferences, which contribute to reproductive isolation. Early vocal learning facilitates rapid, even sympatric speciation.

8.8 Vocal Mimicry

Vocal learning creates the opportunity for evolving an auditory template broad or general enough to learn the songs of other bird species, which is **vocal mimicry.** Roughly 20 percent of the passerine songbirds worldwide practice vocal mimicry. Many of these birds are open-ended learners. They enlarge their repertoires by learning and singing the songs and calls of other species. The most renowned vocal mimics include the Northern Mockingbird, Common Starling, Marsh Warbler, Australian lyrebirds, bowerbirds, scrubbirds, and African robin-chats. Some of these species have templates so open ended that they imitate human-made or mechanical sounds. In Australia, a variety of species now imitate cell phones, and the versatile lyrebirds imitate the buzz of a chain saw, the roar of a motorcycle, and even the clicks of a camera shutter. However, other mimics, like wild Northern Mockingbirds, have more restricted templates and usually imitate only other species of bird.

Male Northern Mockingbirds have repertoires that can exceed 150 songs, which both change from year to year and increase in number with age (Derrickson and Breitwisch 1992). Mockingbirds do not mimic other species to try to deceive them. Rather, Mockingbirds enhance their song repertoire size by imitating other birds. One Northern Mockingbird can imitate dozens of different species, broadcasting in sequence the songs of the American Robin, Blue Jay, Northern Cardinal, and a variety of other common species of the eastern United States. In Texas, mockingbirds broadcast the calls of Bell’s Vireos, Great-tailed Grackles, and Dickcissels, among others.

Some mockingbirds imitate species found hundreds of kilometers away. For example, Jim Tucker of Austin, Texas, was surprised one morning to hear a mockingbird imitate a Green Jay, a species that is found only in the Rio Grande Valley 500 kilometers to the south. Was this song learned directly from a Green Jay in the Rio Grande Valley, or was it passed northward through a series of mockingbird generations?

Migratory species may have international repertoires. Marsh Warblers, among Europe’s most versatile vocal mimics, spend much of the year in Africa. Although they imitate some European species, most of the songs broadcast by Marsh Warblers are those of African birds heard during migration and on the wintering grounds (Dowsett-Lemaire 1979). Territorial male Marsh Warblers may thus inform potential mates where they spend the winter. It could be to a female’s advantage to pair with males adapted for wintering in the same part of Africa as she does and thus to produce young with similar tendencies.

Mimicry has many independent evolutionary origins, but it may be persistent once evolved. Two families of superior mimics—the New World mockingbirds and thrashers (Mimidae) and the Old World starlings (Sturnidae)—are most closely related to each other, indicating an ancient origin of mimicry in their common ancestor.

8.9 Female Song and Duets

Female song is widespread among birds, particularly in tropical species with pairs that reside throughout the year in the same territory. Female song is prominent in antbirds, honeyeaters, bushshrikes, whistlers, wrens, euphonias, and orioles. In these species, both male and female song can function in territorial defense and mate attraction. Because songbirds originated in Australia, where many species are resident and territorial, female song is likely ancestral for all songbirds (Odom et al. 2014). Sexual dimorphism in song is a recently acquired, evolutionary loss for many songbird lineages.

One of the most prominent examples of female song behavior is **duetting,** in which two individuals sing a single song that involves simultaneous or coordinated vocal participation by both individuals. Some birds sing distinctive vocal duets to maintain their pair bond and to communicate their proximity to each other. Vocal duets are bouts of overlapping and precisely synchronized sounds by members of a mated pair or extended family group. To the human ear, the duet often sounds like the song of a single bird. The Rufous Hornero, the national bird of Argentina, sings duets with a strong rhythm in which the female punctuates the male's primary beat with one of her own (Laje and Mindlin 2003; see also Ball 2003). One female note to each three male notes is a common rhythm, but some pairs use different rhythms. As the male increases its song tempo, the female rapidly switches the counterrhythm of its perfectly synchronized notes in predictable sequences that would be impossible for a human musician.

At least 222 species in 44 families are known to sing duets

(Farabaugh 1982). Most of them are tropical birds, such as the Tropical Boubou, an African shrike that defends a year-round territory (Box 8–7). Their duets function both in maintenance of the pair bond and in joint defense of territorial space against encroaching neighbors. They even have a special loud and longer victory duet that they deliver after a protagonist slinks off in defeat (Grafe and Bitz 2004a).

BOX 8–7

Bush Shrikes Duet with Precision

Each pair of Tropical Boubous, a kind of African bushshrike, develops a unique set of duetting patterns that they use to keep track of each other in dense vegetation, to synchronize their reproductive cycles, and to maintain their territorial integrity (Grafe and Bitz 2004b). Either member of the pair can initiate the duet. The respective note contributions are so well synchronized that few people realize that two birds, not one, are singing. A pair of Tropical Boubous increases the complexity of their duet patterns with the density of shrikes which may increase the need for distinction.

Duetting bushshrikes respond to cues—preceding notes—in only a fraction of a second and with astonishing precision (Thorpe 1963). These reaction times can be measured quite accurately in the duets of the Black-headed Gonolek, a bushshrike with a simpler duet than that of the Tropical Boubou. The female gonolek responds to the male’s lead *youck* with a sneezelike hiss. The average response time of one female was only 144 milliseconds, with a standard deviation of 12.6 milliseconds. Another female responded in 425 milliseconds, with a standard deviation of 4.9 milliseconds. These values (12.6 and 4.9 milliseconds) are exceedingly low. Human auditory reaction times, not nearly as precise, have a standard deviation of 20 milliseconds.

B. GOZANSKY/VIREO

Tropical Boubou, an African bird well known for its precision duets.

Duetting requires close coordination in both timing and acoustic structure between vocal phrases sung by each bird, but little is known about the development of vocal coordination. Recently, experiments removing one member of duetting pairs of Canebrake Wrens have shown that new pairs compose their duets using new temporal combinations of the same notes (Rivera-Cáceres et al. 2016). Temporal coordination within the new pair develops very rapidly over a period of two weeks.

The *Chiroxiphia* manakins are a rare example of male–male duetting (Chapter 13). Pairs of cooperating males occupy a common display site and advertise with a very well-coordinated series of similar songs. In the Long-tailed Manakins, frequency matching between cooperating males improves gradually over years (Trainer et al. 2002).

8.10 Songs and Mates

Alarm and begging calls evolve by natural selection, but songs and song repertoires evolve through sexual selection, and both mechanisms of sexual selection are involved. The territorial defense and competition functions of birdsong evolve through male–male competition, whereas the mate attraction function of birdsongs evolves through mate choice.

Territorial songs signal to potential rivals that the resident male is prepared to protect his exclusive use of that space and any associated females. When a territorial male Great Tit, for example, is removed from its territory, another male will take over within 10 daylight hours unless a territorial song is broadcast from loudspeakers on the territory (Krebs 1977). When a song is broadcast, rival males take three times as long (30 daylight hours) to exploit the vacancy.

Male song also functions in attracting potential mates and is often the first step toward courtship and pair formation. Females sometimes respond directly to male song with either precopulatory trills or copulatory postures, and these postures can be used as an assay of female mating preference. Female Song Sparrows and Swamp Sparrows whose sex drives have been experimentally enhanced by the hormone estradiol will respond more strongly to songs of their own species than to the songs of other species. They discriminate between the two by recognizing distinctive syllable structures and patterns of syllable delivery (Searcy and Marler 1981).

Many aspects of birdsong acoustic structure, repertoire size, learning ability, and performance ability have been hypothesized to be **honest indicators** that provide objective information about mate quality (Gil and Gahr 2002; Searcy and Nowicki 2005). Accordingly, the diversity of birdsong has been viewed as myriad solutions to one general challenge: how to get the best-quality mate. For example, larger song repertoire size in male Great Reed Warblers has been associated with larger nestling body size (Nowicki et al. 2000) and greater offspring survival (Hasselquist et al. 1996). However, evidence that song repertoire size generally indicates that mate quality is mixed at best (Gil and Gahr 2002). Swamp Sparrow nestlings raised on stressful, lower-quantity diets do not develop smaller vocal repertoires (Nowicki et al. 2002a). Furthermore, the hypothesis does not explain why repertoire sizes have continued to evolve—and even get smaller—among bird species. For example, both of the "model organisms" for the study of avian song learning—the White-crowned Sparrow and the Zebra Finch—have minimal size, single-song vocal repertoires that have evolved from ancestors with larger vocal repertoires. (Of course, this attribute was selected on purpose because it provided researchers with a better landmark of when vocal learning is complete.) Why evolve smaller song repertoires if bigger is better?

Vocal **performance ability** has also been hypothesized to communicate mate quality. For example, long songs and vigorous singing are preferred by the females of many species studied to date (Nowicki and Searcy 2005). Female House Finches prefer long songs delivered at fast rates (Nolan and Hill 2004). In another study, female Common Starlings preferred males with the strongest immune systems, which would be valuable to pass on to her offspring (Duffy and Ball

2002). Vocal skill, as reflected by the ability to sing rapid, broadband-frequency trills, has also been hypothesized to communicate mate quality (Podos et al. 2009). However, it is not clear that extreme vocal performance abilities evolve because the males are actually better in genetic quality or condition, or because the high-performance songs are merely more attractive.

Alternatively, mating preferences for all of these vocal attributes may evolve merely because they are popular (Prum 2010). Accordingly, the vocal attributes of a species may reflect the arbitrary evolutionary history of preference—like genetic or cultural fashion trends—rather than provide information about objective mate quality. For example, larger vocal repertoires are associated with greater mating success in Song Sparrows but not with greater territory size (Reid et al. 2004).

A huge component of vocal diversity in birds with song learning is a result of cultural evolution. So, does cultural evolution in birdsong parallel with breeding success and natural selection? Apparently not. In an exhaustive eight-year field study of song-type success and mating success in a population of Indigo Buntings, Robert Payne and colleagues found that the cultural success of male song types is completely uncorrelated with male breeding success (Payne et al. 1988). Although young buntings do gain an advantage in male–male competition for territory by copying the song of a near neighbor, variation in which song types were learned was otherwise unrelated to male breeding success. Males with higher breeding success are not copied at higher rates than other mates. Likewise, successful songs are not associated with higher breeding success. In short, the enormous cultural variation in birdsong among populations and species does not appear to provide any potential information about mate quality and may be evolutionarily neutral.

Because learned birdsongs evolve simultaneously through both biological selection on genes and cultural selection on learned aspects of vocal structure, the diversity of learned birdsongs poses a particularly fascinating and important challenge to evolutionary biology. Nowhere in the animal kingdom, outside of humans, has the interplay between biological and cultural evolution been explored more richly than in the realm of birdsong.

REVIEW KEY CONCEPTS

8.1 Physical Attributes

Birds communicate extensively through vocal sounds. Sounds are pressure waves that are characterized by variation in frequency, or pitch, and amplitude, or volume. Many vocal sounds are complex mixtures of a fundamental frequency and its harmonic frequencies, which are multiples of the fundamental. The acoustic structure of avian vocalizations varies extensively with the species, vocal function, and habitat.

There is no clear, universally recognized distinction between a *song* and a *call*, but these traditional categories are used to denote vocalizations that are more and less complex, respectively.

Key Terms: frequency, amplitude, waveform, sonogram, hertz, song, call, harmonic frequencies, fundamental frequency, infrasound

8.2 Repertoire Size and Communication

Birds vary in the diversity of their total vocal behavior, or vocal repertoire, which includes all of their calls and songs. Vocal repertoires vary tremendously among species and even populations. Song repertoires can vary from one to hundreds of songs. Some birds are individually identifiable by their songs and calls.

Key Terms: repertoire, syntax

8.3 Sound Production by the Syrinx

Because the larynx has evolved to become part of the bony avian tongue, birds have evolved a novel structure, called a syrinx, with which to vocalize. The syrinx is located near where the trachea branches into the two bronchi. The syrinx is comprised of supporting elements, membranes, muscles, and nerves, and it is located inside of the air-filled interclavicular air sac. It is usually composed of a combination of tracheal and bronchial elements, but it can be entirely tracheal or bronchial.

The syrinx is incredibly efficient at converting the movements of air into loud, harmonically complex, and rapidly modulated sounds. The control of breathing and the actions of syringeal muscles are critical to avian sound production.

Key Terms: syrinx, syringeal membranes, syringeal supporting elements, syringeal nerves, extrinsic syringeal muscles, intrinsic syringeal muscles, minibreaths

8.4 Post-Source Modulation

In addition to controlling vocal production at the syrinx, or the sound source, birds also engage in post-source modulation, or filtering of the sounds produced by the syrinx by the trachea and mouth cavity. Some birds, from cranes and curassows to manucodes, have evolved elongate trachea that function as resonance chambers to shape the harmonic composition of their songs after the syrinx. To produce a pure tone that changes rapidly in frequency, birds must move their beaks and tracheas quickly to filter out the changing harmonics. This process creates a motor constraint, or a limitation on the kinds of songs that birds can sing. Birds with more powerful, shorter, and robust beaks cannot perform these beak movements as rapidly as those with thinner, less-powerful beaks, creating an unexpected relationship between the foraging ecology and some aspects of the vocal complexity of a species.

Key Terms: post-source modulation, filtering, trill rate, frequency bandwidth

8.5 Learning to Sing

Nearly half of the species of birds of the world—including oscine songbirds, parrots, hummingbirds, and the Neotropical, suboscine bellbirds (*Procnias*)—learn their songs from other individuals. Avian vocal learning, the best-known example of animal learning, requires the acquisition and incorporation of acoustic information into the bird's own vocal output. Song development proceeds through stages of subsong and plastic song to terminal song. A young vocal-learning bird uses an inherited vocal template to select out of its environment appropriate examples of sounds to learn, but vocal learning can also be influenced by individual social interactions.

Key Terms: vocal learning, critical learning period, subsong, plastic song, final song, auditory template

8.6 The Central Nervous System and Song Learning

Experiments on the development of song in young vocal-learning birds have produced a detailed understanding of the neurobiology of song development and the function of brain pathways in this process. The auditory input pathway brings sounds from the ears into the brain stem via the auditory nerves, where these signals are projected into the forebrain’s song-learning nuclei. The posterior pathway receives input from the auditory pathway and controls the mechanics of song production. The anterior pathway receives and sends information to the posterior motor pathway and functions in monitoring vocal output, allowing the bird to improve the fit between the songs it has heard and the songs it is producing.

Key Terms: auditory input pathway, posterior pathway, anterior pathway

8.7 Dialects

Like human accents, song learning in birds creates geographical variation in birdsong, which are called dialects. Young birds sometimes incorporate novel notes or phrases into their songs. When these new vocal structures are learned by other birds, the result is a kind of cultural transmission, called cultural evolution.

Key Terms: dialects, cultural evolution, memes

8.8 Vocal Mimicry

Some birds do not restrict their learning to conspecific vocalization. These species, called vocal mimics, have broad, open neural templates that allow them to consider many bird vocalizations as appropriate vocal models. Vocal mimicry has evolved many times and results in some of the largest vocal repertoire sizes of any birds.

Key Term: vocal mimicry

8.9 Female Song and Duets

In many species, especially of resident, tropical and Australian perching birds, both males and females sing songs. Many of these species also perform vocal duets in which a male and female pair sing a composite song that requires close coordination between the vocal inputs of both individuals. To the human ear, many avian duets sound like the complex song of a single individual bird.

Key Term: duetting

8.10 Songs and Mates

Song evolves by sexual selection, including both mechanisms of male–male mating completion and mate choice. The territorial defense function of song is a clear example of evolution by mate competition. Many aspects of song acoustic structure, repertoire size, learning ability, and vocal performance have evolved by mate choice. Vocalizations have frequently been hypothesized to evolve as honest indicators of mate quality, but the evidence in support of this hypothesis is mixed. Alternatively, mate choice may select purely for the most attractive songs, leading to elaborate and arbitrary diversity in vocal advertisement among species.

Key Terms: honest indicators, performance ability

APPLY YOUR KNOWLEDGE

1. Describe the sonic structures of birdsongs and calls, including the traditional distinctions between these two vocalizations and the nature of whistles, harmonics, pitch and loudness, and timbre.
2. Compare and contrast songs and calls in terms of innate or learned

behavior and natural selection or sexual selection.

3. Explain how the acoustic structure of a sound can hide or disclose the singer. Which structures are best for use in different habitats?
4. Describe how the mammalian larynx and avian syrinx differ in anatomical position and structure.
5. How does the syrinx produce sound, and how can birds produce different, independent sounds simultaneously? What is the importance of the interclavicular air sac?
6. Describe the song-learning sequence from the critical learning period through the silent, subsong, and song-crystallization periods to the production of the final songs.
7. What is the auditory template? How is the auditory template employed in song structure learning, and how does it constrain the scope of sounds that are incorporated into learned songs?
8. How do geographical song dialects develop? Why are dialects described as the result of cultural evolution?
9. Discuss mate selection based on song repertoire in terms of natural selection and fitness versus cultural evolution. What benefits, if any, accrue to the male and to the female due to females choosing the best male vocalist?
10. Describe the three auditory pathways and their interactions and roles in song learning and development.

CHAPTER 9 *Annual Cycles*

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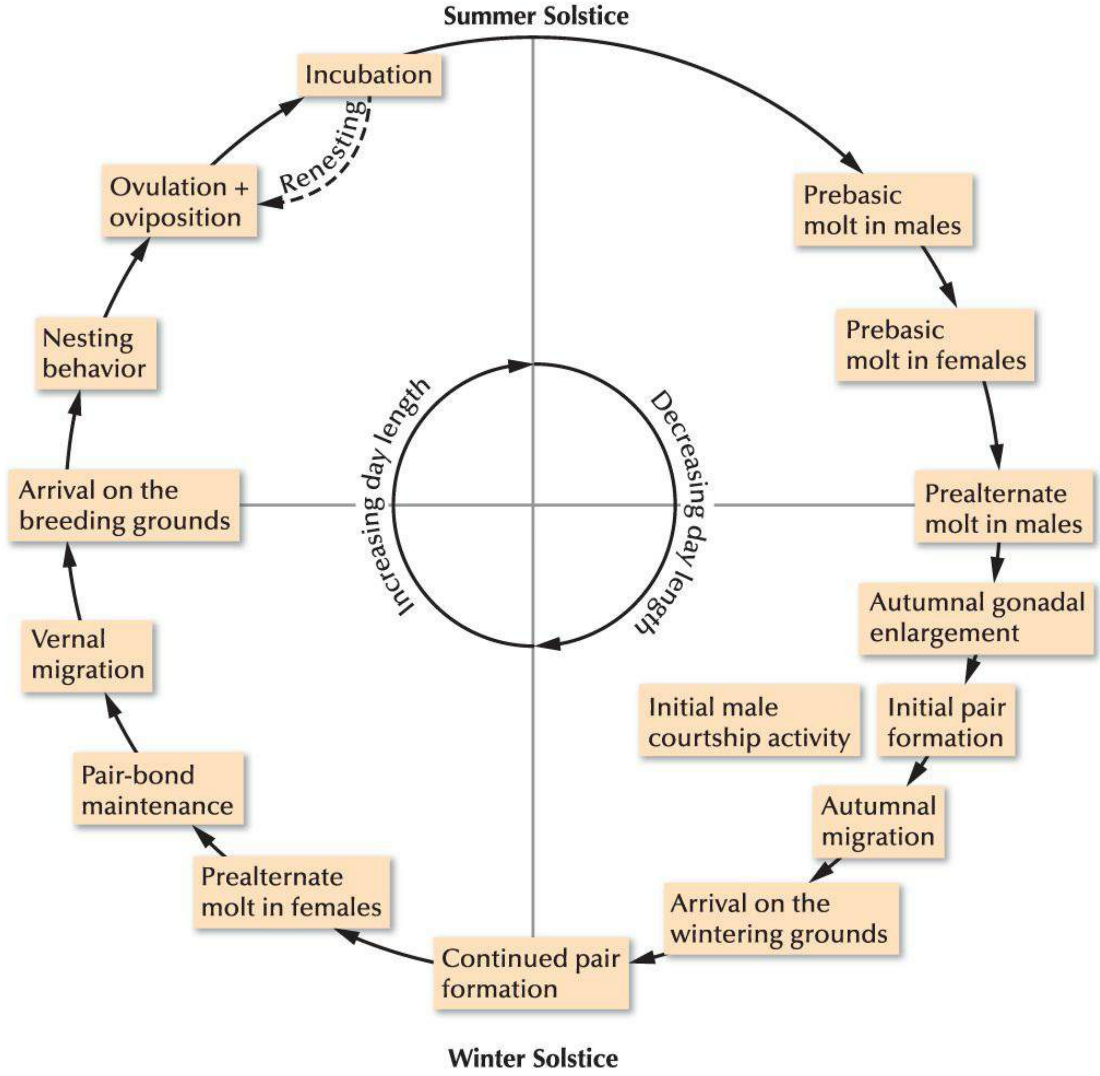
The Dark-eyed Junco is a classic species in the study of mediation of seasonality and speciation by hormones.

> One swallow does not make a summer, but one skein of geese, cleaving the murk of a March thaw, is the spring. [Leopold 1966, p. 19]

Birds face seasons of stress and seasons of opportunity that correspond to predictable calendar changes in day length, climate, and resources, especially food. The primary seasons are usually related to changes in temperature in the temperate zones and to changes in rainfall in the Tropics. Just to survive, much less to breed and otherwise function appropriately at different times of their year, an individual bird must change its appearance, its physiology, and its behavior. It must transition smoothly from one life-history stage to another, with advance notice and preparation so as to time each stage appropriately to the next set of environmental conditions (Jacobs and Wingfield 2000). Environmental and social cues activate internal endocrine management systems that orchestrate the sequencing of life-history stages, with contingencies for the unpredictable.

Each year, an adult bird invests time and energy above and beyond that required for daily survival into three main efforts: reproduction, molt, and, in some cases, migration. The conflicting demands of these efforts combine with seasonal resources and opportunities to define a bird’s annual cycle (Figure 9–1). Tight scheduling, trade-offs, and compromises are often required. Natural selection will favor those individual birds that schedule well and optimize the balance of their seasonal efforts.



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DATA FROM BLUHM 1988

Figure 9–1 Annual cycle of the Mallard. Most individual birds attempt to breed when they are one year old. See Chapter 4 for molt terminology.

This chapter first describes the basic components of avian annual cycles and then proceeds to the physiological clocks, called **circadian rhythms,** that control the avian annual calendars by synchronizing a bird’s internal state with its seasonal environment. The **photoperiod**—the length of daylight—is an essential environmental cue for the clocks. It triggers activity in the brain and then the pituitary gland that leads to a cascade of hormonal controls of physiology and behavior.

The chapter then more closely examines the timing, costs, and trade-offs related to breeding, molt, and migration, including how birds handle stress. We conclude with the effects of global warming on the annual cycles of birds.

9.1 Basic Annual Cycles

The simplest type of annual cycle and the typical year of permanent residents—birds that live in the same place year-round—present three main sequential tasks: breed, molt, and survive until the next breeding season. Consider, for example, the simple life of the Feral Pigeon (Figure 9–2). The pigeons cycle between two life-cycle stages. As long as they have ample food and a mate, they nest until the young fledge (or until the mate is lost). Then they transition to the alternative, nonbreeding stage and remain in that stage until they have a mate in breeding condition and adequate food is available to initiate nesting.

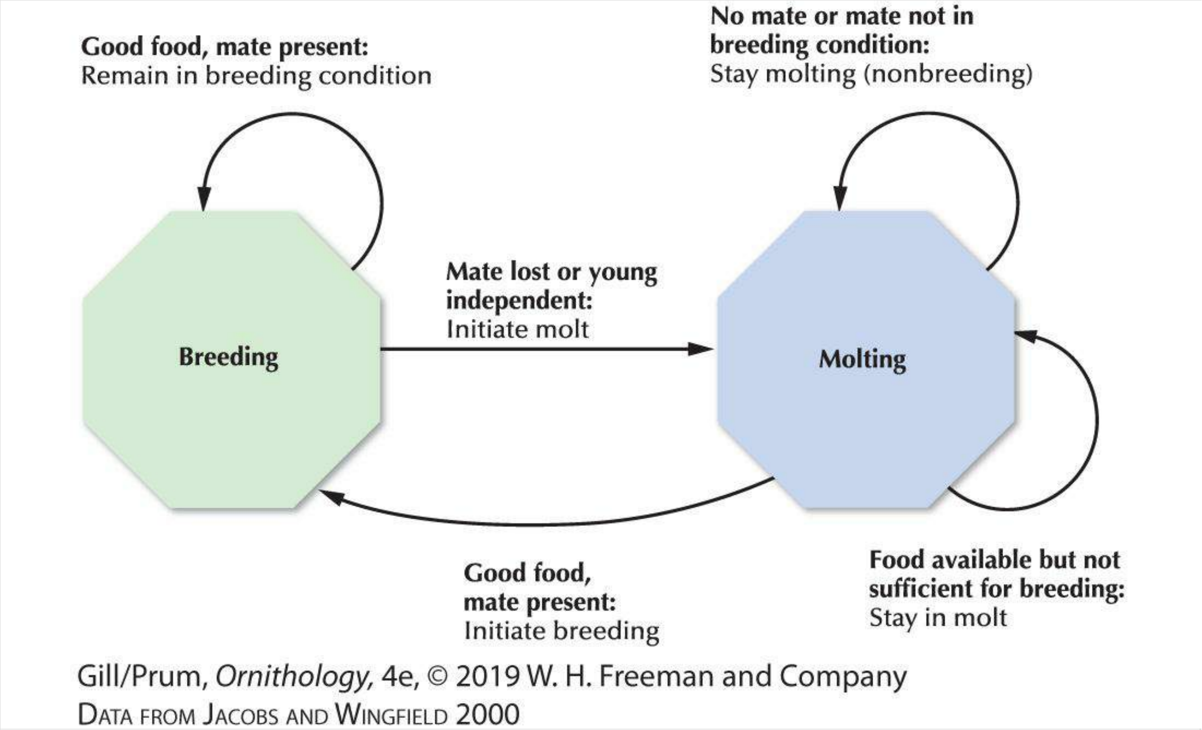

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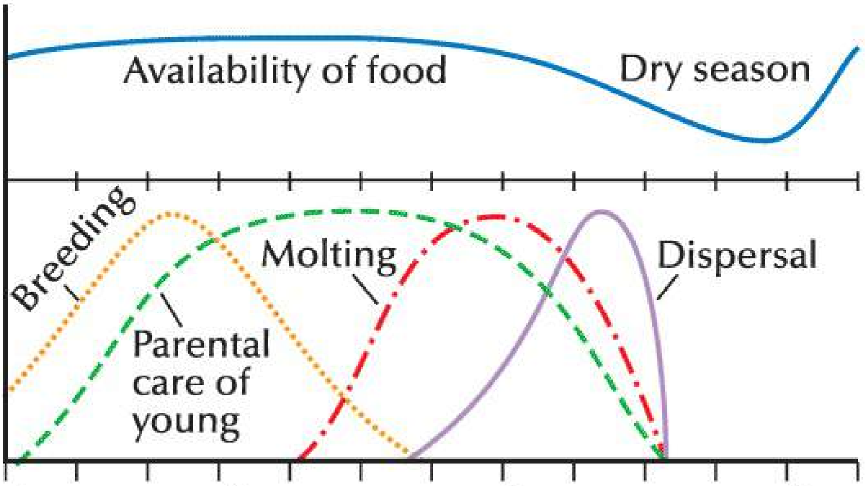
Figure 9–2 Simple life cycle of the Feral Pigeon, which alternates between a breeding stage and a nonbreeding, or molting, stage. Arrows indicate conditions (boldface type) for remaining in one stage or switching to the other. Each condition is followed by a response to the change in environmental cues.

The annual cycles of most forest birds in equatorial Borneo also are simple. Temperature and day length vary little all year. Most small birds start to nest when the heavy rains begin in December. Adults start to molt shortly after the young have left the nest in May and continue molting until the beginning of the two-month "dry" season, when food starts to become scarce. When heavy rains resume and food supplies increase, gonads increase in size, and the cycle repeats itself (Figure 9–3).



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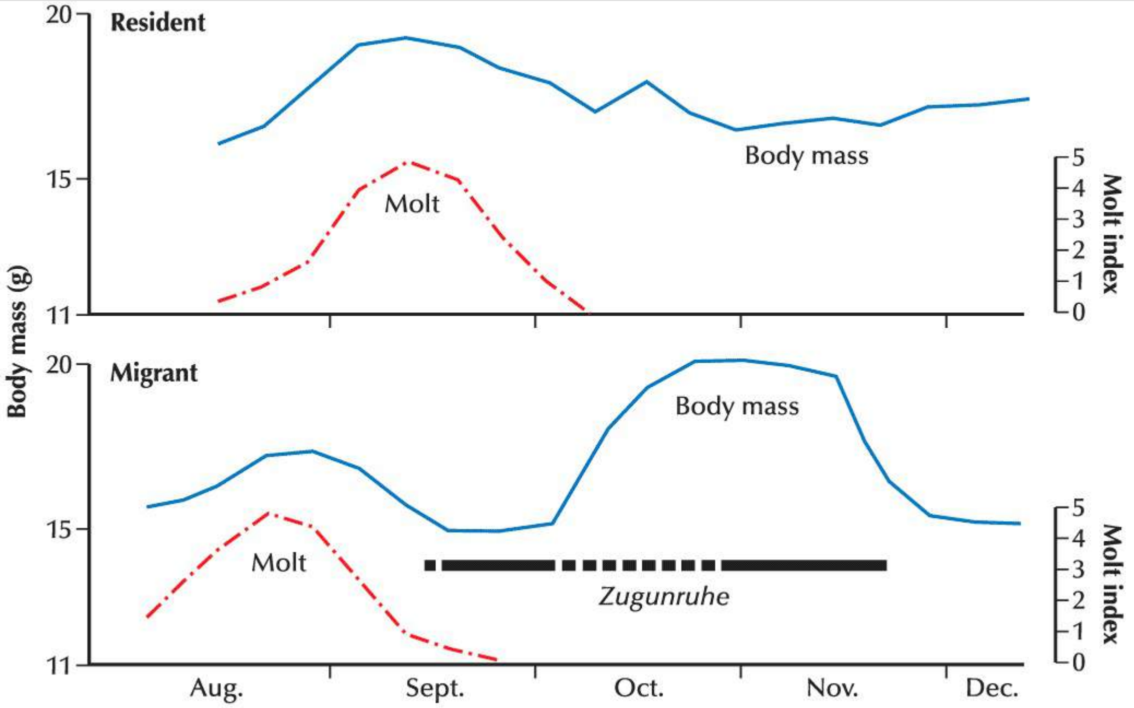
DATA FROM FOGDEN 1972

Figure 9–3 Birds have well-defined breeding and molting seasons that coincide with the months of greatest food availability in the wet season, even in the equatorial rain forests of Borneo.

Similar cycles of reproduction and molt are typical of permanent residents of northern temperate localities, including Song Sparrows in Ohio, Black-capped Chickadees in Wisconsin, and Common Chaffinches in Britain. After the quiescent winter months, sex hormones flow, gonads increase in size, and males proclaim their territories with conspicuous songs and, sometimes, brutal fights. Pair bonds are established or reaffirmed, and mating takes place. Young hatch in May and June, and generally reach independence by late July. Molt follows in August and September. At this time, young birds leave their natal territories, and families aggregate into well-organized flocks for the winter. Social competition for territories, food, and mates—all resources essential for reproduction next spring—may start in the autumn.

Migration adds a complicating challenge to the annual cycle. Major changes in physiology, body composition, and behavior take place (Figure 9–4; Chapter 10). After they breed and molt, migratory birds generally gather in flocks and eat tremendous amounts of food, fueling themselves for their trips. To fuel their marathon flights, many species double their body mass with large stores of fat as fuel. As the date for departure approaches, they become restless after dark and then leave on a major trip to a distant wintering ground. Migratory preparations are repeated the following spring for the return north, where the cycle of reproduction, molt, and preparation for migration repeats. Many temperate-zone birds, especially those that migrate, molt twice a year, once after breeding and again in late winter or early spring.



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DATA FROM BIEBACH 1983

Figure 9–4 Body mass (in grams), molt, and Zugunruhe behavior (migratory restlessness) of a young resident (top) and a young migratory European Robin in the laboratory (bottom). Breeding experiments revealed a genetically based polymorphism for migratory behavior, including early molt, premigratory fattening, and migratory restlessness, in the two forms of this species. A molt index of 1 indicates the beginning or the end of the molt. A molt index of 5 indicates a heavy molt that includes most of the feather coat.

Annual Cycles of the White-crowned Sparrow

The annual cycles of White-crowned Sparrows, including their physiological controls, have been studied in depth (Chilton et al. 1996). The White-crowned Sparrow breeds throughout northern Canada and from southern Alaska to central California (Figure 9–5), which means that different populations that winter together are exposed to seasonal differences in climate on their breeding grounds.

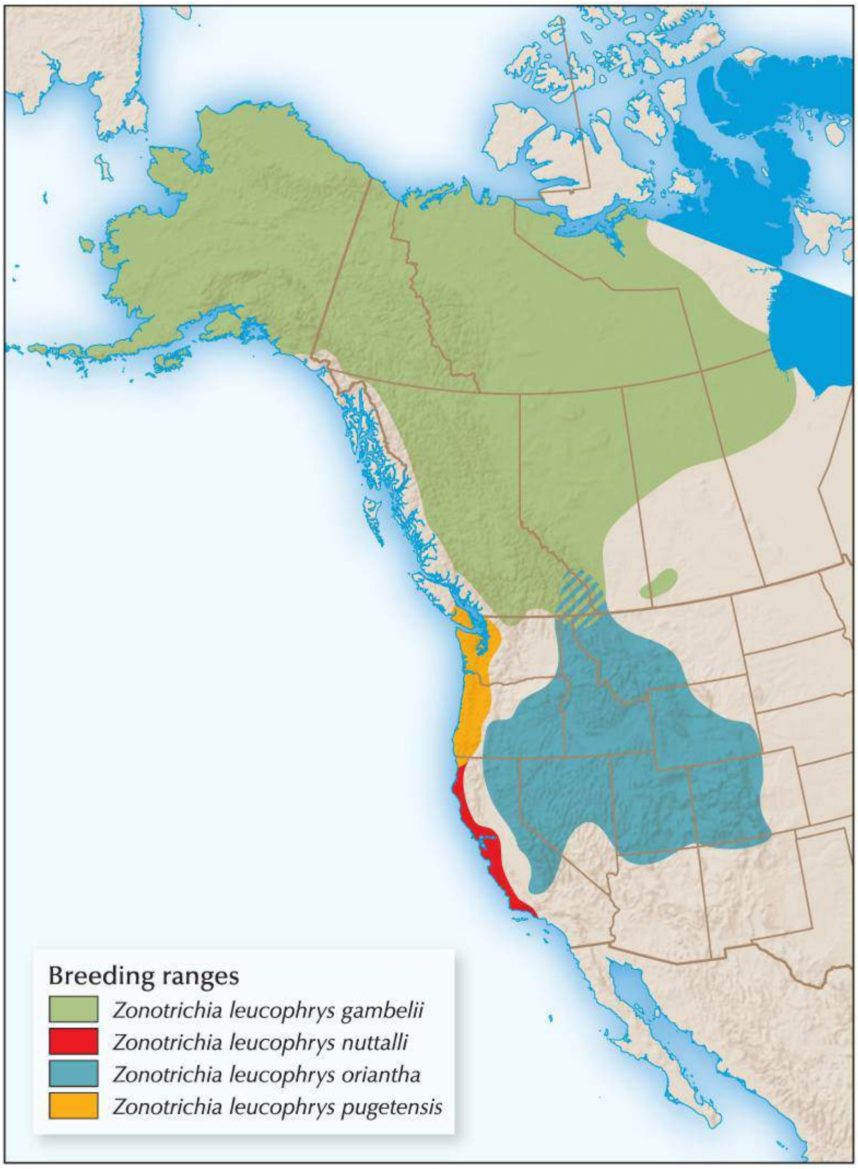

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Figure 9–5 Breeding ranges of four western subspecies of White-crowned Sparrows, *Zonotrichia leucophrys*. The most northern races, *Z. l. gambelii* and *Z. l. pugetensis*, migrate to central California, where they winter with resident *Z. l. nuttalli*. The Rocky Mountain race, *Z. l. oriantha*, migrates south to Arizona and Mexico.

The annual cycle of White-crowned Sparrows can be diagrammed as a series of specific stages activated by environmental cues. The stages are activated by internal (usually hormonal) responses that, in turn, trigger the transition to the next stage in the sequence.

Populations on the Pacific Coast differ in the extent of their annual migrations and in other aspects of their annual cycles. Those that breed in Alaska and in northwestern Canada (subspecies *gambelii*) are long-distance migrants that winter primarily in California, where they mix with winter flocks of the local nonmigratory White-crowned Sparrows (subspecies *nuttalli*). Members of another population (subspecies *pugetensis*), which breed on the coasts of Washington, Oregon, and British Columbia, also mix with *nuttalli* flocks in California during the winter.

White-crowned Sparrows from northern localities nest later in the spring than those from southern localities. The southern resident *nuttalli* come into breeding condition first, then the *pugetensis,* and, finally, the *gambelii* of the far north. Differences in the timing of the enlargement of the gonads and breeding activities characterize not only the three subspecies but also the geographical gradients of populations within each subspecies.

Finally, some (but not all) of these White-crowned Sparrows molt in the spring before breeding. This extra "prenuptial" molt is known as the **prealternate molt** (see Chapter 4).

9.2 Physiological Clocks

The annual cycle requires an orderly integration of behavior and physiology. A network of physiological controls and clocks regulate the schedules of reproduction, molt, sleep, feeding, and migration.

All plants and animals have self-sustained oscillations called **endogenous rhythms** that allow them to precisely time their lives. These biological clocks act at the cellular level. They release the hormones that regulate metabolism, reproduction, and behavior. Birds are no exception. Neuroendocrine systems synchronize cellular rhythms so that an entire bird is internally organized and appropriately synchronized with its periodic environment (Figure 9–6). In addition to regulating the daily activity and cycles of body temperature, these internal clocks measure day length itself and calibrate the sun compass by which birds navigate (Chapter 10). They govern migratory restlessness, premigratory fattening, and egg laying. Some biological clocks, called circadian rhythms, match the daily 24-hour cycle of the Earth's rotation on its axis. Others, called **circannual cycles,** synchronize to the annual cycle of the Earth's revolution around the sun.

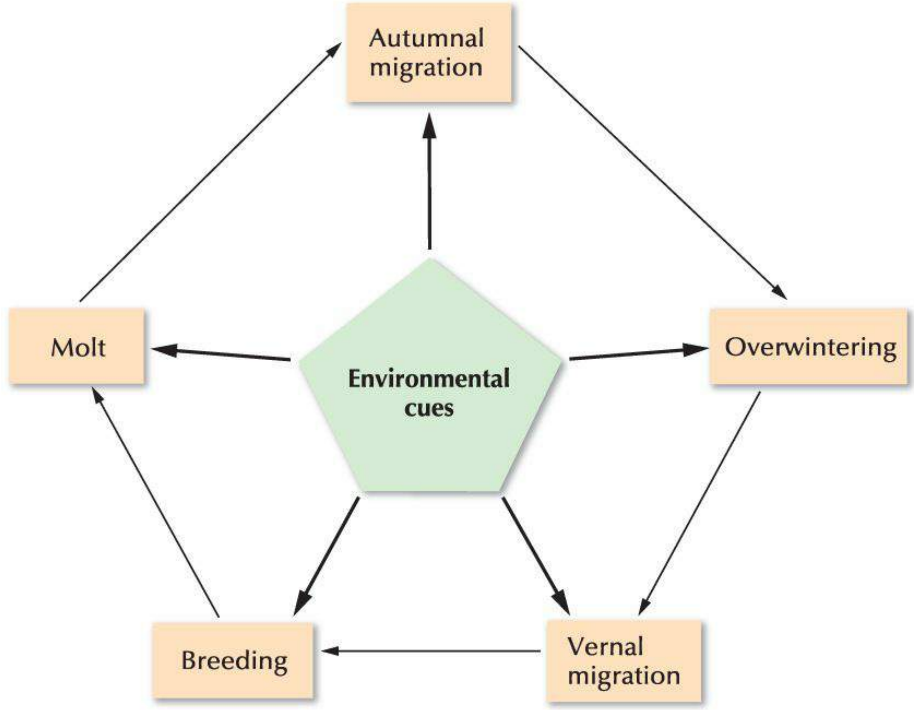

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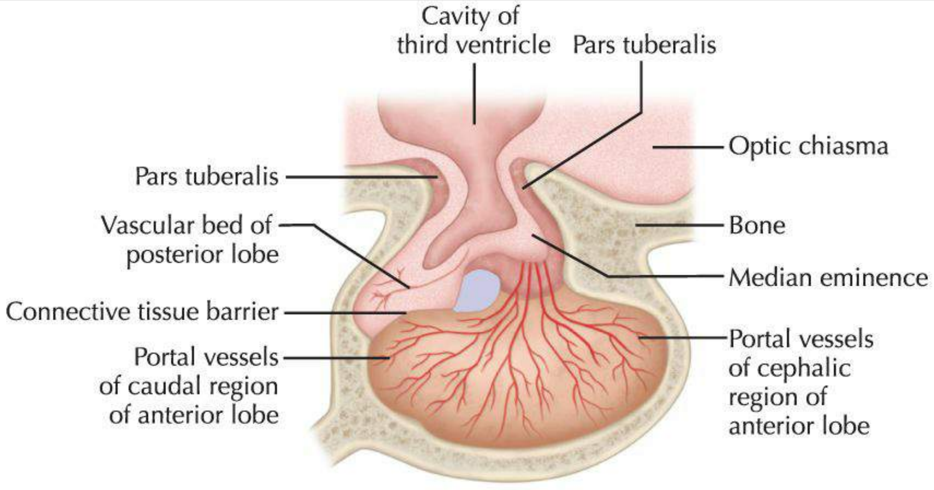
Figure 9–6 Annual life cycle of a migratory population of the White-crowned Sparrow (subspecies *gambelii*). Each seasonal stage (squares) is triggered by environmental cues (large arrows) and by the physiological changes of a preceding stage (thin arrows).

Circadian rhythms are a basic adaptation of cellular organisms to the 24-hour light–dark cycle of the planet. Twilight triggers a switch in physiology from diurnal to nocturnal systems. Most birds have three important self-sustained oscillators in their circadian system: (1) the pineal gland, (2) the suprachiasmatic nuclei of the hypothalamus, and (3) the eyes (Figure 9–7). The triangle-shaped **pineal gland,** which is located on top of the brain, houses the biological clock in birds. Most diurnal birds have a well-developed pineal gland. This gland includes photosensitive cells, each having gene-based pacemakers that direct the rhythmic production of melatonin, the chemical that regulates daily rhythms in concert with daily light–dark cycles. Melatonin is the major circadian messenger in the body and is released directly into the blood, which allows it to reach nearly every part of the body. Experimental removal of the pineal gland in House Sparrows causes normal 24-hour cycles to disappear. The **suprachiasmatic nuclei** are a paired set of brain nuclei located in the hypothalamus that are active during the day and release neurotransmitters that regulate metabolic activity. And the eyes have neuronal and melatonin rhythms of their own that are smaller than those of the pineal. Together, these three circadian oscillators are coupled in a feedback loop through hormonal and neuronal pathways. Light enters the system at three points: through the eyes, through extraretinal photoreceptors, and through the pineal itself, which has its own photoreceptors.



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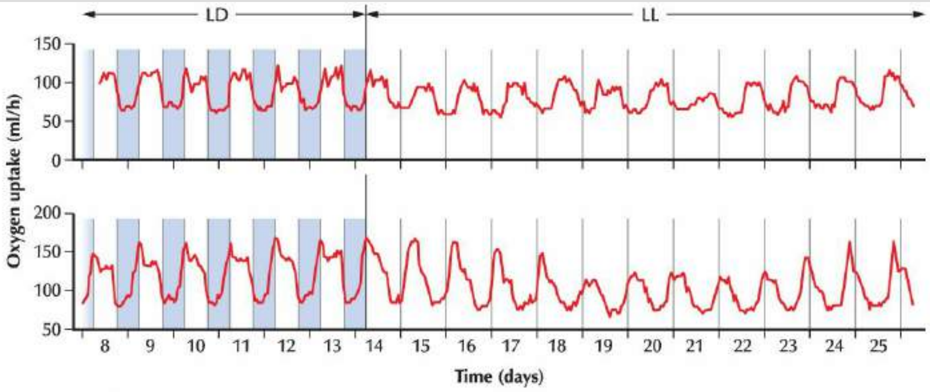
DATA FROM HÖHN 1961

Figure 9–7 Avian pituitary gland and adjacent structures. Daylight stimulates special photoreceptors in the tuberal region (pars tuberalis) of the lower hypothalamus of the midbrain. Neurohormones are released in the median eminence and carried to the anterior pituitary gland through the hypophyseal portal blood vessels. They stimulate gonadal hormone production and, as a result, gonadal activity.

Every individual bird has an intrinsic rhythm approximately 23 hours in length in which body temperature, rate of metabolism, and level of alertness fluctuate in predictable ways. Because they are not exactly 24 hours in length, these internal cycles tend to depart gradually from real time, starting slightly earlier each day, unless they are somehow synchronized or entrained by external cues called **Zeitgebers**—literally, "time givers." When Common Chaffinches are kept in constant dim light, their endogenous rhythms of activity and metabolic rate function in a period of about 23 hours and therefore drift about one hour per day (Figure 9–8). White-crowned Sparrows have a regular cycle of activity and sleep that is just under 24 hours long when they are kept in a dimly lit experimental cage. Natural, external light–dark cycles then synchronize the endogenous rhythm with the 24-hour cycle.



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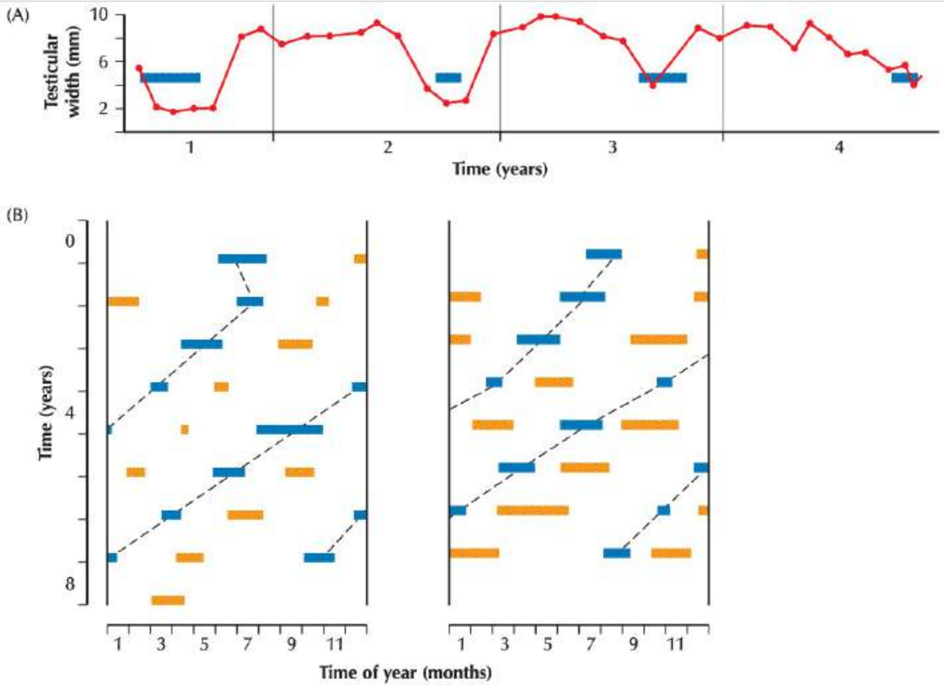
DATA FROM ASCHOFF 1980

Figure 9–8 Common Chaffinches kept in a dimly lit environment have a daily activity cycle (measured here in milliliters of oxygen taken up per hour) of just under 24 hours. This experiment demonstrates that, under constant dim illumination (LL), the cycle drifts one hour of clock time unless it is synchronized by an external stimulus, such as regular 24-hour light–dark (LD) cycles.

Endogenous rhythms control the annual cycles as well as the daily cycles of some birds. We know far less about circannual rhythms because experimental manipulations take many years. Nevertheless, decadelong experiments suggest that endogenous rhythms keep oscillating over many years, even in the absence of Zeitgebers (Figure 9–9). African Stonechats, for example, maintain a cycle of about nine months when kept under constant photoperiods during a 10-year period (Gwinner 1996).



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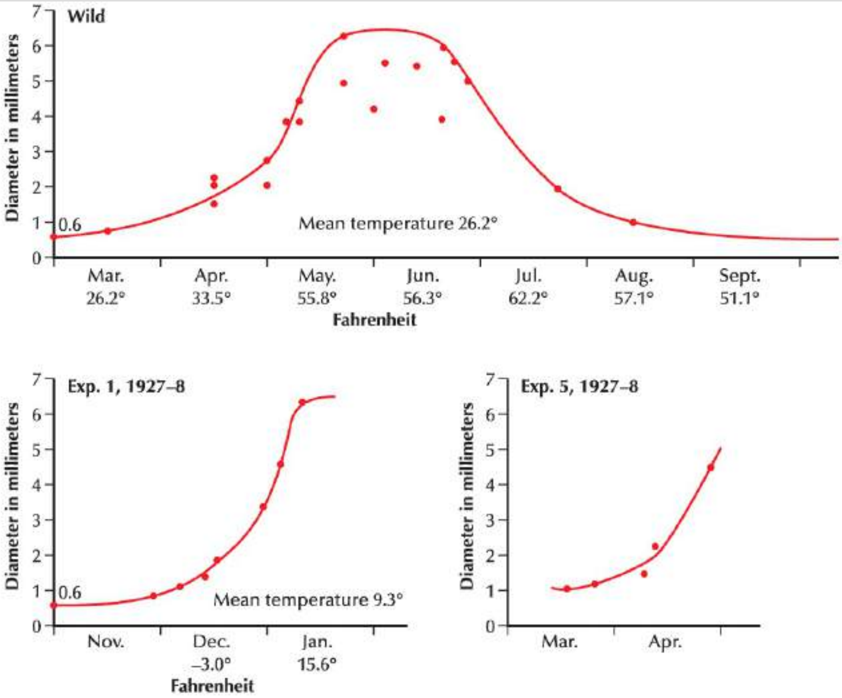
Data from Gwinner 1977, Berthold 1978

Figure 9–9 Circannual rhythms under constant photoperiodic conditions. (A) Rhythms of testicular width (curves) and molt (bars) in a Common Starling. The undamped oscillations in testes size and the intervals between successive molts deviate irregularly from a 12-month cycle. (B) Rhythms of summer molt (blue bars) and winter molt (orange bars) in a Garden Warbler (left) and in a Eurasian Blackcap (right), both maintained in captivity for eight years. Both molts occur progressively earlier each year because the birds have an internal rhythm with a mean period of about 10 months.

The photoperiodic control system couples two kinds of information. Clock information from the internal circadian cycle enables the bird to measure day length by using time windows of photosensitivity. Environmental-light information stimulates neural receptors to translate day-length information into behavior. This two-part system allows birds to respond at the optimal time for reproduction, to synchronize reproductive function in mating pairs, and to terminate reproductive function—three fundamental requirements for control of the annual reproductive cycle.

Day length, or photoperiod, plays a key role in the control system that synchronizes the physiologies of individual birds with their environment. William Rowan (1929) pioneered research on the photoperiodic control of avian gonadal cycles. He showed that increases in photoperiod of only five to 10 minutes per day cause the testes of Dark-eyed Juncos to increase in size, an effect that was reversible and repeatable as many as three times between autumn and spring (Figure 9–10). The phenomenon of the photoperiodic control of gonad cycles has since been recognized in more than 60 north temperate bird species and has been confirmed by experimental manipulations such as the one shown in Figure 9–11, in which manipulations of photoperiod can change the timing of the entire breeding cycle.



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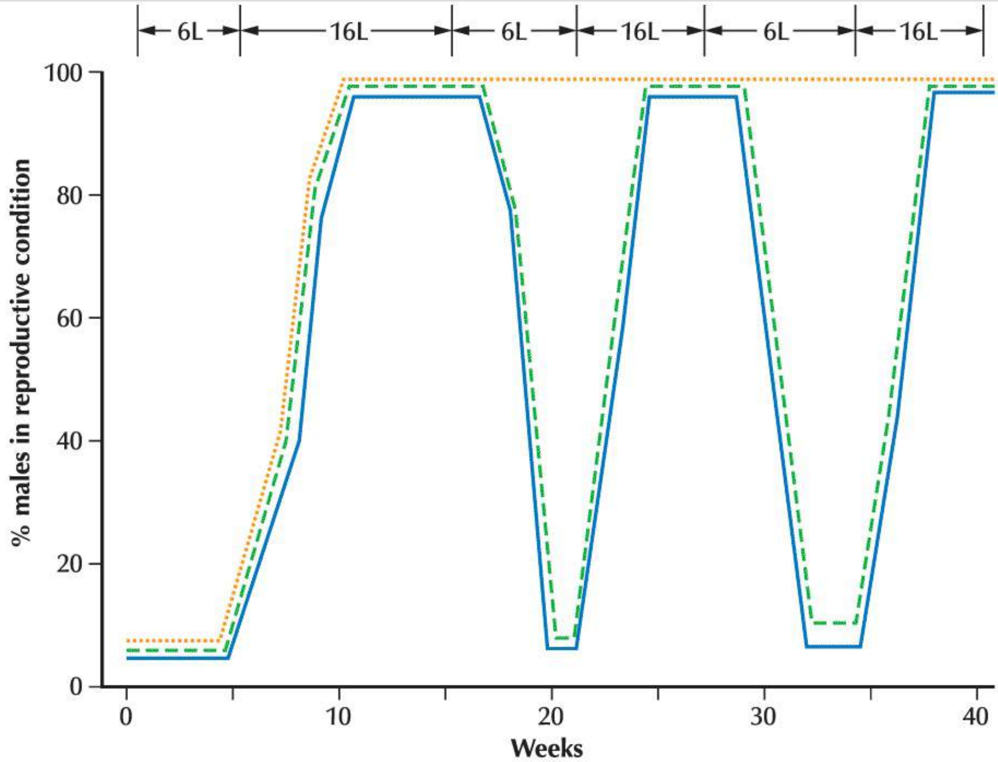
DATA FROM ROWAN 1929

Figure 9–10 In the pioneering study of annual cycle control by photoperiod, William K. Rowan demonstrated that longer day lengths cause the testes of captive Dark-eyed Juncos to increase prematurely to full size in January (lower left) and again in April (lower right) instead of in May and June, as in wild juncos (upper graph). Mean temperature is the average air temperature in that month.



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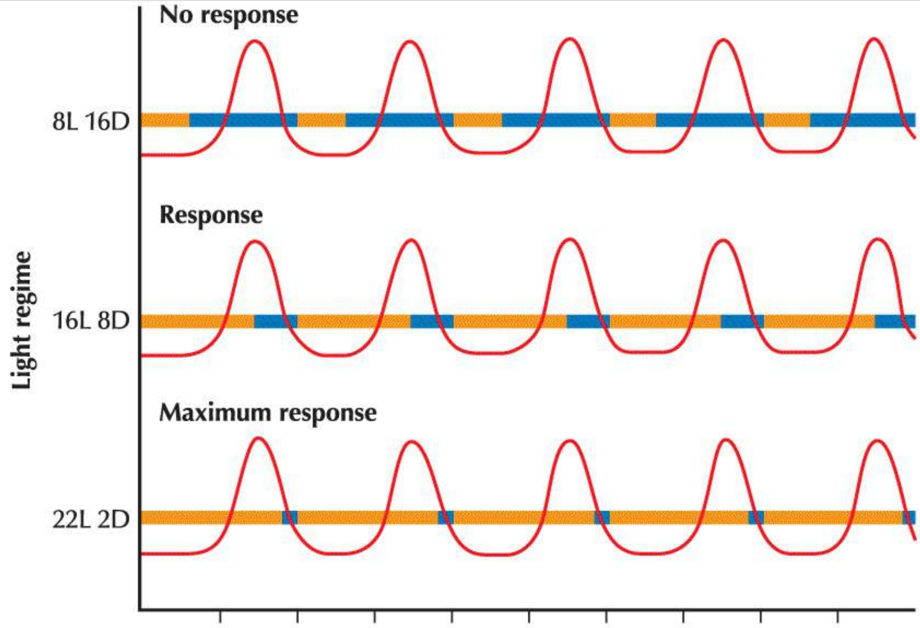
DATA FROM SIOPES AND WILSON 1974

Figure 9–11 Photoperiodic response in male Japanese Quail transferred back and forth between short days (6L:18D) and long days (16L:8D) over a period of 40 weeks. Intact males and males without a pineal gland responded to the photoperiod cycles by entering into reproductive condition on long day cycles and exiting on short days. Blind and pinealectomized males did not cycle.

Molt and preparations for migration also are triggered by changes in day length and can be experimentally manipulated. Stephen Emlen (1969), for example, accelerated the annual cycle of Indigo Buntings, inducing an extra molt into the year by suddenly increasing the length of the photoperiods to which captive birds were exposed.

The circadian rhythms include a limited period of photosensitivity each day. During this period, external light stimulates receptors in the brain, which in turn trigger a series of physiological reactions. As day length increases, so does the chance that there will be daylight during the photosensitive period (Figure 9–12). Not only does the chance of overlap, or coincidence, increase with day length, but the duration of the period of overlap also increases. The amount of overlap enables birds to measure day length. The “external coincidence” model was originally developed for plants, but we now have evidence that this model also applies to many species of birds.



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DATA FROM FARNER 1980

Figure 9–12 The external coincidence model suggests that day length is measured by the increased amount of time that daylight periods (orange bars) coincide with the photosensitive phase of the circadian rhythm (oscillation peaks). Abbreviations: L, number of hours of light; D, number of hours of dark. Response was measured in terms of gonadal enlargement, which was greatest for a 22-hour light–2-hour dark cycle.

After stimulation of the photoreceptors, neurosecretory cells in the hypothalamus induce the release of neurohormones from the pituitary (see Figure 9–7). The released neurohormones then induce the anterior pituitary gland to produce the hormones (Table 9–1) that directly affect the activity of the gonads themselves. Thus, a series of neural and physiological events translate increasing day length into sexual activity.

Table 9–1 *Principal Hormones That Govern the Annual Cycles of Birds*

Hormone	Abbreviation	Source	Role(s)
Adrenocorticotropic hormone	ACTH	Adrenal gland	Stress management Suppresses release of gonadal hormones Reduces resistance to disease (immunocompetence) Migratory restlessness
Estrogens			Progesterone release by pituitary gland Egg production in oviduct Secondary sexual morphology and brain function
Follicle-stimulating hormone	FSH	Pituitary gland	Sperm production by testes Egg-follicle development in ovary
Glucagon	None	Pancreas	Metabolism in liver and

			muscles Release of fatty acids to blood plasma Fasting
Growth hormone	GH	Pituitary gland	Normal posthatching growth Fat metabolism and synthesis Stimulates immune system
Luteinizing hormone	LH	Pituitary gland	Increases production of progesterone and testosterone Induces ovulation
Luteinizing hormone–releasing hormone	LHRH	Hypothalamus	Production of LH and FSH by pituitary gland
Melatonin	None	Pineal gland Retina Gastrointestinal tract	Circadian rhythm of cells throughout body Photoreception and neural transmission Food utilization
Progesterone	None	Ovary	Induces ovulation
Prolactin	None	Pituitary gland	Production of crop milk in pigeons Incubation behavior and broodiness

			Photorefractoriness of testes
Thyroxine	T4	Thyroid gland	Metabolism and thermogenesis Growth and development Onset and pace of molt
Testosterone	None	Testis, ovary	Development of testes Secondary sexual morphology and brain function Ovulation in females

The annual cycle of the White-crowned Sparrow outlined earlier illustrates the translation of seasonal changes in day length into appropriate behaviors. Increasing photoperiods during late winter and early spring trigger events in the annual cycle. The longer days of early spring stimulate gonad development and then the spring (prealternate) molt and migration. Warmer temperatures, rainfall, and the springtime display behavior of other sparrows stimulate the final stages of gonad development on the breeding ground and, as a result, the increased secretion of sexual hormones. After the birds breed, the shortened days of late summer trigger the main (prebasic) molt.

The increasing day lengths of the spring also schedule, in advance, the fall light-insensitive, or photorefractory, period of the testes. After photoperiodic regulation of the annual cycle evolved, some additional safeguards and corrections were essential. Photorefractory physiology is one of them. The gonadal cycle normally concludes with a rapid collapse and reabsorption of gonadal tissue. Then follows the **photorefractory period,** during which long days do not induce gonadal regrowth. The photorefractory physiology of adults seems to be an adaptation for scheduling molt and migratory preparations during the favorable conditions of late summer by discontinuing reproductive activity while days are still long.

Finally, the very short days of early winter inhibit gonad growth and restore sensitivity to long photoperiods by terminating the refractory period. The cycle begins anew as day lengths increase in January. Short winter days are essential to the control of the annual cycle: the testes will not grow in response to the long days of spring unless a bird has experienced a prior period of short day lengths. Thus, White-crowned Sparrows stay in nonbreeding condition for several years when experimentally exposed only to long photoperiods.

9.3 Master Hormones

Much of the annual cycle, including specific behaviors in reproduction, molt, and migration, is directly controlled by hormones. Hormone production is headquartered in the lower midbrain, where the hypothalamus connects to the adjacent pituitary gland, directing it to release master hormones that direct the activities of specific organs (see Table 9–1).

The Pituitary Gland

As instructed by the hypothalamus, the pituitary gland releases two master hormones that directly control gonadal development and function and that indirectly control many other aspects of the annual cycle. One of them—**luteinizing hormone (LH)**—stimulates the production of the male hormone testosterone by Leydig cells in the testes. In the female, it induces the ovulation of mature egg follicles as well as the production of the sex hormones progesterone and testosterone. The other master hormone—**follicle-stimulating hormone (FSH)**—stimulates sperm production in the testes of male birds and the initial development of egg follicles in female birds. Research on male birds has shown that increasing day lengths cause the hypothalamus to release **luteinizing hormone–releasing hormone (LHRH).** As its mouthful of a name suggests, LHRH stimulates the pituitary gland to increase LH as well as FSH secretion. Pulses of plasma LH then travel throughout the bird’s body and stimulate gonadal activity and a host of reproductive behaviors.

In addition to their role in reproductive behavior, endocrine hormones affect the timing and course of molt. The thyroid hormone **thyroxine** plays a primary role in the onset and pace of molt (Jenni-Eiermann et al. 2002). Its effects, however, are subject to the presence of the gonadal hormones—particularly the sex steroid hormones, such as testosterone, which inhibit molt by suppressing the secretion of thyroid hormones. Experimental injections of gonadal hormones into molting birds slow or even stop molt. As a result, nonbreeding and reproductively unsuccessful birds with lower amounts of gonadal hormones begin to molt earlier than successful breeders.

Other hormonal changes take place at the end of the breeding season. In addition to the gonadal hormones, thyroxine, glucagon, corticosterone, and growth hormone all play major roles at different times in the annual cycle. They are central to depositing and using fat as fuel for migration. Among other effects, they stimulate ravenous feeding and fat deposition through the cascade of hormonal controls that starts at the hypothalamus–pituitary headquarters.

Managing Seasonal Stress

Central to seasonal adjustments and the interplay among hormones is the need for birds to manage daily and seasonal stresses. Regular measurements of the amount of the hormone **corticosterone** in tiny samples of blood plasma from living birds allow ornithologists to monitor the patterns of stress that birds experience at different times of year. Corticosteroid hormones are produced by the adrenal glands and are thus also called adrenaline. Corticosterone mediates trade-offs between individual survival and breeding success.

Corticosterone increases rapidly in response to acute stress events, such as escaping from a predator, fighting for a territory, or being hungry. A rapid rise in corticosterone—the stress response—redirects a bird's behavior and physiology toward basic survival efforts, such as looking for food and increasing the rate of food intake. Corticosterone levels stay high until the bird has offset the energetic challenge, perhaps by mobilizing energy reserves or escaping the source of stress. The return to normal baseline levels as soon as possible is important because continued elevation of corticosterone due to sustained or chronic stress suppresses other activities, such as reproduction. Among the effects, high levels of corticosterone suppress the release of gonadal hormones, reduce resistance to disease (immunocompetence), and may have long-term effects on the "personality" of nestlings exposed to chronic stress in the Florida Scrub-Jay (Schoech et al. 2009). Thus, breeding activities, including parental care particularly, are not compatible with high levels of corticosterone in most vertebrate animals. Increases in corticosterone during spring storms, for example, cause birds to stop breeding. Experimental treatments with corticosterone reduce territorial behavior and rates of feeding young. In Florida Scrub-Jays, high levels of corticosterone in bad (food-poor) years are strongly correlated with delayed breeding, and low levels of corticosterone characteristic of birds in suburban populations are associated with early breeding (Schoech et al. 2012).

Because of the potentially severe costs, acute stress responses affect many aspects of a bird's annual cycle, including habitat preferences and breeding behavior. Some birds, however, live in difficult, high-stress environments that would seem to promote debilitating, high levels of corticosterone. Examples include desert birds, such as the Cactus Wren and Curve-billed Thrasher, which endure intense heat and aridity during the summer (Wingfield et al. 1992). At another extreme, species that breed in the Arctic, such as White-crowned Sparrows and American Tree Sparrows, face severe time and energy constraints imposed by the short summers and unpredictable weather (Holberton and Wingfield 2003). Do such birds avoid the trade-off costs by moderating their corticosterone responses? They seem to do so. The desert-adapted wrens and thrashers suppress the classical adrenocortical response to stress during the hot summer season but reactivate it during the winter. Similarly, the Arctic-nesting sparrows exhibit low responses to stress throughout the season, though males are more sensitive to stress before the young hatch. Then they settle down to the unchanging low levels of their mellow mates. The mechanisms of this modulation are unknown.

9.4 Breeding Seasons

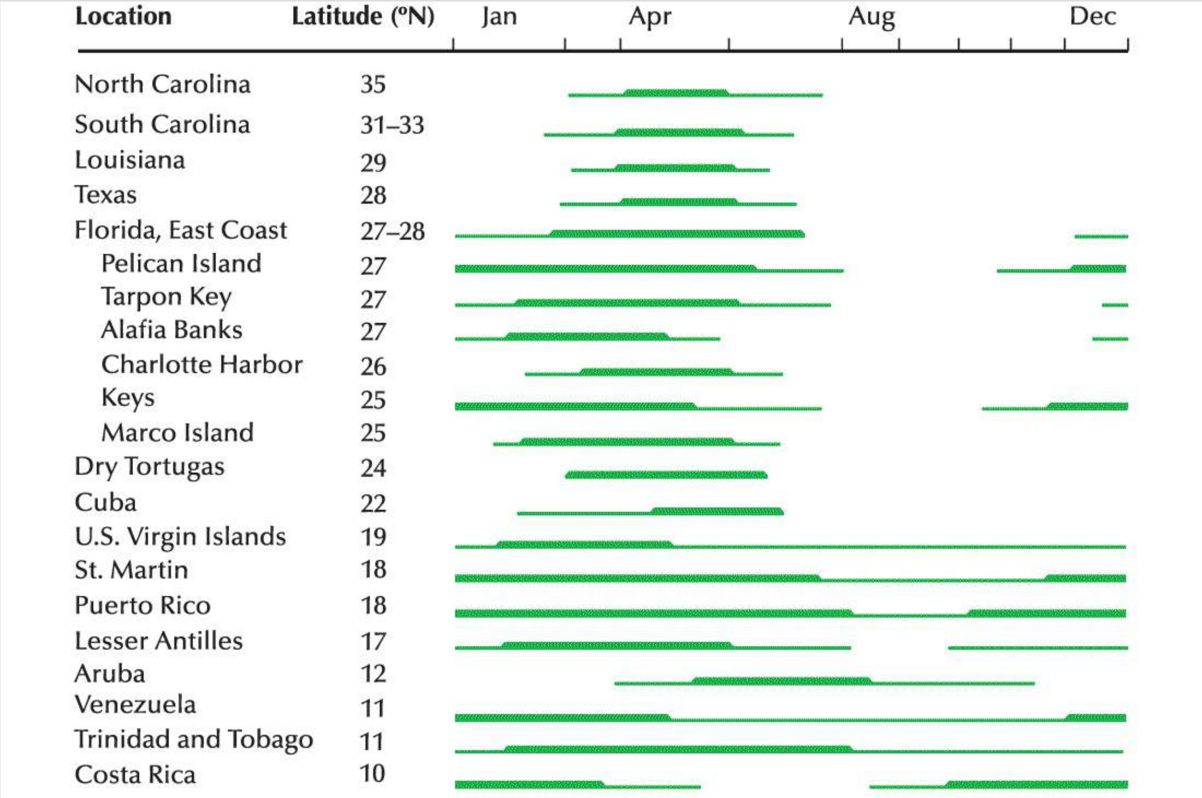
Guiding the evolution of the controls of seasonal behavior cycles have been such factors as the timing of adequate food supplies for both parents and their young, the availability of nest sites, the locations of favorable climates, and areas or times of low predation risk. These so-called ultimate factors tune the control systems to the best times for reproduction. However, they provide no guarantee against the vagaries of particular years. Drought or parasites may cause widespread nesting failure in some years. Birds, of course, cannot predict such disasters before starting to nest, but they can make last-minute adjustments.

Proximate factors are the external conditions that actually induce reproduction. Temperature is probably the most important modifier of annual gonadal cycles. The correct habitat, new vegetation or abundant food, ritualized displays of aggression among neighbors, and social stimulation in general all help to consummate the final stages of gonad enlargement and ovarian development. The annual cycle of Pinyon Jays in New Mexico, for example, is closely tied to the availability of the seeds of the pinyon pine, one of their primary foods. Just the sight of green pine cones is sufficient to trigger gonadal enlargement and timely breeding by these jays. Similarly, Red Crossbills in the Rocky Mountains will nest in January and February surrounded by snow if conifer seeds, their primary food, are abundant.

Tropical nesting seasons last longer than those in the temperate zones. Favorable tropical climates permit nesting for six to 10 months or even, in some cases, throughout the year. Although some individual birds can be found breeding in most months in the Tropics, nesting activity for most birds in lowland Costa Rica, for example, reaches a peak at the end of the dry season and early in the rainy season. Kingfishers are an exception, preferring to breed during the dry season when streams run shallow and clear, making fish easier to capture. Hummingbirds, too, nest at the beginning of the dry season when flowers begin to bloom.

Nesting seasons at temperate latitudes usually last from three to four months or less. In the high Arctic, where only a month or so is suitable for breeding, birds must start nesting immediately after arrival, and sometimes they gain a few days' head start by reusing old nests.

Local populations of a species respond to local conditions. Nesting by Brown Pelicans, for example, is strongly seasonal at northern sites, but is prolonged at tropical sites. Low water temperatures, which depress food supplies, appear to delay the onset of nesting at all sites. After food availability, the hurricane season is the second most important factor controlling the onset of nesting in these pelicans (this observation holds true for tropical seabirds in general). Pelicans nest irregularly throughout the year in the Caribbean and northern South America, more predictably after the hurricane season during the winter and spring in Florida, and from March to June in Louisiana and the Carolinas (Figure 9–13).



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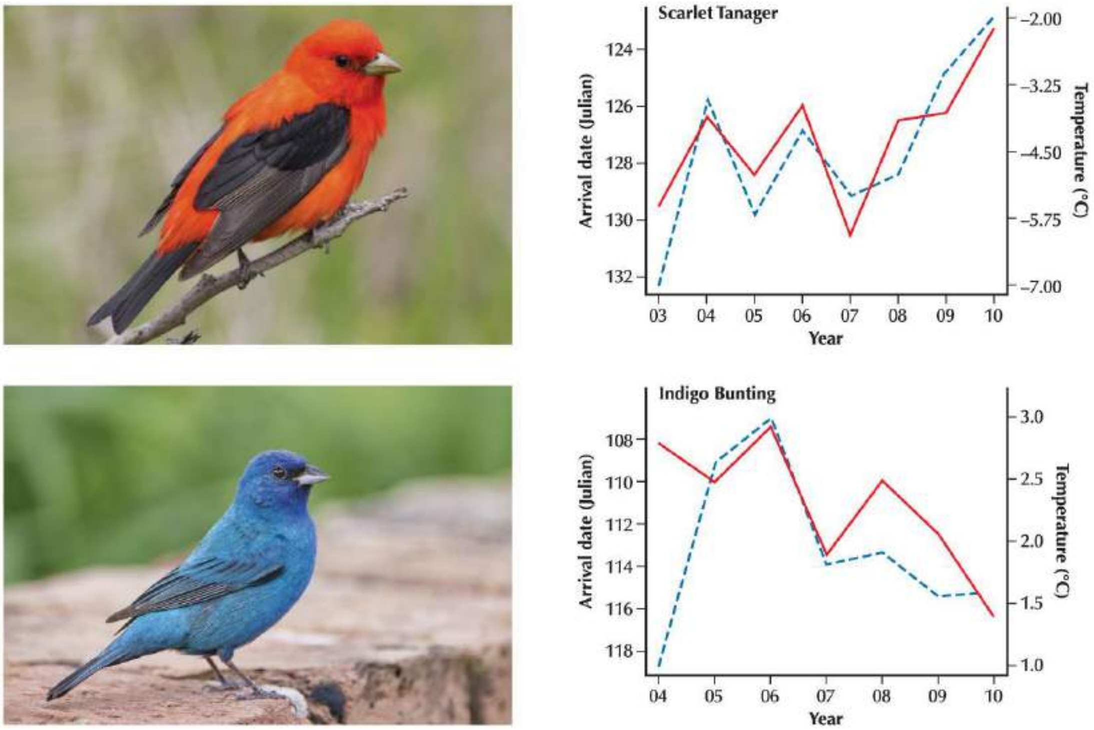
DATA FROM SCHREIBER 1980A

Figure 9–13 The time and length of the breeding season of the eastern race of the Brown Pelican vary geographically as shown by the date that eggs are laid. The thicker part of the lines indicates the probable presence of eggs.

Precise arrival and departure dates are an impressive feature of migration. Every year, after their transequatorial migration, Short-tailed Shearwaters arrive at their breeding colonies off southern Australia within a week of the same date. The traditional return of American Cliff Swallows the week of March 19 to the San Juan Capistrano mission in California has become a symbol of the arrival of spring itself. Year-to-year fluctuations track minimum spring temperatures, with implications for the effects of climate change (Figure 9–14).



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DATA FROM HURLBERT AND LIANG 2012. PHOTOS: (SCARLET TANAGER) TREVOR JONES/SHUTTERSTOCK, (INDIGO BUNTING) BONNIE TAYLOR BARRY/SHUTTERSTOCK

Figure 9–14 Spring arrival dates (dashed blue line) of Scarlet Tanagers and Indigo Buntings correspond to minimum spring temperatures (red line).

Nonannual Cycles

Not all birds follow a 12-month cycle. Year-round availability of adequate food fosters double breeding seasons among some tropical bird species. The Sooty Terns of Christmas Island breed every six months, although the individual birds that breed twice in the same year are those that failed in the first breeding season. Successful birds wait from eight to nine months before breeding the following year (Ashmole 1963a). In only a few cases is the breeding cycle independent of calendar year. Unlike the Sooty Terns on Christmas Island, the Sooty Terns on Ascension Island in the tropical Atlantic nest every 9.6 months, in different months in successive years. Successful nesting is possible at any time of the year, so ample food must be available every month (Figure 9–15).

DAVID HOSKING/ALAMY

Figure 9–15 Sooty Terns on Ascension Island do not have a regular 12-month breeding cycle; instead, they breed approximately every 9.6 months and, consequently, in different months in successive years.

A few very large birds cannot fit their extended reproductive efforts into a single year and hence may skip a year between nestings. Frigatebirds, Crowned Eagles, Griffon Vultures, and Wandering Albatrosses nest once every two years. King Penguins take two months to incubate their eggs and from 10 to 13 months to raise their nestlings, and then they molt. As a result, they breed only twice every three years.

9.5 Timing of Migration

Internal rhythms that are linked to other aspects of the annual cycle guide the timing of migration. Caged migratory passerines predictably become restless just before the time at which they would migrate in the wild. This phenomenon—called **migratory restlessness (Zugunruhe)**—has been familiar to bird fanciers for more than 200 years. Typically, a captive bird wakes shortly after dark and then jumps or flutters in the cage until at least midnight. Because the amount of activity is easily measured, it lends itself to experimental study of both the physiology of migration and orientation behavior. Nonmigratory birds do not exhibit Zugunruhe behavior. Adrenocortical hormones are known to act in concert with prolactin in stimulating this behavior in White-crowned Sparrows.

We now know that increasing day length in winter stimulates early spring restlessness, hyperphagia (eating to excess), fat deposition, and weight increases in many migratory birds. Extending Rowan’s findings about the photoperiodic control of the annual cycle (see section 9.2), Albert Wolfson showed, in another classical study, that Dark-eyed Juncos from migratory populations respond to increasing day length by adding fat stores, whereas sedentary juncos do not (Wolfson 1942). The spring fat deposition and migratory activity of White-crowned Sparrows are under the direct control of increasing day length, mediated by an internal clock. The average date of onset of springtime premigratory fat deposits in captive White-crowned Sparrows has been shown to remain virtually constant for a period of eight years.

The timing of preparations for fall migration is indirectly set by the spring activities. The normal fall sequence of photorefractory testes, prebasic molt, and preparations for migration in White-crowned Sparrows, for example, depends on prior exposure to long photoperiods, but the pace is proximately influenced by shortening days. Rowan suggested some causal relations between gonadal cycles and migration, but the available evidence now indicates that sex hormones do not directly regulate migration. In one set of pioneering experiments, for example, castration did not prevent male Golden-crowned Sparrows from becoming restless and putting on their premigratory fat deposits at the appropriate time of the year (Morton and Mewaldt 1962).

The timing of migration relates first to internal physiological rhythms, but extrinsic weather factors also play a role, primarily one of fine tuning. Northward movements of migrants in the spring correlate with the warming of the higher latitudes. Both the American Robin and the Canada Goose move north in the eastern United States, just behind the main spring thaw, along a front of regions that have a mean daily temperature of 2°C. A line connecting these points is called the 2°C isotherm. Willow Warblers in Europe move north with the 9°C isotherm.

Daily weather conditions and favorable winds, in particular, also influence departure times. In spring, major northward movements in the United States coincide with a depression (lowering of barometric pressure) toward the southwest, followed by a strong flow of warm southern winds from the Gulf of Mexico toward the northeast. The sizes of migration waves relate directly to the intensity of the depression and the strength of the favorable winds. The value of favorable winds is clearly seen in records of arrivals of northbound migrants at Baton Rouge, Louisiana (Gauthreaux 1971). Migrants from Central America usually reach Louisiana in mid-afternoon after crossing the Gulf of Mexico, but when they have strong southern tailwinds, they arrive several hours earlier, in the late morning. On rainy days with adverse winds, they arrive later in the evening, and they do not arrive at all on days when there are cold fronts or east winds.

Fall migration departures also are stimulated by favorable weather conditions. Good flights of large numbers of raptors at Hawk Mountain, Pennsylvania, and of land birds at the tips of peninsulas such as Cape May, New Jersey, are the result of strong northwest winds due to a barometric depression moving east from the Great Lakes region. Departures from the New England coast are related to favorable tailwinds, and peak flights south across the Gulf of Mexico in early October coincide with improved flight conditions to the north.

Exactly how migrants forecast weather conditions is a mystery, but birds are sensitive to changes in barometric pressure and feed more intensely as storms approach and barometers fall. Wind directions aloft, however, are not easily judged from the ground. Meteorologists track weather fronts by monitoring infrasound with a special system of microphones. Pigeons, too, seem to be sensitive to infrasound and may use this source of information in some way.

9.6 Scheduling High-Cost Efforts

The correspondence between breeding season and food availability is central in defining the annual energy budgets of birds. Birds can assume the costs of reproduction, molt, or migration only after they have first met the costs of self-maintenance, their highest priority. Basic social interactions to obtain food or a roost site are their second-highest priority. Some seasons, such as a north temperate winter, permit only self-maintenance for most species, whereas others accommodate additional activities. Reproduction and molt must be scheduled during the months when a bird's requirements for self-maintenance are lowest or when extra food is available. Usually, the costs of only one extra activity can be accommodated. The energetic costs of reproduction and molt favor the segregation of these stages in the annual cycle.

Reproduction

Peak reproductive activities increase total daily energy expenditures by as much as 50 percent. Daytime activity costs may actually double or even triple, but overnight costs remain relatively constant. At the beginning of the breeding season, courtship, territoriality, and nest building demand significant effort. Only minor amounts of productive energy are channeled into the growth of the gonadal tissues themselves, but subsequent egg formation and egg laying by females impose new demands on energy and nutrition (Chapter 12). The large clutches of the big, richly provisioned eggs of waterfowl are especially expensive to produce. They may temporarily double a female's total daily energy requirement. Large waterfowl, such as the Snow Goose and the Canada Goose, therefore, can rely on their substantial body stores of nutrients and energy to produce their large eggs; smaller ducks must feed to supplement their endogenous reserves. Incubation also can create an energy shortage because it limits the amount of time during which a bird can forage for its own maintenance. The parents then face another surge of demands on their time and energy when the hatched chicks require food and brooding.

Molt

Molt is a costly effort that typically follows breeding in the warmest months of the year and precedes migration. But a bird strategically adjusts the timing and sometimes the pace of its molt.

The complete molt is a major undertaking. The bird sheds and then regenerates thousands of feathers, roughly from 25 to 40 percent of its lean dry mass (i.e., excluding fat and water content). Molt draws significantly on protein and energy reserves to synthesize feather structure and to offset the costs of poorer insulation and flight efficiency. Thomas Bancroft and Glen Woolfenden (1982) estimated that adult Blue Jays and Florida Scrub-Jays must increase daily metabolism from 15 to 16 percent during peak periods of feather production. Reduced insulation while molting requires increased heat production, doubling the cost of molt in Brown-headed Cowbirds at low temperatures (Lustick 1970). Molting during the warm summer months can thus be advantageous.

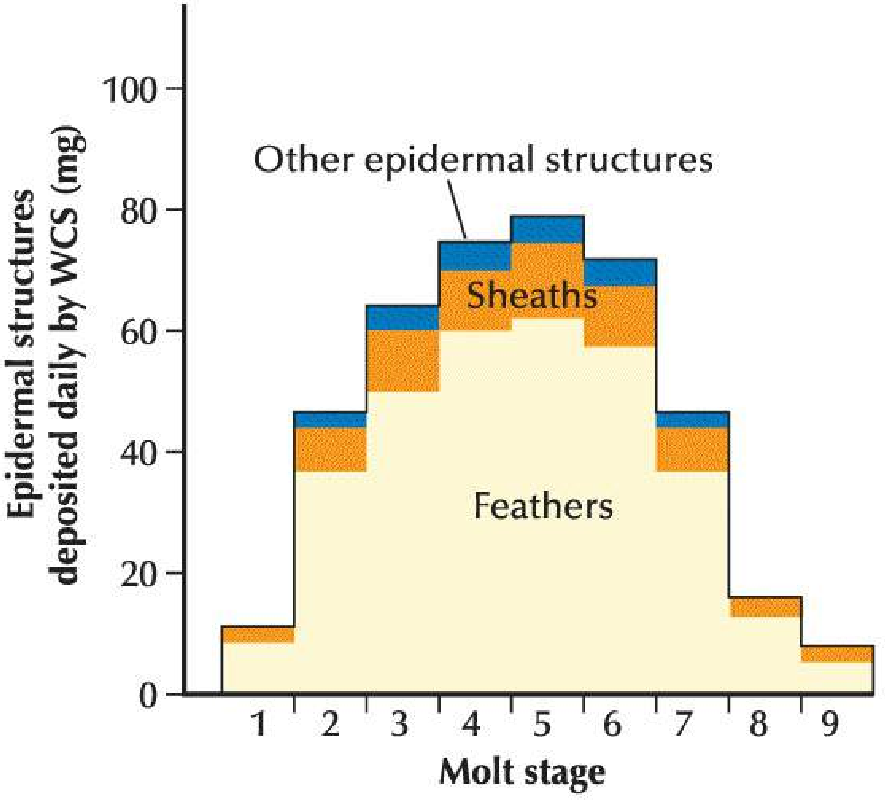
Molt is also a period of intense physiological change (Box 9–1). Accompanying the replacement of worn feathers is the synthesis of beta-keratin by the skin, increased amino acid metabolism, and increased cardiovascular activity to supply blood to the growing feathers. The long list of changes also includes the shunting of water to the developing feathers, changes in bone metabolism and calcium distribution, and an increased need for iron for red blood cell production. Together, these and other metabolic changes impose substantial hidden costs beyond the conversion of amino acids into feather proteins. Only about 7 percent of the energy used by molting birds is incorporated into the feathers themselves.

BOX 9–1

Molt by White-Crowned Sparrows Requires Energy and Special Nutrition

Mary Murphy and Jim King (1992) deciphered the costs—in both energy and nutrition—of the rapid fall (prebasic) molt in the *gambelii* subspecies of the White-crowned Sparrow. The complete molt of this sparrow lasts about 54 days, with peak feather production and energy costs from day 18 to day 36 (see graph). The actual energy costs of molt total 605 to 876 kilojoules, with daily investments that are proportional to the molt intensity. The daily energy costs of peak molt (58 percent of basal metabolic rate) are higher than those associated with reproduction.

Obtaining adequate nutrition for the molt is probably not a major problem for sparrows in the wild. Muscle tissues can be broken down as needed to provide most of the amino acids required. Beta-keratin synthesis, however, requires disproportionately high proportions of sulfur-containing amino acids, especially cysteine. To have cysteine available in amounts sufficient to continue feather growth overnight when the sparrows fast, they store extra reserves in the liver during the day, feeding selectively on foods containing such amino acids, if needed; the stored cysteine is liberated for use at night.



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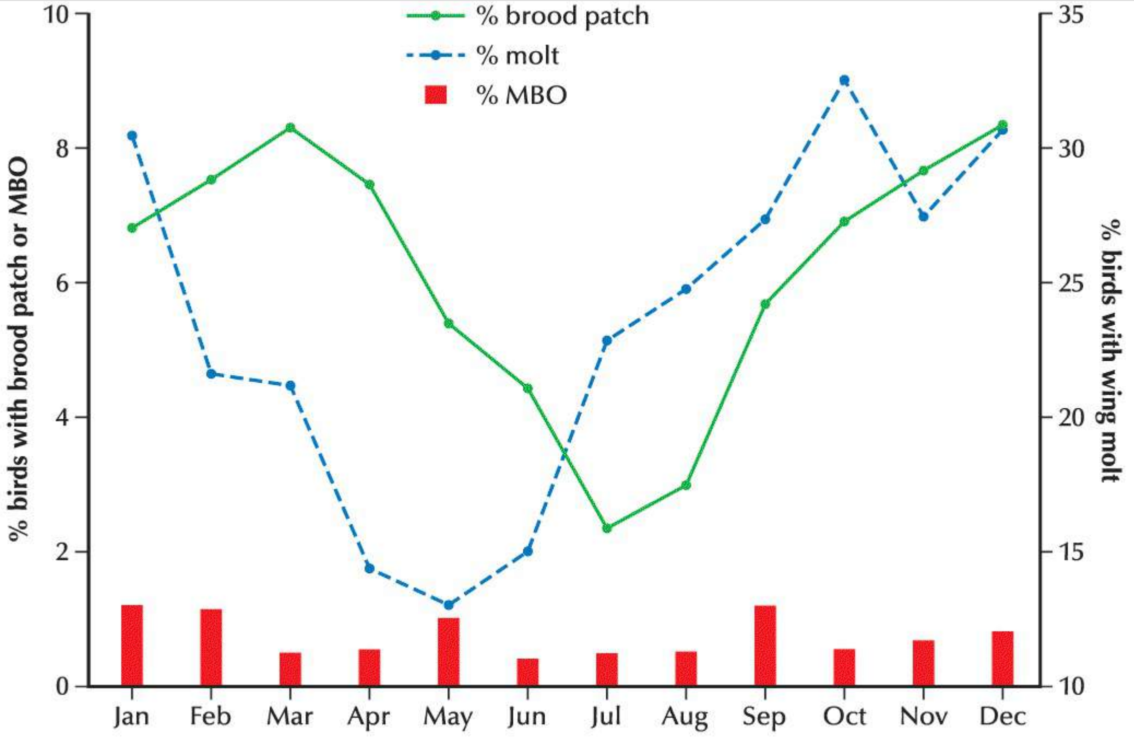
DATA FROM MURPHY AND KING 1992

Plumage, sheaths, and other epidermal structures deposited daily in the 54-day prebasic molt period of the White-crowned Sparrow (WCS). Each of the nine molt stages lasts six days.

Few species breed and molt at the same time. They mostly are species that live in productive, tropical environments with minimal seasonal variation. There, prolonged molts apparently minimize daily costs in the absence of strong seasonal constraints. Roughly 13 percent of breeding bird species near Manaus, Brazil, in the Amazon Basin also showed signs of molt (Figure 9–16). Molt–breeding overlap was extremely variable among different families of birds; most showed only slight overlap at the beginning and end of the molt cycle, but many antbird species, which have very long breeding seasons, showed extensive overlap. Exceptions to the rule are instructive. Some female hornbills molt while sealed in their nest cavities to incubate eggs and brood young. Their energy requirements for self-maintenance are minimal; as a result, the added costs of molt can be accommodated. Additionally, the flight feathers are not essential during this sedentary period. The high temperatures that build up inside the nest cavity may favor loss of feathers and reduced insulation. In contrast, male hornbills, which feed the incubating females, wait to molt until their families leave the nest.



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DATA FROM JOHNSON ET AL. 2012

Figure 9–16 Molt-breeding overlap (MBO) in 87 species of Amazonian birds.

Tropical birds molt more predictably than they breed because reproduction may be tied to irregular periods of rain, or may require several renesting attempts due to high rates of nest loss to predators. To give breeding priority, some birds interrupt their molts. Desert birds, such as Darwin's finches of the Galápagos and the Zebra Finch of Australia, stop the regular seasonal molt to nest whenever the unpredictable rains begin. They resume the interrupted molt after nesting is completed.

Tropical terns, such as the White Terns on Christmas Island, turn the molt on and off to breed whenever possible (Figure 9–17). This delicate seabird has no pigment in its flight feathers, which consequently wear easily and must be replaced more often than those of most other terns. Wave after wave of molt is initiated in the flight feathers. The innermost primaries often begin to molt again before the outermost primaries are replaced in the preceding molt. As many as three successive molts may be in progress simultaneously. When a White Tern starts to nest (it simply lays an egg precariously on a bare branch), the molt stops suddenly no matter which feathers may be missing—the molting equivalent of musical chairs. After the tern has finished nesting, molt resumes as if there had been no interruption in the complicated pattern of feather replacement.

ALL CANADA PHOTOS/ALAMY

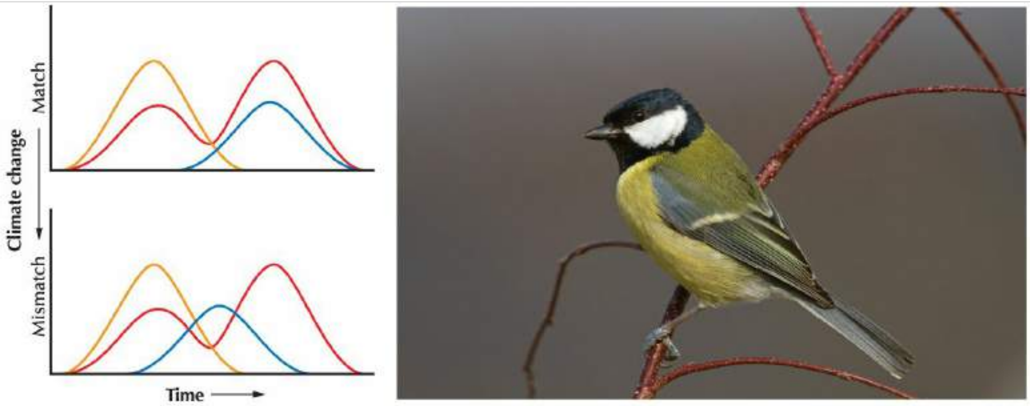
Figure 9–17 The White Tern molts almost continuously to replace its worn, unpigmented feathers, but it interrupts the molt upon laying an egg.

Birds adjust the pace of molt in relation to the time available. Gulls and sandpipers that breed in the high Arctic, where the reproductive season is short, start molting before they finish breeding to be ready for migration. The Dunlin, for example, begins to molt its primaries just before incubation and then finishes from four to five weeks later. The northernmost populations of the White-crowned Sparrow complete their molt speedily in 47 days, just over half of the time (83 days) that it takes their slow-molting southern (*nuttalli*) relatives. Renesting White-crowned Sparrows molt so fast at high latitudes that they become almost flightless for a short time. Peregrine Falcons and American Golden Plovers, as well as many other shorebirds, begin their molts on their Arctic breeding ground, but are unable to complete the process in time to leave for the south. They stop the molt of their flight feathers just before migration and then resume it for several more months after reaching their wintering grounds.

9.7 Climate Change

Major changes in global climates, whether yearly or long term, affect the annual cycles of birds. Year-to-year changes cause bird populations to fluctuate, often dramatically (Chapter 18). Periodic climate cycles cause populations to have good years followed by bad ones. The El Niño Southern Oscillation in 1982 and 1983, for example, severely disrupted nesting by Christmas Island seabirds (Schreiber and Schreiber 1984). El Niño was known historically as the periodic warm-water disruption of cold upwelling off the coasts of Ecuador and Peru; it destroys the anchovy fishing industry and causes severe crashes in the local seabird populations. Now we understand that it is not just a local phenomenon. The entire equatorial Pacific Ocean changes in concert with atmospheric changes that influence global climates. The sudden changes in ocean currents and temperatures and associated flooding rains from August 1982 to July 1983 caused wholesale reproductive failure, severe adult mortality, and the disappearance of the entire seabird community on Christmas Island. With the return of normal oceanic and atmospheric conditions, representatives of all seabird species returned to nest again. This event revealed to ornithologists for the first time the sensitivity of tropical bird populations to unpredictable, anomalous global climate changes.

Timing of annual cycles is one of the major potential problems created by global warming. If birds are unable to advance their breeding season to match changes in their major food resources, then a “mismatch” between them and their resources may occur (Figure 9–18). Birds generally time their breeding or migration to match resource availability. If global warming causes resources to become available earlier, there will be strong selective pressure on birds to nest earlier as well. At least two species of North American birds nest earlier in response to global warming. Arizona populations of the Mexican Jay now lay their first clutch 10 days earlier than they did in 1971 (Brown et al. 1999). This significant trend corresponds to a local increase in monthly minimum temperatures, not a maximum monthly temperature. More broadly, climate change has affected the breeding date of Tree Swallows throughout North America (Dunn and Winkler 1999).



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DATA FROM DURANT ET AL. 2007, VISSER ET AL. 1998. PHOTO: MARK L. STANLEY/GETTY IMAGES

FIGURE 9–18 Example of a match/mismatch induced in the Great Tit by climate change. Whereas the abiotic environmental cues (orange line) that trigger onset of egg laying (red line) stay the same, food sources (blue line) emerge earlier and out of synchrony with the peak energy demands of the chicks.

Resident species and early-arriving migrants, such as the Tree Swallow, can respond to the same cues (e.g., local temperatures) that fine-tune the onset of nesting. Long-distance migrants, on the other hand, generally arrive later and therefore have less of an opportunity to match the timing of their breeding season with that of their resources.

Late-breeding waterfowl, for example, have declined as global warming promotes earlier food availability due to decreased spring snow. Conversely, ducks that arrive earlier have adjusted their breeding season to nest earlier and are increasing their numbers (Drever et al. 2012). Global warming therefore has the potential to cause shifts in the composition of entire communities.

Global climate change has the potential to change evolutionary trajectories of some species. Migratory European Blackcaps warblers, for example, have established new wintering populations in northern latitudes in western Europe. These more northerly populations arrive earlier and mate before the birds from their historical African wintering grounds have arrived. As a result, they are now mating assortatively, a possible first step in the speciation process.

Human alterations of the environment have also led to other changes in the timing of the breeding season. Birds in urban settings, for example, often breed earlier than those in more rural settings, an effect that has been attributed to the warmer temperatures in cities, the availability of additional food sources (e.g., bird feeders), and the presence of light at night that may stimulate earlier breeding. Not all of these changes, however, are proving to be adaptive. The Florida Scrub-Jays in suburban settings, for example, nest earlier but suffer higher egg failure and nestling mortality, possibly as a result of the lower quality of food available (Aldredge et al. 2012).

REVIEW KEY CONCEPTS

9.1 Basic Annual Cycles

Birds experience seasonal cycles of stress and opportunity accompanied by major changes in physiology, body composition, and behavior. Cellular clocks guide the physiological cycles that prepare a bird for each season. Migration adds additional challenges to the annual cycle. The annual cycles of White-crowned Sparrows have been well documented as a series of specific physiological stages activated by environmental cues. The diverse populations of this species differ in the extent of their annual migrations and the photoperiodic controls of their annual cycles.

Key Terms: circadian rhythms, photoperiod, prealternate molt

9.2 Physiological Clocks

The avian circadian rhythm comprise three important self-oscillating components: (1) the pineal gland, (2) the suprachiasmatic nuclei of the hypothalamus, and (3) the eyes. Individual birds have an intrinsic rhythm of about 23 hours in length in which body temperature, rate of metabolism, and levels of alertness fluctuate. Seasonal changes in day length, called photoperiods, adjust the daily rhythm and control gonadal activity for reproduction. They do this by directly stimulating receptors in the midbrain and, in turn, the secretion of gonadal hormones by the pituitary gland.

Key Terms: endogenous rhythms, circannual cycles, pineal gland, suprachiasmatic nuclei, Zeitgebers, photorefractory period

9.3 Master Hormones

A set of master hormones, including those of the pituitary gland, controls seasonal behaviors related to reproduction, molt and migration, and levels of stress. Birds must regulate their responses to acute stress because corticosteroid hormones from the adrenal gland suppress the release of gonadal hormones and reduce immunocompetence.

Key Terms: luteinizing hormone (LH), follicle-stimulating hormone (FSH), luteinizing hormone–releasing hormone (LHRH), thyroxine, corticosterone

9.4 Breeding Seasons

The simplest annual cycles proceed from breeding to molting to surviving seasons of reduced food availability to breeding again. Seasonal migrations and extra molts complicate the annual cycles of many birds. Departures from annual breeding cycles occur in seabirds with year-round food availability and large species, such as the Wandering Albatross, that cannot fit their extended reproductive effort into a single year. A few, mostly tropical birds have six-month cycles, breeding twice a year. Others, with nine- or 10-month cycles, breed in different months each year. Ultimate factors, such as food supplies, nest sites, climate, and predator risk, determine the evolution of breeding seasons in birds. Proximate factors, such as temperature, rainfall, and green vegetation, adjust the actual onset of reproduction to local conditions. Warm spring and summer months constitute the main breeding season in temperate zones. Rainfall usually defines tropical breeding seasons.

9.5 Timing of Migration

Internal physiological rhythms drive the timing of migration, but extrinsic weather factors also play a role, primarily one of fine tuning. Migratory birds become restless and prepare for departures by eating to excess, adding fat, and increasing weight sometimes twofold.

Key Term: migratory restlessness (Zugunruhe)

9.6 Scheduling High-Cost Efforts

Birds generally do not breed and molt at the same time but undertake these efforts, which require substantial energy, in different months. In some exceptional cases, molt and breeding do take place simultaneously; for example, female hornbills, confined to the nest and fed by the males, can afford to molt. Some sandpipers molt while nesting to accommodate the short Arctic summer. Opportunistic breeders, such as the White Tern of tropical oceans, interrupt molt while they nest.

Key Terms: molt

9.7 Climate Change

Human-caused changes in global climates and resource availability affect the annual cycles of birds. Short-term responses to global warming are now well documented, including earlier nesting and changes in arrival dates. Some of these are changing the evolutionary trajectory of different populations. Urban settings favor some species that can take advantage of supplemental food and warmer conditions to start breeding earlier. These changes may affect the long-term future of many species and alter the composition of communities.

APPLY YOUR KNOWLEDGE

1. Compare the fundamental annual cycles of nonmigratory birds living in tropical and temperate biomes.
2. Using the White-crowned Sparrow (*Zonotrichia leucophrys*) populations of the western United States, compare and contrast the migratory and breeding patterns of the long-range migrants, short-range migrants, and nonmigratory subpopulations.
3. Describe the endogenous rhythms referred to as biological clocks and the locations and functions of the three primary oscillators that control them.
4. Define the term *Zeitgeber*. How are Zeitgebers important to the maintenance of 24-hour circadian rhythms?
5. Describe the changing day lengths through the year and how photoperiod and the photorefractory period control the annual cycle of growth and regression of gonadal tissues and the timing of migration.
6. Describe the roles luteinizing hormone (LH), follicle-stimulating hormone (FSH), luteinizing hormone–releasing factor (LHRH), thyroxine, and corticosterone in controlling reproductive behavior and molting.
7. Compare and contrast the direct and hidden costs of reproduction and molting, explaining why reproduction and molting generally do not occur simultaneously. Include exceptional examples of birds that do molt during the breeding season.

8. Using El Niño as an example of periodic climate change, describe the local events in the equatorial eastern Pacific near Ecuador and Peru and the global result on seabird populations 18,500 kilometers away on Christmas Island.
9. Explain the impacts of global warming on the mismatch of migration to breeding grounds and availability of food and the impacts of the changing wintering grounds of subpopulations of birds that could lead to speciation and how the resultant community structures will change.
10. How have human urban settings disrupted the natural behaviors of birds?

CHAPTER 10 *Migration and Navigation*

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Bar-tailed Godwits are champions of long-distance migration. Each fall, they migrate nonstop from Alaska to New Zealand by draining energy reserves and muscle tissues.

> Bird migration is the world's only true unifying natural phenomenon, stitching the

> continents together in a way that even the great weather systems fail to do.
> [Weidensaul 1999]

Ancient records of the seasonal appearances and disappearances of birds perplexed early naturalists, who were not certain whether birds migrated or hibernated. Aristotle understood that cranes moved seasonally from the steppes of Asia Minor (then Scythia) to the marshes of the Nile, but he believed that swallows, larks, and turtle doves hibernated. Later anecdotes about swallows that were found frozen in marshes and that flew off after being thawed fueled this misconception.

We now know that, every fall, billions of land birds of about 200 species each leave Europe and Asia for Africa and leave North America for Central and South America. The migrations of Arctic shorebirds regularly exceed 13,000 kilometers one way from the high Arctic to distant South America or the South Pacific. Red Knots, for example, fly from Baffin Island above the Arctic Circle to Tierra del Fuego with selective stopovers. Millions of raptors, as well as waterbirds such as American White Pelicans, fly past a single migration hot spot in Veracruz, Mexico, on peak days. Some of them have been fitted with digital recorders, providing valuable data that are transforming our understanding of the powers and consequences of migration.

Migratory birds connect ecosystems locally and globally, including ecological services and the spread of diseases. Migrant birds cycle annually between precise locations thousands of miles apart in opposite hemispheres; others relocate up and down mountain slopes, or back and forth across Amazonia. Broadly speaking, migratory behavior integrates avian physiology with the extrinsic environment to achieve some of birds’ most demanding physical feats. Direct extensions of the physiological and ecological controls integrate the timing of migration with other aspects of the annual cycles of birds.

This chapter first presents the main patterns of bird migration and a selection of the extraordinary feats that some birds achieve. The use of new technologies reveals new patterns of population dynamics and connectivity; seasonal passages connect some populations and separate others. We then review the costs and benefits of migration, which are subject to natural selection. Long-distance migration requires both physiological endurance and ample fuel supplies or regular refueling stopovers. Optimality models help us to explore alternative migration strategies. Direct extensions of the physiological and ecological controls integrate the timing of migration with other aspects of the annual cycles of birds. The final section of this chapter looks more closely at the cues and compasses that birds use to orient themselves toward their destinations thousands of miles away. Magnetic fields, time-compensated solar compasses, the night stars, and polarized light in the evening provide complementary and backup navigational tools. Young birds calibrate their skills starting with their first flights from the nest and observing the rotation of the night sky. So begins the acquisition of skills needed for their first migratory flights.

10.1 Migration

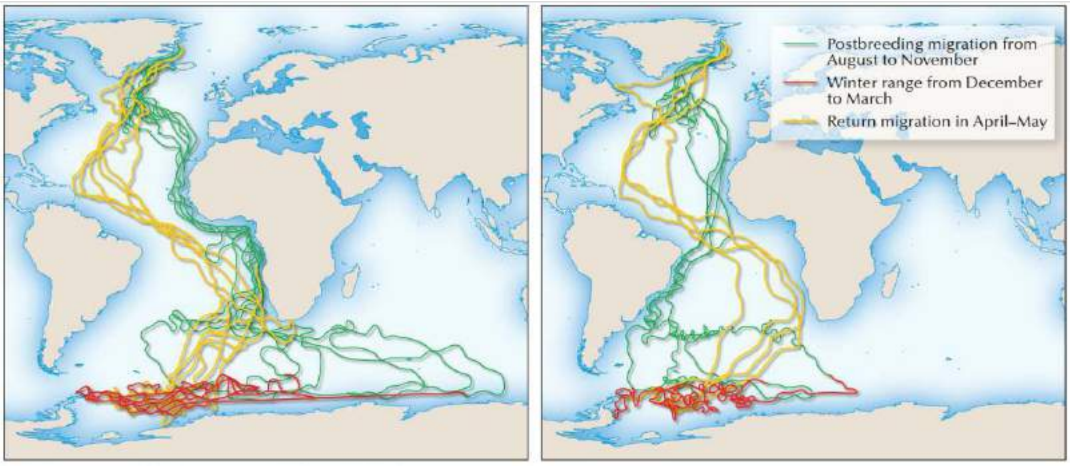
Patterns

Migration is a major part of the annual cycle of many birds. Photoperiod, gonad cycles, and hormones guide the preparations for migration and migratory behavior itself. Proximate factors, such as weather and food availability, trigger day-to-day departures and stops to refuel.

Migration takes advantage of predictable, seasonal opportunities. It is different from nomadic wandering or irruptions tied to unpredictable, aseasonal opportunities. Scattered pine-seed crops or insect infestations attract opportunistic feeding by nomadic species such as Red Crossbills, which breed wherever food is abundant. In the tropics, fruit-eating and nectar-feeding birds wander locally in search of their unpredictable sources of food, but this type of behavior is distinct from the predictable cyclic behavior of seasonal migration. Seasonal cycles of climate or insect abundance generate corresponding cycles of breeding, flocking, and migratory relocation.

To take advantage of predictably favorable conditions, birds undertake both local and long-distance movements. On a local scale, tropical hummingbirds migrate up and down mountain slopes. On a global scale, Arctic Terns famously leave their nesting colonies in the far northern Atlantic and Arctic Ocean for the waters of Antarctica (Figure 10–1). One tern, a female, recently completed a world-record 96,000-kilometer round-trip between Northumberland, United

Kingdom, and its winter home in the Weddell Sea, Antarctica (Bevan and Redfern 2016). More commonly, birds migrate to closer wintering grounds. Many species of wood warblers that breed in the northern United States and southern Canada spend the winter in Central America and in the West Indies.



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From Carsten Egevang, Iain J. Stenhouse, et al., “Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration,” PNAS, 2010, February 2; 107(5) 2078 – 2081 ; Figure 1. https://doi.org/10.1073/ pnas.0909493107

Figure 10–1 Geolocation tracks of 11 Arctic Terns that migrated from breeding colonies in Greenland and Iceland to wintering grounds in Antarctica.

Migration routes and patterns are almost as varied as the migrants themselves. The routes trace the histories of populations, their abilities to cross large barriers, the positions of topographical barriers, and the relative locations of summering and wintering grounds. Extensive marking and recovery programs in the past 50 years mapped the general migration routes for hundreds of species (Figure 10–2). But new technologies, including satellite tracking, digital data loggers, weather radar, and feather chemistry, allow real-time tracking of individual migrant birds on a global scale and offer insight into the global structure of populations (Webster et al. 2002; Figure 10–3).

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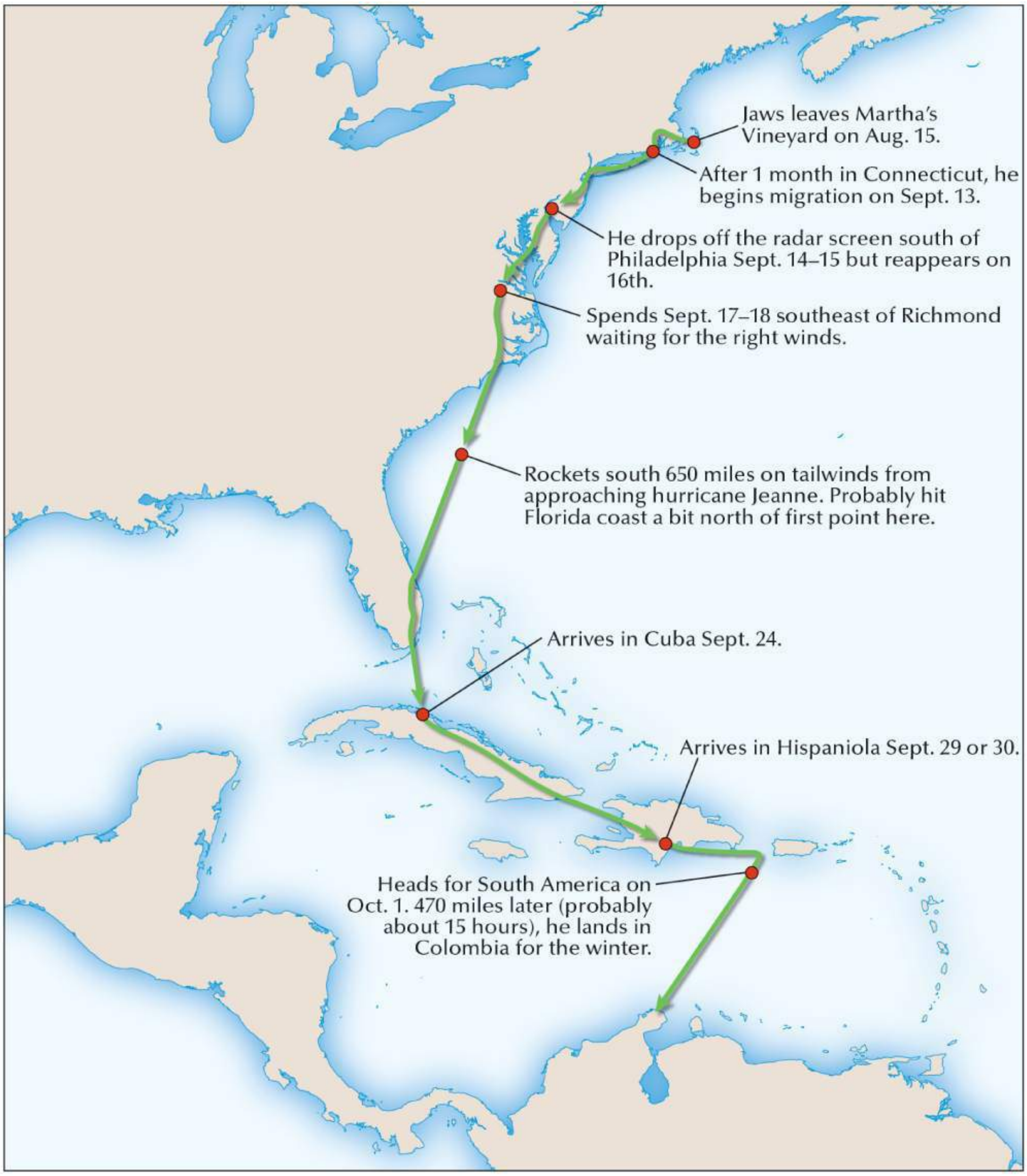
DATA FROM CORVEN 1998

Figure 10–2 Major migration routes of shorebirds and their stopover sites in the Western Hemisphere Shorebird Reserve Network.



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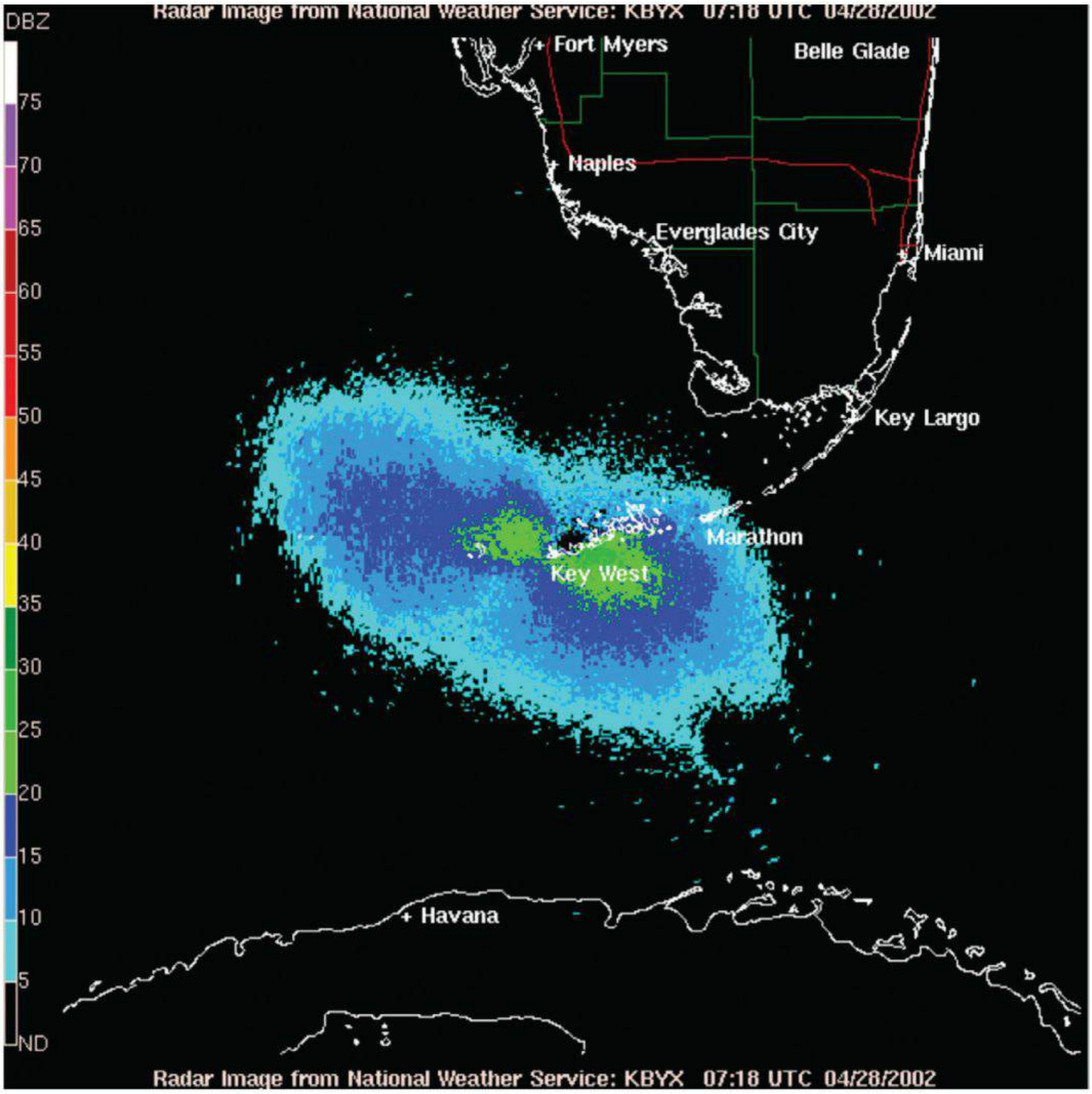
Data from R. O. Bierregaard

Figure 10–3 Satellite tracking map of the first fall migration of a young Osprey named Jaws, which was fledged on Martha's Vineyard in the summer of 2004. He moved south in September, reaching Florida on September 21–24 as shown. From there, he flew to the north coast of Cuba, moved overland to its eastern end by September 28, crossed to eastern Hispaniola, and then, from the waters off western Puerto Rico, flew straight down to Colombia, where he wintered successfully.

Radar Ornithology

On peak occasions in spring and fall, millions of migrant birds course through the night sky; the general public is largely unaware of this phenomenon. In the 1960s, George Lowery and Robert Newman at Louisiana State University pioneered the quantitative study of nocturnal migration by counting the birds silhouetted briefly as they crossed in front of the full moon. Now we use radar.

We all follow the weather reflected through Doppler radar images. The weather images, however, can be filtered out, leaving just images of birds in flight (which radar operators initially called “angels”). Military radars can track and identify single birds (e.g., by using flap rates) and assess their flight speeds, altitudes, and compass orientation. Weather surveillance radar stations also provide continuous monitoring of migration activity. Some of these images are massive clouds that span hundreds of square miles and include millions of birds (Figure 10–4; Box 10–1). Doppler radar studies through the years have documented when birds travel en masse in relation to continental weather patterns. They have also documented the decline of migrants (Gauthreaux 1992).



NOAA

Figure 10–4 Doppler radar image of cloud of migrating birds over Key West, Florida, after crossing the Gulf of Mexico.

BOX 10–1

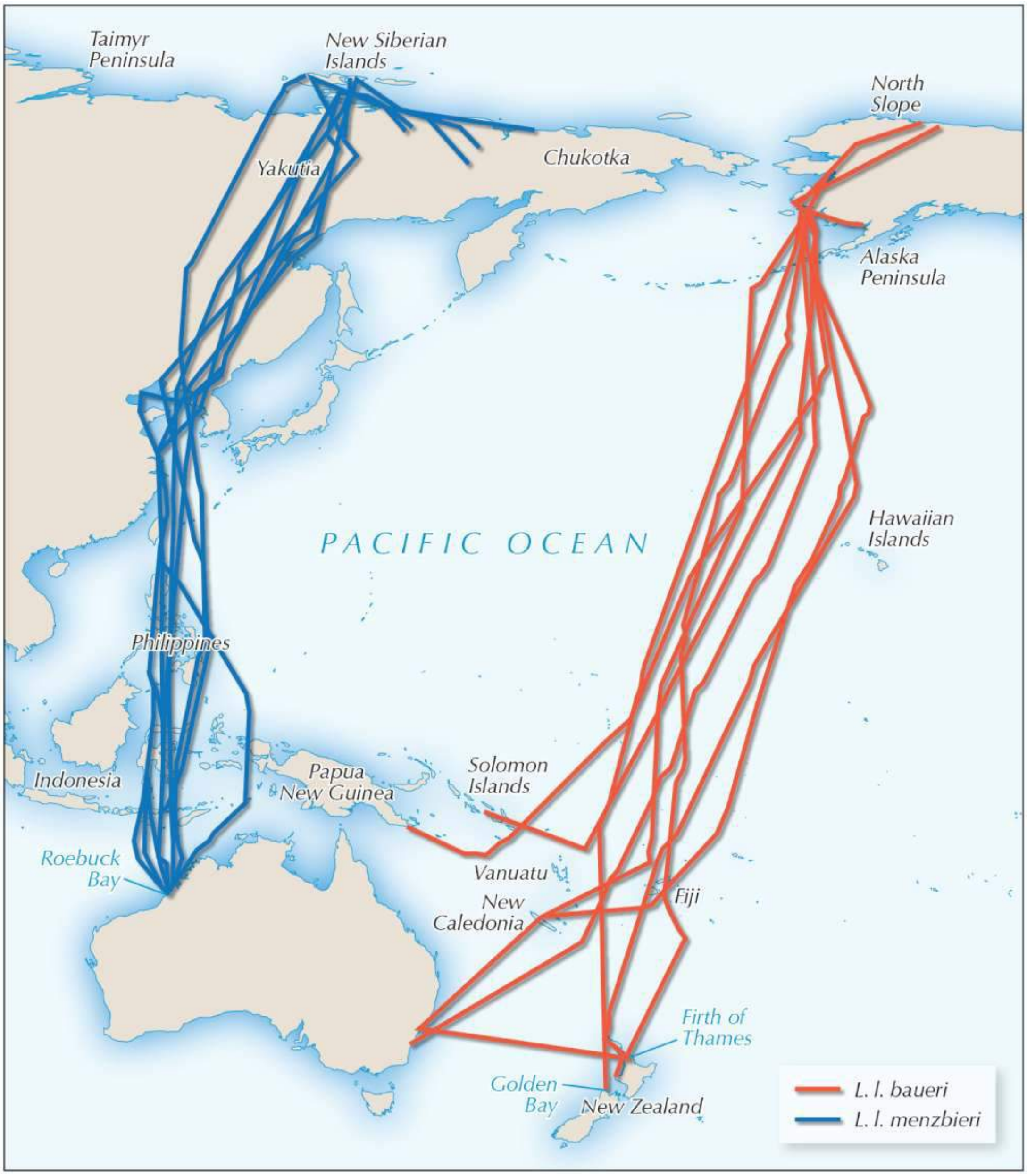
Bird Migration Forecasts

Experts on the interpretation of Doppler radar images can identify warblers, ducks, or shorebirds by their distinctive airspeeds and patterns of movement. Radar images, however, do not allow us to identify exactly what species of birds are flying through the night skies. But there is another way to do so: nocturnal migrants call regularly, enabling expert ears to identify them by their notes (Farnsworth 2005).

Project BirdCast (http://birdcast.info) integrates diagnostic call notes with radar images in a new era of predictive analysis of daily migration dynamics. Bird-sound experts team up with radar experts and citizen scientists to forecast nocturnal bird migrations in real time. They supplement radar images with the calls of migrants recorded by microphones placed on rooftops. The calls are stored on computers in the volunteers' home study and uploaded the next day for analysis. Volunteer birders then census the new arrivals in their backyards each morning and submit their ground-truth data to eBird, a real-time, online database of bird observations. The frequencies of different call notes and appearances of new backyard arrivals align with the radar-measured volumes of birds passing overhead.

Routes

The classical description of migration emphasized major migration routes called **flyways,** routes that follow the topographies of coasts, mountain ranges, major river valleys, and great deserts: north/south in the Americas, east/west in Eurasia. This traditional description of migration flyways, however, oversimplifies the routes and obscures the feats of traveling birds. Data recorders and satellite transmitters reveal the precise tracks of individual migrants and their extraordinary feats. Members of one subspecies (*baueri*) of the Bar-tailed Godwit fly 11,000 kilometers nonstop across the Pacific from Alaska to New Zealand and eastern Australia (Gill et al. 2005; Figure 10–5). These migrants and others cross thousands of kilometers of open ocean or inhospitable terrain without stopping, thereby stretching their fuel reserves and physical abilities to the limit.



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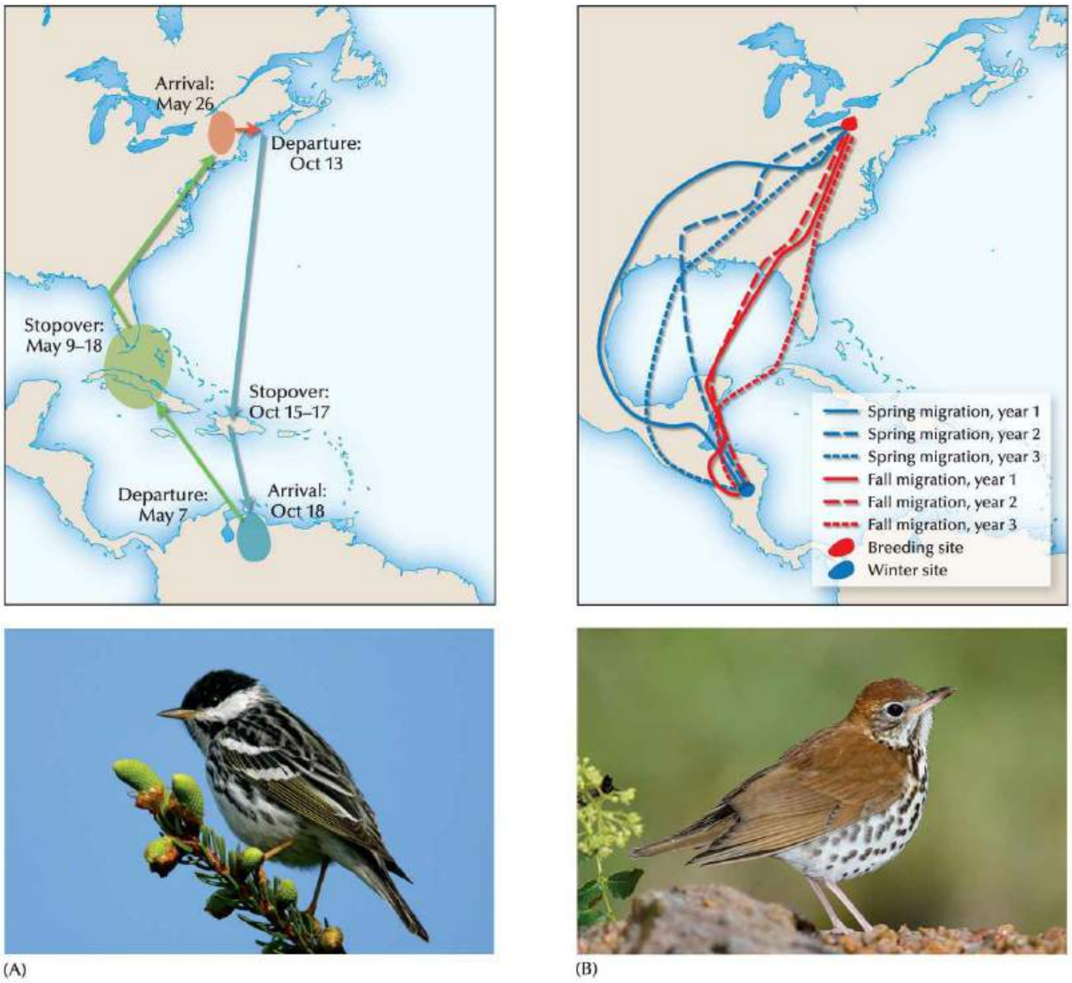
Data from Battley et al. 2012

Figure 10–5 Tracks of satellite-tagged Bar-tailed Godwit subspecies (*L. l. baueri* and *L. l. menzbieri* on southward migration.

Every fall, for example, vast numbers of migrants leave coastal New England and Canada, heading southeast over the Atlantic Ocean. The capacity for such flights by larger, faster shorebirds, such as the American Golden Plover, has been known for many years. Radar studies now reveal similar efforts by small songbirds (Figure 10–6). One of these athletes, the 12-gram Blackpoll Warbler, undertakes marathon flights from New England to stopovers in the Antilles and then the coast of South America (DeLuca et al. 2015). These three-day nonstop transoceanic flights cross 3,000 miles of open ocean. Tim and Janet Williams (1978) put this feat in perspective:

> For a man, the metabolic equivalent would be to run 4-minute miles for 80 hours. . . . If a Blackpoll Warbler burned gasoline for fuel instead of its reserves of body fat, it could boast of getting 720,000 miles to the gallon!



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(A) Data from DeLuca et al. 2015. Photo: Nature Photographers Ltd./Alamy. (B) Data from Stanley et al. 2012.
Photo: Nature Photographers Ltd./Alamy

Figure 10–6 (A) Millions of fall migrants, such as Blackpoll Warblers, fly directly from northeastern North America to the Greater Antilles and northern South America, often with a several day refueling stop. They return to their northern breeding grounds more leisurely up the Atlantic Coast. (B) Wood Thrushes tracked from Pennsylvania to winter territories in Costa Rica vary their return routes the next spring.

Evidence of the strenuous nature of that trip can be seen in the exhausted condition of birds that stop at Curaçao, short of their destination, when flight conditions have been poor. Little more than feathered skeletons, they have depleted their fat reserves, metabolized much of their protein, and drained the remnants of their precious body water (Voous 1957).

Newly appreciated also are the mirror migrations of tropical and Southern Hemisphere species (Jahn et al. 2004; Figure 10–7). South American flycatchers and swallows, among others, migrate seasonally from temperate-zone South America to the tropics of Brazil. Fork-tailed Flycatchers are one of the champions, regularly overshooting their northern breeding grounds to the joy of rarity-seeking birders in North America (Figure 10–8). The annual cycles of birds in Africa and Australia also feature austral (southern) migration systems.

Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
Data from Faaborg et al. 2010

Figure 10–7 General patterns of migratory movements of birds in Central and South America. Solid arrows indicate intratropical latitudinal migration and dashed arrows South American austral migration.

JUAN JOSE ARANGO/VWPICS/ALAMY

Figure 10–8 Fork-tailed Flycatcher, a champion austral migrant.

Eurasian migrants also face Herculean challenges (Lövei 1989; Bairlein 1988). Each fall, many of them fly 1,100 kilometers directly across the Mediterranean and then, almost immediately thereafter, 1,600 formidable kilometers nonstop across the Sahara. They are vulnerable to diurnal predators, such as Eleonora's Falcon, which breeds in the fall so that it can feed its nestlings on migrants trying to cross the Mediterranean.

Migration routes sometimes trace the recent distributional histories of birds; individual birds that colonize new areas tend to retrace the population's historical expansion routes. Pectoral Sandpipers colonized Siberia from Alaska. Instead of migrating south through the Orient, as do most Siberian shorebirds, these "Siberian" Pectoral Sandpipers fly back to Alaska and then south with the rest of their species to South America. Other Arctic shorebirds stage in eastern Canada and then migrate across the western Atlantic, some nonstop, to South American wintering grounds, returning north the next spring through Latin America and the Great Plains.

Such circular or loop routes also are features of seabird migrations. Shy Albatrosses, for example, circumnavigate the Antarctic continent in as little as 46 days (Croxall et al. 2005). To call attention to the plight of the world's albatrosses, BirdLife International joined the world's largest bookmaker, Ladbrokes, to track the 10,000-kilometer race of 18 young albatrosses from Australia to South Africa. They were released on April 27, 2004, wearing satellite transmitters. Celebrities throughout the world sponsored the birds and placed bets on which individual bird would reach South Africa first. The winner, Aphrodite, was first detected in South Africa waters on July 13.

Conditions for flying are a key variable for successful migratory flights. Migrants fly at times of the day and at heights where travel is least costly, safest, and most rapid. Some birds migrate by day and others by night and still others, such as waterfowl and shorebirds, at both times. Diurnal and nocturnal flights offer different advantages. Hawks migrate during daylight hours when they can take advantage of warm rising air currents. Swifts and swallows, which feed on the wing, also migrate by day. Many small land birds, including most flycatchers, thrushes, and wood warblers, as well as rails and woodcocks, depart shortly after sunset and migrate by night. Predation by hawks and gulls is less likely at night, and these migrants can then refuel by day. Cooler and more humid night air also favors heat loss and water retention. Most important, more stable night atmospheres with weaker horizontal winds and less turbulent vertical motion create favorable flight conditions. Most migrants fly at fairly low altitudes, usually below 700 to 800 meters, although they climb to more than 3,000 meters. Waterfowl have set some of the record altitudes—for example, almost 9,000 meters high for the Bar-headed Goose seen flying over Mount Everest. At the top of the list, however, is the record of a Rüppell’s Vulture that was sucked into a jet engine at 12,000 meters over Ivory Coast, Africa. The physiological mechanisms that prevent fatal hyperventilation at such altitudes remain unknown.

Some (perhaps most) birds throttle back and coast with tailwinds, thereby saving energy and potentially increasing their flight range. The land birds that fly to South America pick up the trade winds as they enter the tropical Caribbean region. They backtrack to land on their first night at sea if wind conditions seem unfavorable for intercontinental flight.

Headwinds are a different story. Migratory passages across deserts or across major bodies of water may be followed by local groundings, or **fallouts,** of thousands of exhausted birds, especially when they encounter strong headwinds. Legendary are the spectacular fallouts on the coasts of Louisiana and Texas of Neotropical migrants after they have flown across the Gulf of Mexico. These fallouts take place in April when bad weather and opposing winds force the northbound migrants to land on the first available land, with high mortality. Victor Emanuel, who grew up in Houston, Texas, and has probably witnessed as many fallouts as anyone, describes his experience when the entire trans-Gulf migration was grounded in late April 1960:

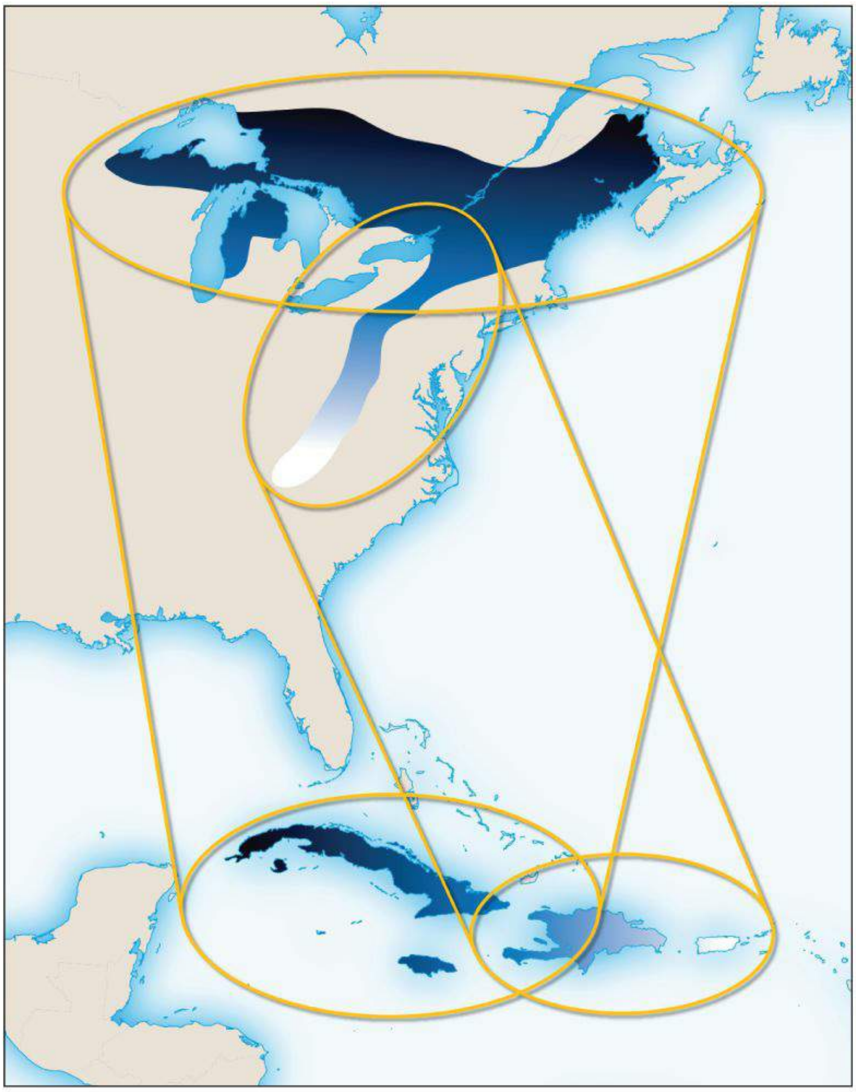
> There were trees decorated with tanagers, orioles, and grosbeaks. Trees dripped with warblers of many species—ten or more varieties in one tree. Birds were everywhere. In the trees, in the bushes, on fence posts, on fence wires, around houses, and most remarkably, in the grass. Sometimes a hundred orioles and buntings would fly up from the grass and perch in dead stalks. What impressed and delighted me most was seeing warblers in the grass, and even hopping on the ground! Here were these tiny birds, the “butterflies of the bird world,” not hidden amid the foliage of tall trees but literally at my feet. I’ve seen

> twenty or more Bay-breasteds, a dozen Blackburnians, and many others on the ground. In such a situation, you can approach warblers quite closely and enjoy every detail of their brilliant plumage. [Emanuel 1993, p. 1]

10.2 Connectivity

Why birds migrate as they do, connecting distant locales, is still a challenging question. The benefits of migration logically offset its risks and costs for many species. Many species that migrate to high northern latitudes are tropical birds that temporarily exploit the favorable opportunities of the long days and abundant resources of high-latitude summers. Attractive nesting opportunities invite migration to temperate latitudes. The large expanses of northern temperate-zone habitats facilitate dispersed, low-density breeding. Reduced predation of nests may be one result of low densities, breeding opportunities for yearlings another. Several years' wait for a breeding space is often the case in the Tropics. Such factors, contributing to reproductive success in one season and survival during another, are incentives to migrate.

New tracking technologies reveal the global connections of seasonal bird populations (Figure 10–9). The Black-throated Blue Warbler, for example, is a widespread Neotropical migrant that winters in the Caribbean and breeds in the cool forests of the Appalachian Mountains, New England, and eastern Canada. Its southernmost populations have been declining for the past 30 years, whereas northern populations are doing well. Conservation initiatives required knowing where warblers from particular breeding locales wintered so that both parts of the annual cycle could be addressed (Rubenstein et al. 2002). So a group of ornithologists turned to their feather chemistry. The ratio of carbon 13 to carbon 12 in plants and animals increases with latitude. This local chemical signature is deposited in new feathers from food eaten while a bird is molting.



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DATA FROM HOLMES 2007

Figure 10–9 Migratory connectivity of breeding and wintering grounds of Black-throated Blue Warblers. Shaded colors map specific sets of isotopes in feather samples. Warblers that nest in the northern part of the species range tend to winter in the Caribbean west of warblers that nest in the Appalachian Mountains.

Analysis of the carbon isotope ratios in the feathers of more than 700 Black-throated Blue Warblers from throughout their breeding range and from major islands in the Caribbean revealed that warblers from the southern Appalachians (from Georgia to West Virginia) winter on the easterly islands of Hispaniola and Puerto Rico. Warblers from northern populations winter in Cuba and Jamaica. The severe deforestation of the island of Hispaniola is likely responsible for the decline in the Appalachian breeding populations and will be the focus of new conservation initiatives. Discovering the connections between breeding and wintering grounds not only improves targeting of conservation initiatives but also offers unprecedented opportunities to understand the costs and benefits of migration (Bowlin et al. 2010).

Optimality models aid our understandings of the trade-offs and interconnections of migration strategies, including flight, fuel deposition, routes and detours, daily timing, wind selectivity and wind drift, and annual molt schedules, among many others (Alerstam 2011). Consider the energetic benefits for Red Knots that spend the winter in West Africa compared with those that stay in England. Red Knots that fly all the way to West Africa use at least 40 percent less energy each winter day compared with those that winter in Britain (Wiersma and Piersma 1994). Substantial energy is required to offset the cold winter temperatures, higher wind speeds, and reduced sunshine in Britain. Knots wintering there sustain energy expenditures of four to five times resting rate, which is at the upper limit possible for warm-blooded animals and equivalent to the physical effort of cyclists in the Tour de France. Using another analogy, Theunis Piersma suggests that a knot wintering in Britain would drain the power from a car battery in a day, whereas the battery would last a week in tropical Africa. Further, the costs of migration to West Africa from Siberia are relatively modest because they make good use of tailwinds. Flying to West Africa is a good investment of time and energy.

As their solutions to different trade-offs, the sexes and age classes of fully migratory species move different distances, called **differential migration.** At least 53 species (and possibly three times that number of species), of diverse taxonomic groups and habits, are differential migrants. Typically, females migrate farther than males, and young migrate farther than adults. The classes of birds that migrate farthest are usually smaller in body size, subordinate in social behavior, and later arriving on the breeding grounds. The classic study of differential migration by Ellen Ketterson and Val Nolan (1983) focused on Dark-eyed Juncos, which migrate south from Canada and the northern United States to wintering grounds throughout the eastern United States. Adult females migrate farthest to the southernmost states, young males stay farthest north in Indiana and Ohio, and adult males and young females settle at intermediate latitudes. Greater mortality among the young of both sexes, compared with adults, selects for their shorter migrations. Males that get back to the breeding grounds first to establish a territory tend to win, so they stay farther north than females. Young males, especially, must hurry back to succeed in the competition for breeding territories. Adult females migrate farther south to regions of lower junco densities and higher probabilities of overwinter survival.

Finally, there is a dark side to connectivity: the global transmission of diseases. The migration routes of birds around the planet unite into a vast global network full of opportunities to exchange viruses, such as avian influenza and West Nile virus. Because it provides breeding grounds for birds that winter in both Asia and North America, Western Alaska, for example, is a gateway for the transmission of contagious diseases from eastern Asia into the Western Hemisphere. Waterfowl exposed to new and deadly flu strains, such as H5N1, which emerged in the Asian poultry industry, are especially susceptible to them. The global spread of new and deadly strains carried by migratory birds can be rapid, with fatal consequences for local bird populations, livestock, and humans. West Nile virus, for example, which was detected first in Uganda in 1937, spread globally to the United States within 60 years (Rappole 2013).

10.3 Fat, Fuel, and Flight Ranges

Preparations for a major migratory flight can be intense and transforming. Migrants fatten rapidly just before migration by consuming enormous quantities of energy-rich food. Blackpoll Warblers nearly double their weight, from an average of 11 grams to an average of 21 grams. Ruby-throated Hummingbirds, which cross from 500 to 600 miles of open water in the Gulf of Mexico, also nearly double their normal weight of three grams to make this trip.

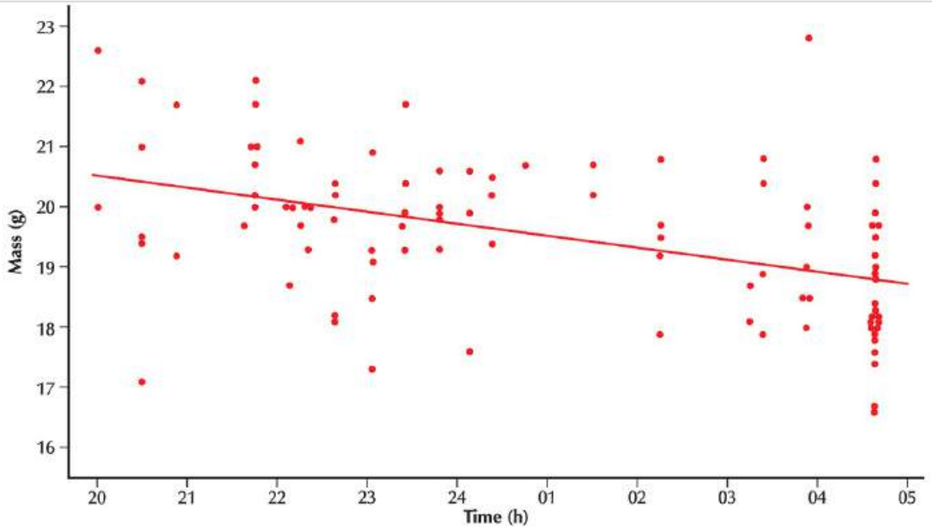
Fat yields twice as much energy and water per gram metabolized, as does either carbohydrate or protein (Table 10–1). Fat is stored in adipose tissues under the skin, in the muscles, and in the body cavity. For example, White-crowned Sparrows deposit subcutaneous fat initially at 15 separate sites. With continued deposition, the fat stores spread laterally and coalesce into a continuous layer between the skin and muscles. Some fat is also stored in most muscles and in internal organs. Unlike the human heart, the avian heart does not accumulate much fat, even when a migrant reaches peak obesity.

Table 10–1 ***Fuels for Migration***

Fuel	Energy Yield (kJ)	Metabolic Water (g)
Fat	38.9	1.07
Carbohydrate	17.6	0.55
Protein	17.2	0.41

Adipose tissue does not consist simply of large, inert globs of fat. Instead, it supports a dynamic system for the synthesis, storage, and release of lipids (George and Berger 1966). The enzyme lipase breaks down fat into free fatty acids and glycerol for transport to sites of use. Lipase activity, which is a good index of the capacity of muscles for fat metabolism, increases in relation to migratory activity.

How far migrants can fly nonstop depends both on their fat reserves and on how quickly they use their fuel. David Hussell and his associates at Long Point Observatory on the north shore of Lake Ontario captured and weighed nocturnal migrants arriving at various times of the night after flying north across Lake Erie (Hussell and Lambert 1980). These data suggest average weight losses of 0.9 percent of body weight per hour of flight and 0.2 gram per hour for the Ovenbird (Figure 10–10). Weight losses of about 1 percent project to expenditures of about 418 joules of energy per gram of body weight per hour of flight. Blackpoll Warblers were more fuel efficient than most other migrants; they lost weight at 0.6 percent per hour of flight or expended 250 joules of energy per gram per hour of migration.



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Data from Hussell 1969

Figure 10–10 Ovenbirds, weighed on arrival at Long Point Observatory on the north shore of Lake Ontario, decreased in mass by an average of 0.2 gram per hour as the night proceeded. Assuming that those that arrived later had flown longer than those that arrived earlier, one can use such data to estimate the energy costs of migratory flights.

Estimates of energy expenditure allow us to project total flight range. Small birds that expend 418 joules per gram per hour during migratory flight and that have fat reserves of 40 percent of total live weight can fly about 100 hours and cover about 2,500 kilometers. At that rate, they should be able to cross the most extensive barriers with energy to spare, unless they encounter strong headwinds. Migrant shorebirds, such as the Dunlin, have estimated flight-range potentials of 3,000 to 4,000 kilometers.

Ornithologists long wondered how such a tiny bird as the Ruby-throated Hummingbird could carry enough fuel to cross the Gulf of Mexico. Some doubted that hummingbirds crossed at all, suggesting instead that they took a less direct route overland to Central America. Others proposed that hummingbirds hitched rides on the backs of larger migrants. Laboratory measurements suggested that a hummingbird in flight consumes fat at the rate of 2,880 joules per hour. If the hummingbird carried two grams of fat and flew at a velocity of 40 kilometers per hour, it should be capable of flying more than 1,000 kilometers nonstop in about 26 hours, more than enough to cross the Gulf of Mexico (Lasiewski 1962).

Long-distance migrants may need more fuel than is available in their fat deposits. They then turn to stores of protein in their muscles and organs, and consume those stores in flight (Battley et al. 2000).

Great Knots, medium-sized shorebirds, fly 5,400 kilometers from Australia to stopover sites in China. In addition to having used most of their fat, arrivals had used and reduced the size of seven organs while in transit. Only the brain and lungs seemed to be exempt from use as fuel.

Stopover Sites

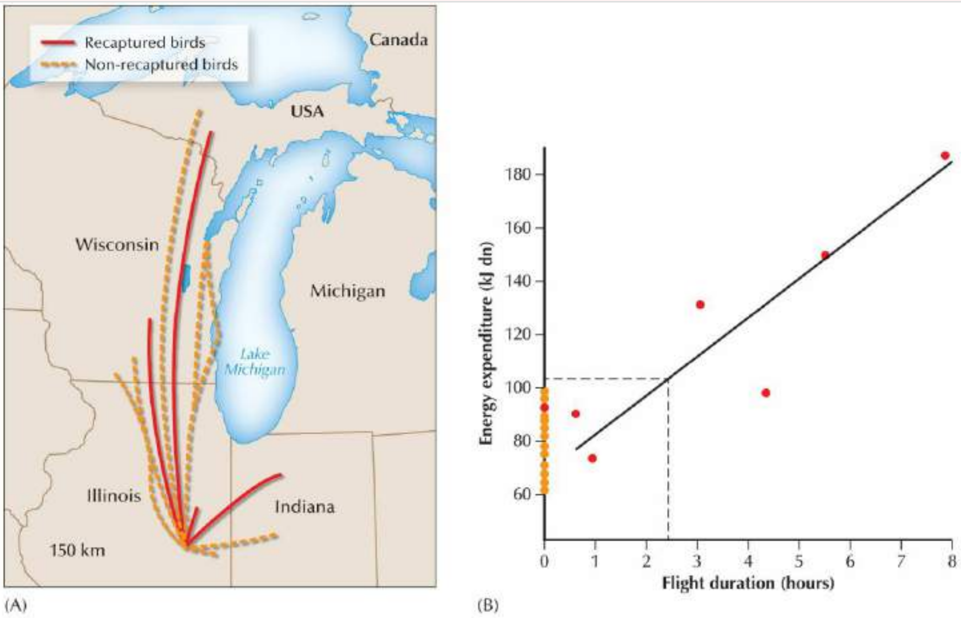
Regular refueling usually accompanies migrations. Songbirds typically fly several hundred kilometers overnight and then pause for one to three days of rest and refueling (Winker et al. 1992a, 1992b). Some songbirds press on for several nights in succession until their reserves are nearly exhausted. Beyond their expenditures of energy in the air, they also need energy to find food at a **stopover** site. The stopover ground costs of thrushes migrating north in the spring in the United States, due to cold weather and foraging efforts, were greater than their flight costs (Wikelski et al. 2003; Box 10–2). High-quality stopover sites with plenty of food—avian service stations, or McDonald’s for birds—are critical to successful migrations.

BOX 10–2

Tracking Thrushes on Overnight Flights

Real-time tracking of individual nocturnal migrants such as *Catharus* thrushes provides firsthand insights into the abilities and energetic costs of their overnight flights. In the pioneering study, a Gray-cheeked Thrush outperformed the ornithologists. William Cochran and his coworkers (1967) captured the migrating thrush in central Illinois one afternoon and attached a tiny radio transmitter to it. At dusk, the thrush took off on the next leg of its journey, followed by the ornithologists in a small plane. A severe thunderstorm and shortage of fuel forced their plane down that night, but the thrush flew on. After refueling, the Cochran group took off again and, remarkably, relocated the thrush in the vast night sky by dead reckoning. The thrush landed at dawn in Wisconsin after flying 650 kilometers on a firm compass bearing all night—without refueling.

Thirty-three years later, Martin Wikelski and his coworkers (2003) followed Swainson’s and Hermit thrushes injected with doubly labeled water, the use of which measures energy expenditures. The treated thrushes were followed by plane up to 600 kilometers, from evening takeoff to landing the next morning, and retested for the loss of the labeled water. The thrushes spent 15.5 kilojoules per hour of flight. Their measurements indicated that the actual flight costs would be 29 percent of the total energy costs of the 42-day migration (including 18 flights) from Panama.



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DATA FROM WIKELSKI ET AL. 2003

Migration routes and energetics of thrushes. (A) Overnight flight paths of thrushes released in Illinois. Red lines indicate recaptured birds; dashed orange lines indicate birds that were not recaptured. Ends of lines indicate stopover sites. (B) Daily energy expenditures of migrating (red symbols) and stopover (orange symbols) birds.

The Bar-tailed Godwits that migrate directly from Alaska to New Zealand could fly instead down the coast of eastern Asia with opportunities to refuel. Optimality models, however, suggest that a two-step migration with one stop-over site on the Asian coast would not reduce the energy costs of migration, including the heavy costs of fuel transport (Alerstam 2011). A flight plan with more stopovers could bring about a slight reduction in total energy cost, but other issues, such as wind conditions and absence of predators and pathogens, seem to have tipped the balance in favor of a direct fall flight. Interestingly, the Bar-tailed Godwits favor the westerly coastal route with one stopover on their migration back to Alaska. This route may be beneficial for exploiting spring winds and especially for arriving on the breeding grounds with extra reserves (Gill et al. 2009).

The nonstop flights of the Bar-tailed Godwits from Alaska to New Zealand, mentioned above, are exceptional. Three or four refueling stopovers are a strategic aspect of the extraordinary migrations of most Arctic shorebirds, which fly from the Arctic tundra of North America to the southern tip of South America and back, as many as 30,000 kilometers round-trip. Migrating shorebirds congregate by the millions at key staging areas. For example, from 5 million to 20 million shorebirds pass through the Copper River Delta in Alaska every spring, including almost the entire Pacific Coast populations of two species: Western Sandpipers and Dunlins (Figure 10–11). They time their movements to coincide with the appearance of abundant food at these sites, where they build up fat reserves required for the next leg of their journey.

STEVE KAUFMAN/GETTY IMAGES

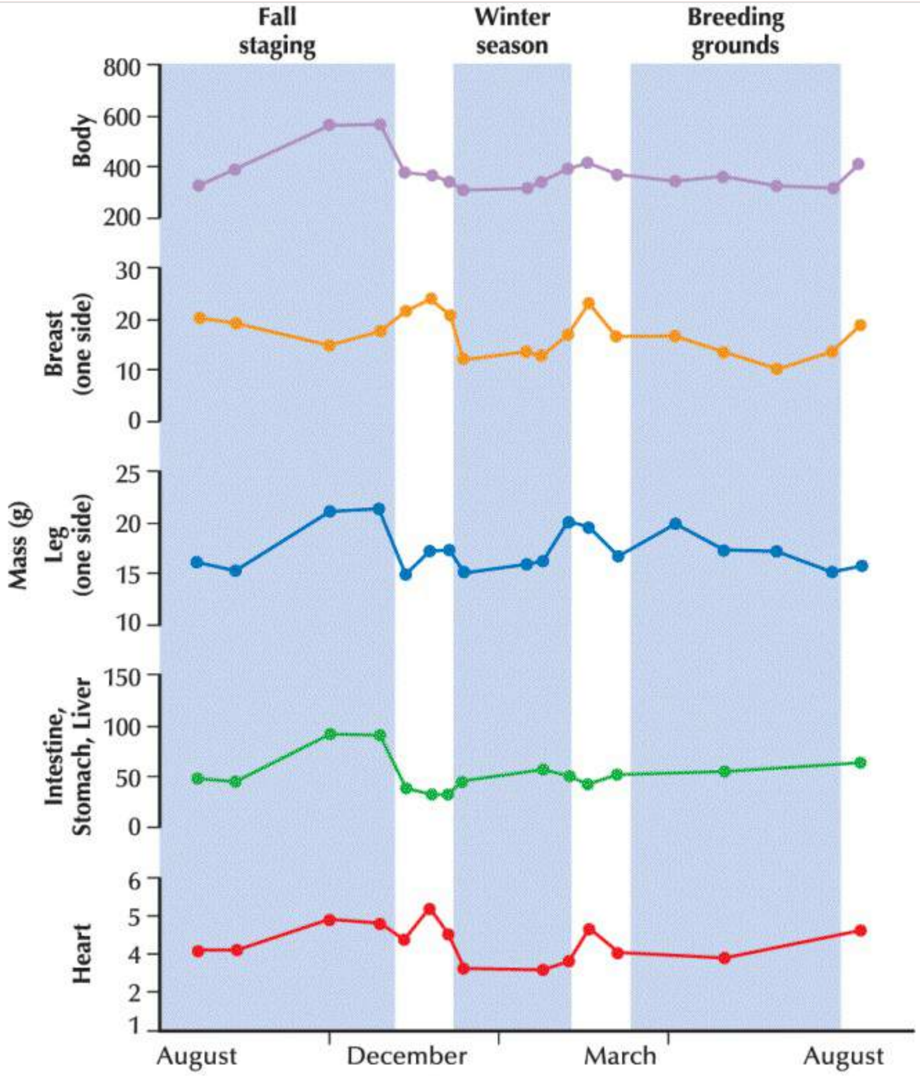
Figure 10–11 Millions of shorebirds gather at key staging areas, such as the Copper River Delta in Alaska, to refuel for the next (in this case, final) leg of their migration to northern breeding grounds.

Good stopover sites can be few and far between. Bar-tailed Godwits require good mudflats with soft sediments and lots of worms and small mollusks. Spring migration of the Eurasian populations requires a series of 1,000-kilometer flights from West Africa to Siberia, first to estuaries in Mauritania on the edge of the Sahara, then to Morocco, then all the way to the coast of France, and then to the Wadden Sea on the north coast of Europe, followed by a final 4,500-kilometer nonstop flight to their final destination in Arctic Siberia (Piersma 1994). At Wadden Sea, their final refueling station, they undergo a cycle of organ changes quite like that of Eared Grebes (Landys-Ciannelli et al. 2003; Box 10–3). The lean dry mass of the digestive-tract organs (stomach, liver, kidneys, and intestines) increases rapidly in the early stages of refueling and then shrinks before departure. Flight muscles increase steadily in lean dry mass, peaking at departure.

BOX 10–3

The Eared Grebe Reorganizes Its Whole Body

Beyond just adding fat for the trip ahead, long-distance migrants also reorganize the organs of their bodies. Studies of Eared Grebes staging for migration on Mono Lake in California revealed this phenomenon (Jehl 1997; Cullen et al. 1999). They quickly more than double their weight from about 260 grams to more than 600 grams, mostly with added fat (see illustration). To process the large quantities of food (brine shrimp) that they need for this change, they almost double the size of the organs of their digestive tracts. Conversely, their pectoral flight muscles shrink by half, rendering the grebes flightless even before they drop their flight feathers in the major molt of the year. Then the grebes fast for two to three weeks before leaving on migration. They lose weight, shrink their digestive systems to one-third of their former mass, reduce their leg muscles, increase the size of their hearts, and double the mass of their pectoral flight muscles back to their former size. They trade locomotory organs and muscles for digestive organs to build fat deposits, then they trade digestive organs for the muscle and heart power needed for the migration itself. The endocrine and physiological controls of this cycle of body reorganization remain unknown.



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DATA FROM CULLEN ET AL. 1999

Changes in body mass and in the size of organ systems of Eared Grebes over the annual cycle. Shaded areas indicate periods of migration. Breast and leg mass determined for one side of body.

The shores of Delaware Bay in the eastern United States are a key stopover place on the Red Knots’ northward migration. Here, in late May, they fatten rapidly on horseshoe crab eggs to fuel the final leg of the flight to the Arctic. Spring tides and warming water temperatures stimulate horseshoe crabs to emerge from the ocean depths, to mate, and to lay their nutritious eggs in the beach sand. The sheer abundance of tiny greenish crab eggs attracts thousands of gulls and shorebirds to feast and fatten up in a true spectacle. By consuming an estimated 1,000 grams of crab eggs, the average knot adds 54 grams of fuel and nutrients (Castro and Myers 1993). Rough calculations suggest that, at their peak numbers in the 1990s, 95,530 knots stopping at Delaware Bay in the spring would have consumed 226.1 metric tons of horseshoe crab eggs, and would have gained 5.2 metric tons of fat (Harrington 2001).

The Red Knots compete with local fishermen, who exploit the horseshoe crabs for conch-fishing bait, fertilizer, and a biochemical reagent extracted from horseshoe crab blood that is used in medical tests. Consequently, more and more of the knots fail to adequately refuel on Delaware Bay, underscoring the vital importance of stopovers. From 1997 to 2002, a larger proportion of knots failed each year to attain a mass of 180 to 200 grams, the critical size required to complete the journey and breed successfully. Reduced nutrient storage and organ shrinkage increased mortality, especially for late-arriving adults, and lowered reproduction. As a result, adult survival dropped 37 percent. Young birds in wintering flocks dropped 47 percent. This population is in serious trouble: it declined precipitously from 51,000 birds to 27,000 in the period from 2000 to 2002 (Baker et al. 2004).

Conservation of Staging Areas

International alliances for the conservation of shorebirds are directed toward the protection of critical staging areas, such as Delaware Bay. One of these alliances, the Western Hemisphere Shorebird Reserve Network (WHSRN), was formed by Pete Myers in 1985 to address shorebird-conservation problems. Many species of shorebirds were declining in numbers, apparently as a result of habitat loss. WHSRN, a voluntary collaboration of private and government organizations, gives international recognition to critical shorebird habitats and promotes their cooperative management and protection. The shorebirds serve as a symbol for uniting countries in a global effort to maintain the Earth's biodiversity.

Using data from private and government sources, this voluntary network helps protect 95 sites (as of July 2016) of the globally most important nesting, stopover, and wintering sites in 15 countries (see Figure 10–2). These sites contain 33 million acres of wetlands on which the continued existence of millions of shorebirds depend. More broadly, a worldwide network of **Important Bird Areas (IBAs)** targeted by BirdLife International and its partners now helps to protect birds in more than 200 countries and territories. IBAs worldwide are important stopover sites for a variety of migratory species. The stewardship of such sites will be essential to continue the natural connections among ecosystems through the hemispheric migrations of birds (Chapter 21).

10.4 Evolution

Migration is a package of complex behaviors that have separate genetic controls. Zugunruhe behavior (nocturnal restlessness; see section 9.5), hyperphagia, and navigation systems are each independent systems with deep evolutionary roots (Berthold 1999). Despite those roots, however, migration is a labile and facultative behavior. It has evolved and has been lost repeatedly in different species and lineages of birds. Within species—for example, White-crowned Sparrows and Common Ringed Plovers—some populations migrate, whereas others do not. In other species, such as the Red Knot, some migratory populations travel farther than others do. Still other species, such as the European Robin, mix migratory and nonmigratory birds in the same population. Unpredictable winter conditions favor a mixture of migrant birds and resident or nonmigrant birds. Mild winters favor residents; severe winters favor migrants. Resident birds make up about one-fifth of the robin population in southwestern Germany. They remain within five kilometers of their breeding territories, do not put on large reserves of premigratory fat, and do not exhibit sustained migratory restlessness in the laboratory. In contrast, migrant birds fatten in the fall, exhibit intense migratory restlessness, and travel an average of 1,000 kilometers to their winter habitats. Resident birds suffer higher overwinter mortality but benefit from early access to high-quality territories in the spring.

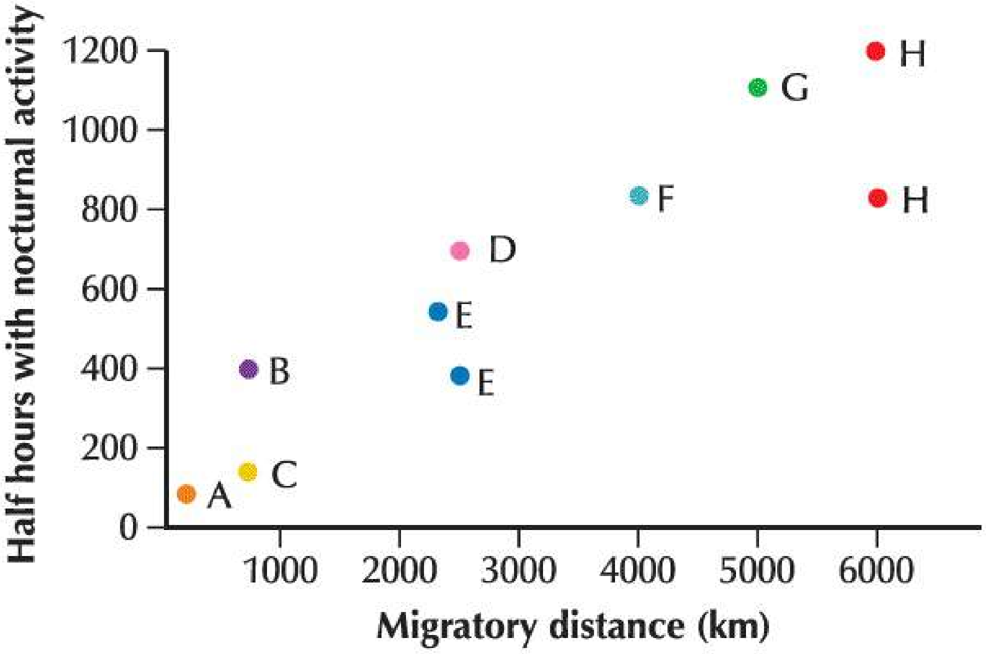
Within a species, increasingly sedentary populations can competitively replace migratory populations (or vice versa) in a few generations. The composition of migratory compared with nonmigratory birds and their offspring in populations, such as those of the European Robin, can shift quickly in relation to natural selection. House Finches introduced from sedentary western populations into the eastern United States in the 1950s quickly evolved to be migratory (Able and Belthoff 1998). Conversely, Barn Swallows wintering in Argentina during the austral (southern) spring and summer stayed to nest there (Martinez 1983).

The Eurasian Blackcap, a familiar songbird of Europe, added Britain to its list of wintering grounds in the twentieth century. Instead of migrating southwest to the Mediterranean (the Eurasian Blackcap’s historical wintering grounds), increasing numbers of Eurasian Blackcaps that nest in Germany and Austria migrate northwest each year to winter in England and Ireland. The offspring that winter in England exhibit an innate orientation to the northwest, suggesting a rapid evolutionary change in the genetic program that controls their migratory behavior.

The evolution of some Eurasian Blackcaps to new wintering grounds has benefits, including a shorter migration (Bearhop et al. 2005). In combination with faster changes in day length that stimulate the warblers to migrate earlier, shorter migration times lead to earlier returns to the breeding grounds and capture of the best-quality territories. One result is that a female Eurasian Blackcap from England lays one more egg than does a female that winters in Spain, in turn fueling an increase in the new wintering population. Both males and females from England arrive early with another important result. They pair assortatively with each other, not randomly with those that winter in other places. Assortative pairing potentially leads to the evolution of a genetically distinct population and, in time, a new species. Speciation among migratory bird populations often involves a mixture of geographical overlap (sympatry) as well as isolation (allopatry), termed heteropatry (Winker 2010). Reproductive isolation between such populations is driven by ecological factors (i.e., adaptation to different environments and adjustments of the annual cycle) rather than by sexual selection (Chapter 19).

Endogenous Controls

Not only are migratory preparations and migration itself linked directly to endogenous circannual rhythms (see Chapter 9), but the duration and pace of migration are linked to these rhythms as well. The length of Zugunruhe activity in the laboratory relates directly to the distances migrated by these warblers to their respective winter ranges (Figure 10–12). The Willow Warbler normally takes from three to four months to migrate from Europe to southern Africa; this warbler's intense migratory restlessness in the laboratory lasts more than four months. The Common Chiffchaff takes only one to two months to migrate from southern Europe to northern Africa; intense migratory restlessness in the laboratory lasts 60 days.



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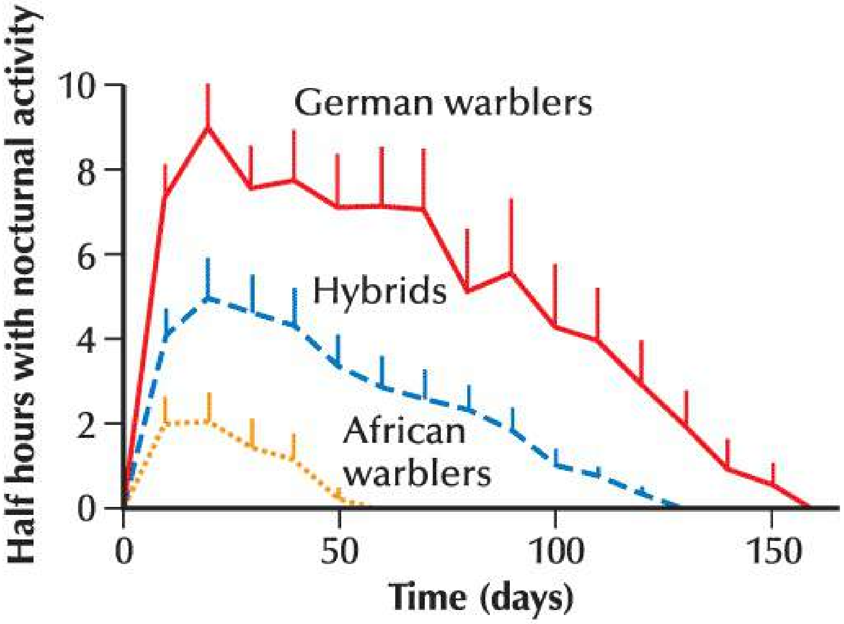
DATA FROM GWINNER 1977

Figure 10–12 The lengths of time of nocturnal restlessness in the laboratory correlate with the migration distances covered by eight species of European warblers: (A) Marmora’s Warbler, (B) Dartford Warbler, (C) Sardinian Warbler, (D) Eurasian Blackcap, (E) Common Chiffchaff, (F) Subalpine Warbler, (G) Garden Warbler, and (H) Willow Warbler. Results for Willow Warblers and Common Chiffchaffs tested under different conditions are shown separately.

Populations of the Eurasian Blackcap differ from one another in the seasonal course and magnitude of Zugunruhe. The differences correspond directly to the normal migration distance of each population. Evidence of direct genetic control of their directional migrations comes from the study of hybrids. Hybrids between the migratory German population and the nonmigratory African population hybrids exhibit intermediate Zugunruhe activity (Figure 10–13).



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Data from Berthold and Querner 1981

Figure 10–13 Eurasian Blackcaps from migratory populations in Germany show intense and prolonged migratory restlessness, whereas birds from a nonmigratory population in Africa show little migratory restlessness. Hand-raised hybrids of these forms have intermediate migratory behavior.

Hand-reared, caged migrants not only exhibit well-defined orientation behavior but also change their compass direction in ways that correspond to their natural migration routes. Garden Warblers change direction in the course of their fall migration from southwest initially to south–southeast from Spain to southern Africa. Devoid of cues other than magnetism, the orientation of migratory restlessness in the laboratory shows a corresponding shift. Restless, caged Garden Warblers orient southwest in August and September and then shift their heading to south–southeast from October to December. Such internal programs, however, cannot guide migrants precisely to their final winter residences. External forces, including food availability, climate, and competitive interactions, come into play at various stages of the journey and may be the dominant factors, especially in short-distance migration.

10.5 Navigation

In addition to the physical feats, migration requires precise **navigation** between breeding territories and wintering stations. On hemispheric scales, individual birds return to a particular tree in Canada after wintering in South America or migrate annually between particular sites in Europe and Africa. Legend has it that, in one of the earliest experiments, an Eastern Phoebe, wearing a silver thread placed on its leg by John James Audubon in 1803, returned the next spring to Audubon's house in Mill Grove, Pennsylvania, after wintering somewhere in the southern United States. Conversely, banded Northern Waterthrushes, which breed in the northern bogs of Canada, returned predictably every year to the exact same wintering sites in Venezuela.

The choice and maintenance of a compass direction are only part of the challenge of navigation. If a bird is to reach a goal, such as a loft in regard to homing pigeons, it must also know its own position relative to its goal.

The homing feats of displaced birds testify to their navigational abilities. Homing pigeons return to their lofts by flying as much as 800 kilometers per day from unfamiliar places. Ancient Egyptians and Romans developed these messengers by selecting for the natural orientation abilities of Feral Pigeons. Both shearwaters and sparrows can return to a home site after having been transported thousands of miles away. A Manx Shearwater returned to its nest burrow in Wales only 12.5 days after having been released in Boston (Mazzeo 1953). White-crowned Sparrows that were shipped to Baton Rouge, Louisiana, returned the following winter to their wintering grounds in

San Jose, California, where they were recaptured. They returned to California again after a second displacement to Laurel, Maryland (Figure 10–14).

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DATA FROM MEWALDT 1964

Figure 10–14 White-crowned Sparrows returned to their wintering grounds in San Jose, California the following year, after having been carried by aircraft (green dashed lines) to Baton Rouge, Louisiana, and to Laurel, Maryland. These marked sparrows apparently spent the intervening summers on their nesting grounds in Alaska. The solid blue lines show their probable flight paths.

The orientation systems of birds include a tool kit of complementary and interactive compass senses, including landmarks, the positions of the sun by day and the stars by night, the topology of the Earth's magnetic fields, and odors in the atmosphere as well as the position of the setting sun and its bands of polarized light in the evening. Next, we review each of these compass systems, including the history of their discovery, which illustrates the way in which ornithologists have developed a detailed understanding of complex bird behaviors. How birds themselves build and calibrate the whole tool kit is the final section of this chapter.

Visual Landmarks

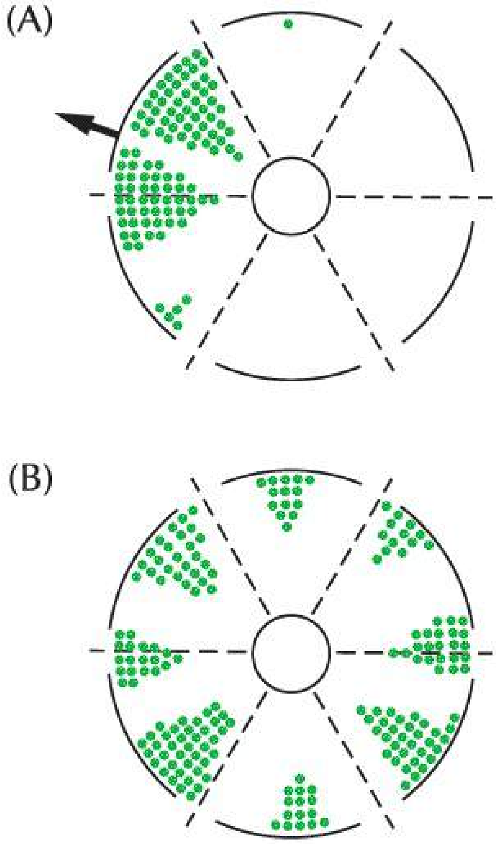
First and foremost, birds rely on visual landmarks for both local travel and long-distance migration. Pigeons routinely follow highways, railways, and rivers, even if not the most direct route home. Both diurnal and nocturnal migrants, especially waterfowl, follow watercourses and coastlines but are reluctant to cross large, open bodies of water unless the winds are favorable. As a result, great numbers concentrate where restricted corridors function as funnels. The Strait of Gibraltar and the Bosporus at Istanbul are major funneling points for Eurasian migrants that detour around the Mediterranean Sea. The coasts of Central America funnel thousands of migrating raptors—Broad-winged Hawks, Swainson’s Hawks, and Turkey Vultures—over Panama City. Crowds of bird-watchers gather to view the spectacle of migrants funneled to the tips of peninsulas such as Point Pelee, Ontario, and Cape May, New Jersey.

Naive young birds cannot use visual landmarks to guide them on their first migrations across new landscapes. Underlying the experienced use of visual landmarks are more sophisticated navigational compasses. Birds start their orientation with cues other than landmarks and senses other than sight.

In a now classic early experiment, well-trained homing pigeons were fitted with frosted contact lenses that eliminated image formation beyond three meters (Schlichte 1973). These severely myopic birds flew "blind" for more than 170 kilometers directly back to their lofts. When they reached the vicinity of their lofts, they hovered and then landed like helicopters. Not all such pigeons performed perfectly (some crashed and some missed the loft altogether), but many oriented well without being able to see landmarks. Orientation by birds is based on a framework of navigational compasses that include the sun, the stars, and the Earth's magnetic fields.

The Sun Compass

Scientists long suspected that birds navigated by the sun, but proof of this ability awaited experiments conducted with starlings and homing pigeons in the 1950s. In Germany, Gustav Kramer studied the orientation of Zugunruhe in Common Starlings (Figure 10–15). The birds were housed in circular cages and placed in a large pavilion with windows through which they could see the sun, including its change of position as the day progressed. As long as they could see the sun, they focused their attention toward the northeast, the correct direction for spring migration. On overcast days, however, the starlings showed no directional tendency.



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Data from Kramer 1951, Emlen 1975a

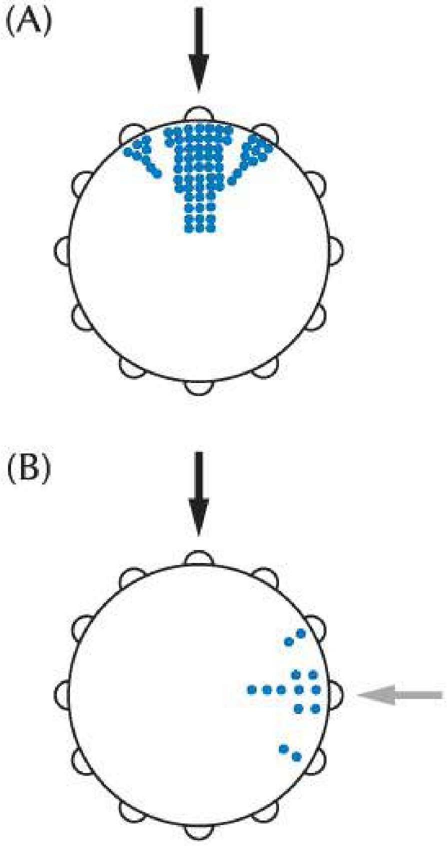
Figure 10–15 Common Starlings use the sun to orient in a circular cage. (A) As long as they could see the position of the sun in the sky, they oriented their restless spring migratory behavior toward the northeast. (B) On overcast days when they could not see the sun, they showed no directional orientation. Each dot represents 10 seconds of fluttering activity.

At about the same time, in Britain, Geoffrey Matthews (1951) released homing pigeons from unfamiliar sites away from the loft under a variety of weather conditions. The pigeons flew directly home when they could see the sun, but they fared poorly under overcast skies. Matthews discovered a key feature of this orientation behavior:

not only could the pigeons use the sun for directional information but they also compensated for its changing position as the day progressed, as if they could “tell the time.”

Testing the so-called **sun-arc hypothesis,** Gustav Kramer and his colleagues demonstrated that birds, indeed, compensate for the apparent motion of the sun. They trained starlings (and some other birds) to feed from the northwest cup of a series of cups placed around the perimeter of a circular cage. The birds reliably chose the correct cup when they could see the sun. However, when trained to accept a stationary lightbulb as a substitute for the sun, they fed from cups increasingly farther to their left as they compensated for the expected hourly change in the position of the “sun.”

The next step in the study of a time-compensated solar compass was to trick a bird into misreading the sun’s position by changing the bird’s internal clock. Konrad Hoffman kept Common Starlings on a 12-hour-dark and 12-hour-light cycle that was six hours out of phase with natural daylight (the lights went on at 1200 instead of 0600). Accustomed to this schedule, the starlings predictably misread the sun’s position in the sky. The clock-shifted starlings interpreted the midday position of the sun to be its dawn position. Their “east” was really south, so they looked for food at a position 90 degrees clockwise from the correct bearing (Figure 10–16). This result is standard: six-hour clock-shift experiments with many other birds, including homing pigeons, produce a 90-degree disorientation and confirm the widespread use by birds of time-compensated solar cues.



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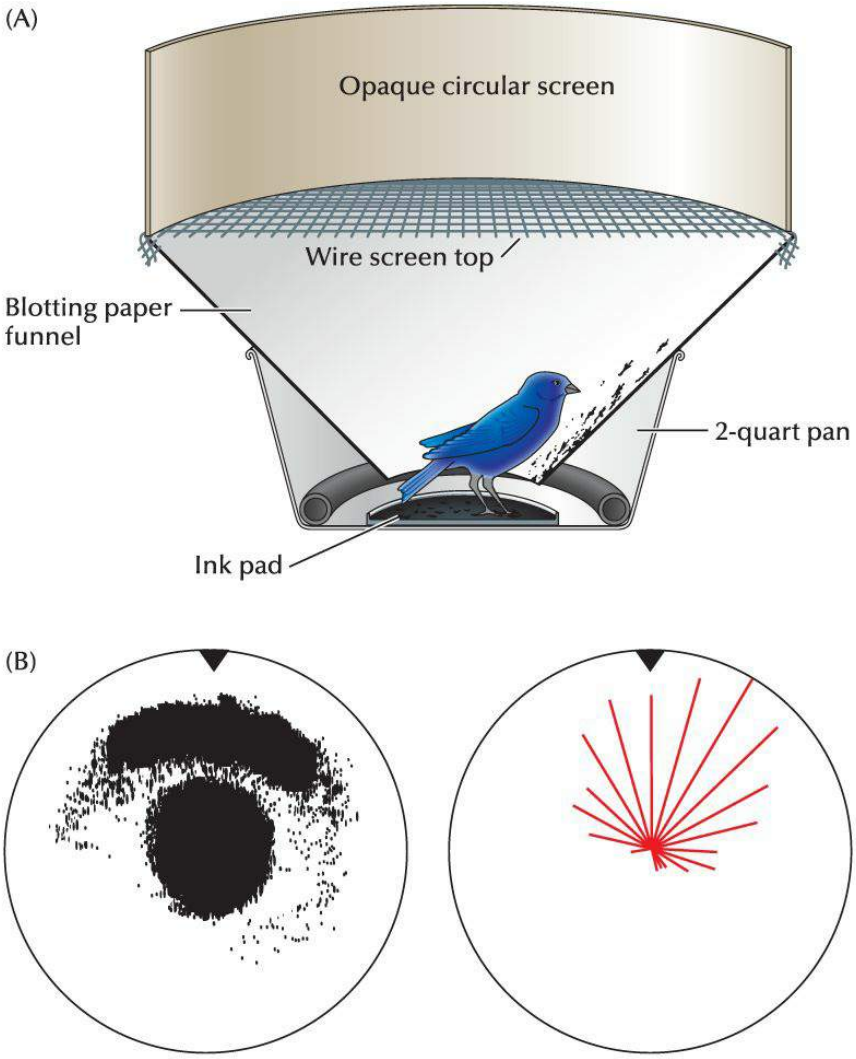
Data from Hoffman
1954, Emlen 1975a

Figure 10–16 When the internal clock of a Common Starling is set six hours behind natural time (by changing the schedule of light and dark), it misreads the sun’s position and looks for food 90 degrees (gray arrow) from the correct location (black arrows). (A) Behavior during training, showing correct orientation. (B) Behavior after the six-hour clock shift in internal schedule. Each dot shows an attempt to find food.

The Star Compass

Land birds and waterfowl maintain their direction when they migrate at night by using the stars as a source of directional information. Franz and Eleanore Sauer first demonstrated the ability of migrating passerine birds to use the stars for navigation in experiments with hand-reared Garden Warblers (Sauer 1958). The warblers were kept in circular experimental cages in a planetarium. When ready to migrate, they became restless and hopped and tried to fly or hop in their migratory direction. The Sauers watched the birds through the glass bottom of their cage. The warblers oriented north in the "spring" and south in the "fall" under the simulated night skies of the planetarium. When the Sauers turned off the "stars," the warblers became disoriented. When the Sauers rotated the north–south axis of the planetarium sky 180 degrees, the warblers also reversed their compass headings.

Stephen Emlen duplicated the Sauers' results with a North American migrant, the Indigo Bunting (Figure 10–17). These buntings oriented north when a spring night sky was simulated in a planetarium and south when a winter night sky was simulated. Like the warblers, the buntings became disoriented when the planetarium sky was turned off and reversed their orientation when the axis of the sky was reversed (Figure 10–18). Then Emlen (1967b) tried to identify the stars that buntings use for orientation by systematically blocking out various constellations. He assumed, logically, that the buntings orient by the North Star, the one obvious, fixed point in the night sky, but they did not. Instead, they used the constellations that were within 35 degrees of the North Star. Moreover, the buntings were familiar with most of the major constellations in the Northern Hemisphere, including the Big Dipper, the Little Dipper, Draco, Cepheus, and Cassiopeia; if one of these constellations was blocked from view, the buntings used the others. Such redundancy is useful when sections of the sky are overcast; it also allows the birds to be flexible in their choice of guideposts in the complex, ever-changing night sky. The axis of rotation of the night sky is a key compass for many nocturnal migrants.



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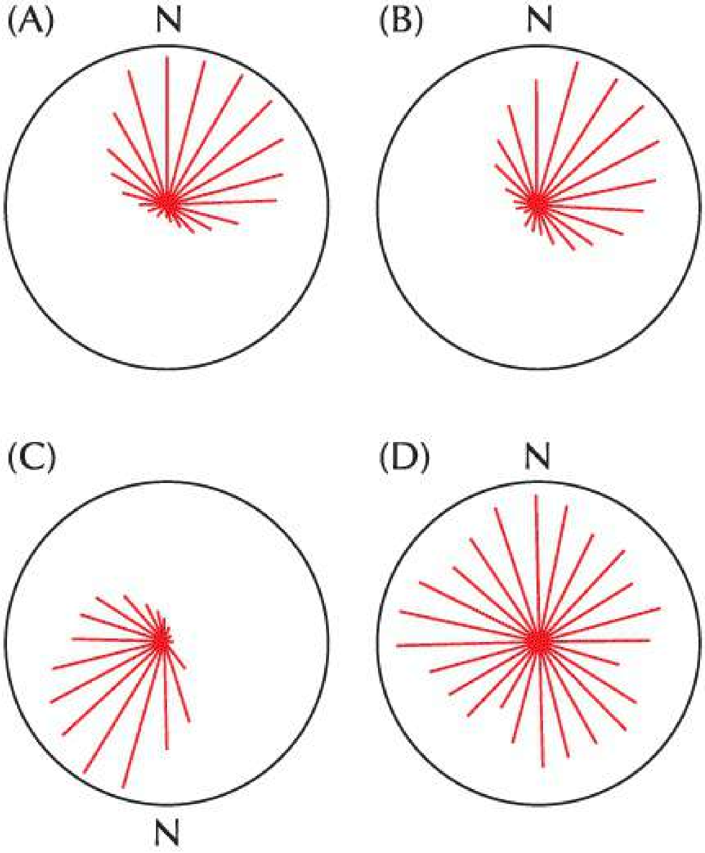
DATA FROM EMLEN AND EMLEN 1966, EMLEN 1967A

Figure 10–17 (A) The Indigo Bunting migrates at night between its summer range in the eastern United States and its winter range in Central America. Buntings in a state of migratory restlessness orient by the stars at night, even when confined to a funnel-like cage placed under a planetarium sky. (B) Inky footprints record the orientation direction; the lengths of line vectors measure the intensity of ink left in each 15-degree sector.



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DATA FROM EMLEN 1975B

Figure 10–18 Line vectors, such as the ones described in Figure 10–17, show how Indigo Buntings use the stars to orient north in the spring. They do so under (A) natural night skies and (B) simulated night skies in a planetarium. (C) When the planetarium stars are shifted so that the North Star, N, is at true south, the birds reverse their orientation. (D) When the stars are turned off and the planetarium is diffusely illuminated, the buntings do not orient.

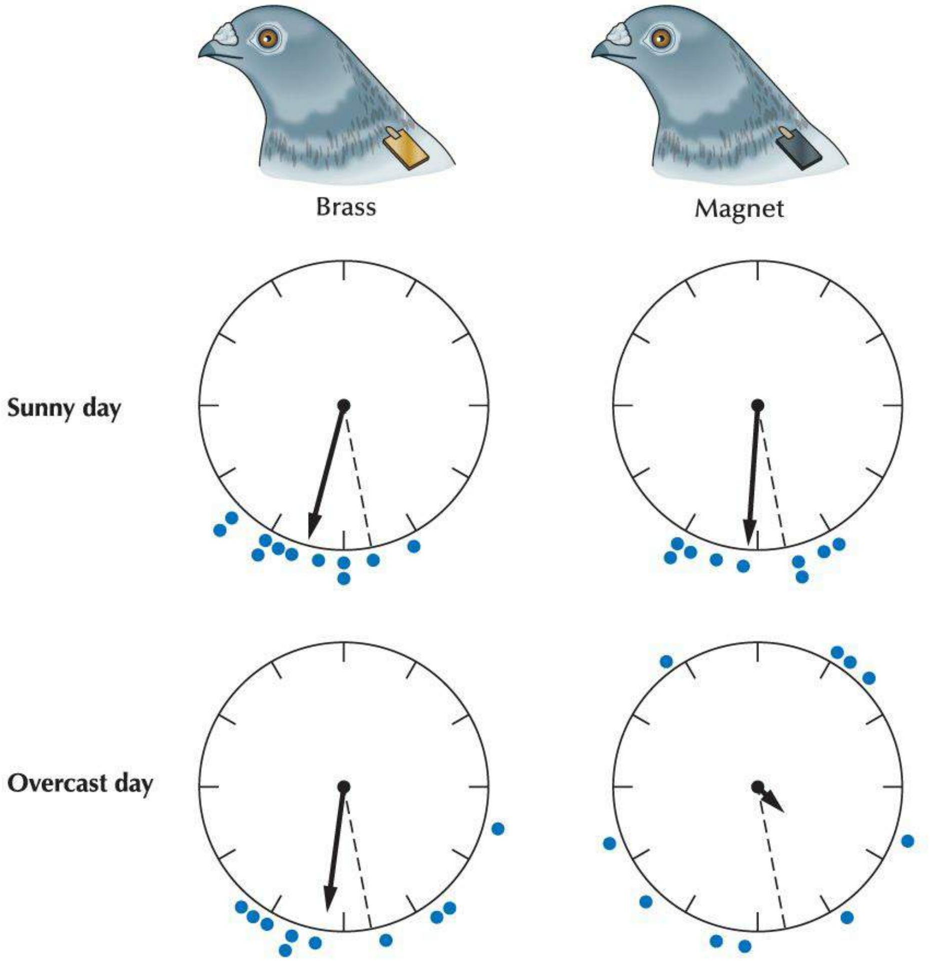
A bird’s hormonal physiology is easy to change by changing day length, or photoperiod (see Chapter 9). Simulating the seasons by increasing or decreasing day lengths can bring caged birds into breeding condition, can cause them to molt more often than is natural, and can cause them to accumulate premigratory fat at the wrong time of the year. Using unnatural photoperiod regimes, Steve Emlen (1969) manipulated the seasonal physiology of two groups of Indigo Buntings. He induced readiness for northward spring migration in one group and readiness for southward fall migration in the other group. Exposed to the same planetarium sky, buntings in the two groups oriented north and south, respectively. These results showed that migratory orientation is under physiological control, at least in some birds.

Geomagnetism

The **geomagnetic fields** of the Earth provide a map of horizontal space, just as gravity and barometric pressures give information about vertical space. The intensity and dip angle—or inclination of the magnetic field—change with latitude in ways that provide reliable, omnipresent information about geographical orientation and position.

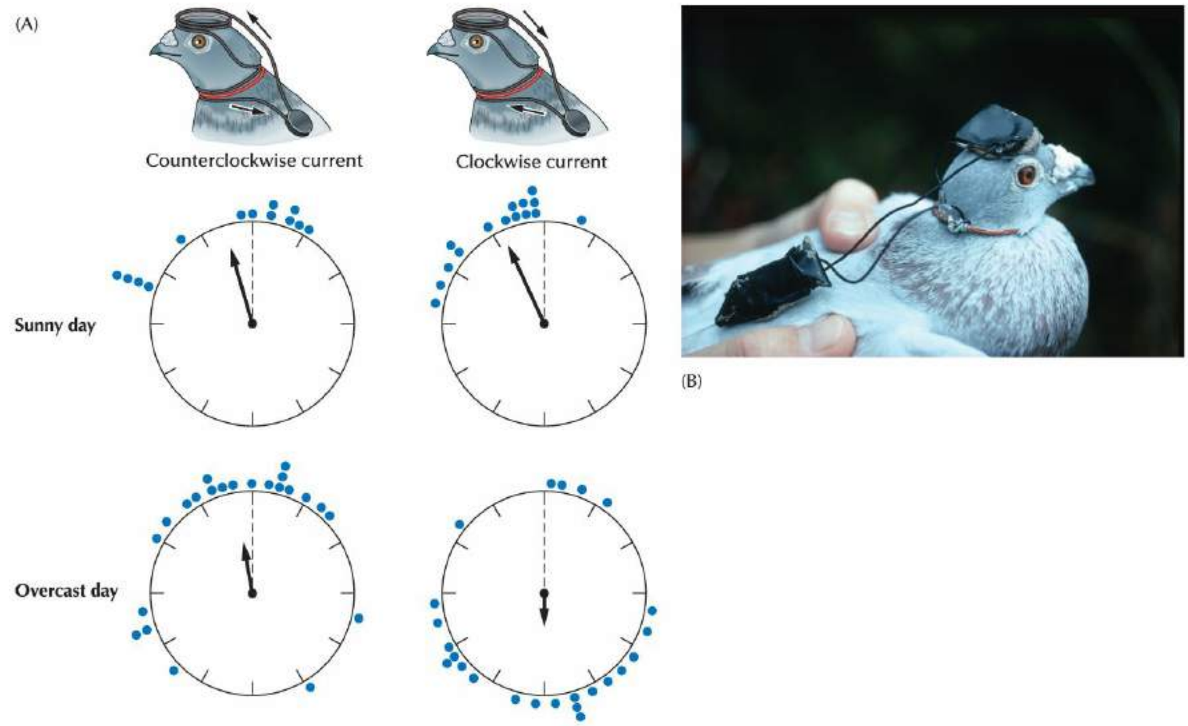
Ornithologists were slow to accept the hypothesis that birds might use the Earth’s magnetic field for orientation. An early report that magnets disrupted a pigeon’s homing ability (Yeagley 1947) was discredited, largely because the results could not be repeated. Then Frederick Merkel and Wolfgang Wiltschko (1965) showed that captive European Robins could orient in experimental solid steel cages without celestial cues.

Years later, William Keeton showed that free-flying homing pigeons wearing bar magnets often did not orient properly on cloudy days, whereas control pigeons wearing brass bars usually did (Figure 10–19). Failures to repeat Yeagley’s earlier experiments were due in part, Keeton revealed, to the use of the solar compass in preference to the magnetic compass on sunny days. Finally, in experiments that swayed the skeptical, Charles Walcott and Robert Green (1974) fitted homing pigeons with electric caps (containing Helmholtz coils) that produced a magnetic field through the birds’ heads. Under overcast skies, reversing the field’s direction by reversing the electric current caused free-flying pigeons to change their heading (Figure 10–20). The sensitivity of these systems to extremely weak magnetic fields is one reason why some early experiments succeeded and others did not. Natural fluctuations in the Earth’s magnetic field, such as those caused by sunspots and hills of iron ore, can disrupt the orientation of passerine birds migrating at night.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
DATA FROM KEETON 1974

Figure 10–19 A bar magnet interferes with a homing pigeon’s ability to return to its loft on overcast days. On sunny days, both pigeons wearing magnets and control pigeons wearing brass bars adopt accurate home bearings at unfamiliar release sites. On overcast days when they cannot orient by the sun (their preferred cue), the pigeons wearing magnets become disoriented. The control group, however, orients by means of the Earth’s magnetic information. Vectors (arrows) show mean direction and consistency of orientation among individual birds: long vectors show consistent orientation, and the short vector shows variable orientation. Dots represent bearings recorded for each pigeon tested. The dashed line represents the correct orientation.



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(A) Data from Keeton 1974, Walcott and Green 1974. (B) Dr. Charles Walcott, Cornell University.

Figure 10–20 (A) By attaching Helmholtz coils to the heads of homing pigeons, Charles Walcott and Robert Green generated artificial magnetic fields by allowing an electric current to flow through the coils. The reversal of electric current, which reversed the magnetic field, caused the pigeons to reverse their orientation direction on overcast days. Vectors are portrayed as in Figure 10–19. (B) A homing pigeon equipped with Helmholtz coils.

We now understand that many migrating bird species navigate by using the Earth’s magnetic fields. Bobolinks rely on their magnetic compasses to undertake extraordinary long-distance migrations annually from North America across the equator to wintering grounds in the pampas grasslands of Argentina and back. One nine-year-old female Bobolink flew the equivalent of 4.5 times around the Earth (at the equator) on this annual 20,000-kilometer round-trip (Martin and Gavin 1995).

How birds actually detect and “read” the Earth’s magnetic fields has been both mysterious and controversial. The discovery of magnetite (iron oxide) elements in the beaks of birds seemed at first to provide the answer (Winklhofer et al. 2001; Davila et al. 2003; Mora et al. 2004). Receptors in the ophthalmic branch of the trigeminal nerve were sensitive to very small changes in the intensity or topography of the Earth's magnetic fields. They seemed to help a bird determine its location relative to a goal. Sensory physiologists have also found specialized photopigments, or **cryptochromes,** in birds' retinas that were sensitive to magnetic direction, specifically to the "poleward" or "equatorward" angles of inclination of a magnetic field (Maeda et al. 2012).

It seemed, therefore, that Bobolinks and other birds used two sensory systems to navigate via a magnetic beak–eye dualism. They could process geomagnetic information by means of a map location system based on magnetite in the upper beak and trigeminal nerve and a direction-finding magnetic compass based on photopigments in the eye (Beason 2005). But the magnetite elements in the beak proved not to be part of this intriguing sensory system. They are instead mineral artifacts inside macrophages, or white blood cells that engulf foreign objects, especially iron compounds (Treiber et al. 2012). Conversely, the magnetoreceptor cells in the retina are key elements of avian biocompasses (Qin et al. 2016).

A bird's brain and body are more sensitive to magnetism than we once thought. Cells in the **hippocampus,** the part of the brain that controls spatial memory and orientation, are sensitive to magnetism, as are neurons in the brain stem of birds. The role of the inner ear, especially, is gaining prominence in studies of magnetoreception by birds (Wu and Dickman 2011; Winklhofer 2012). The lagena section of the inner ear contains magnetic iron compounds that are linked to directionally selected receptor cells. Removal of the lagena disrupts a pigeon’s homing ability.

Odors and Twilight Cues

Supplementing the principal features of a bird’s tool kit for navigation are cues as subtle as chemical odors in the prevailing winds, polarized light in the atmosphere, and sunset itself.

Navigation by smell once seemed improbable, but it is now clear that pigeons at least obtain information about their location from trace gases in the atmosphere (Wallraff 2004). Maps of compounds, such as volatile hydrocarbons, are reliable sources of information and are even resistant to disruption by wind, at least in urban environments. Early experience with local smells is important: a young pigeon does not orient well after fledging if its nest was screened from prevailing winds and the odors carried by them.

The sky at dawn and dusk also is full of directional information (Able and Able 1993). The direction of the setting sun establishes a primary direction (west). In addition, the rays of the setting sun include a band of strongly polarized light that runs (north–south) perpendicularly to the sun’s daily arc. Migratory songbirds may use both of these sources of information to define their departure directions after dark. Experiments with freely migrating birds show that they also recalibrate their magnetic compasses each evening by using the setting sun. William Cochran and his colleagues (2004) tricked Gray-cheeked and Swainson’s Thrushes by exposing them to false magnetic fields (80 degrees off to the east) at sunset, and then released them with radio transmitters. They flew in the wrong direction on the first night but recalibrated to the correct heading the following night after recalibrating their magnetic compass using celestial cues during the next, natural sunset.

Learning and Calibration

The navigational abilities of birds are partly innate and partly learned, with the result that inexperienced young migrant birds become lost more often than experienced adults. The rare visitors that excite birders, for example, are often lost immature birds (DeSante 1983).

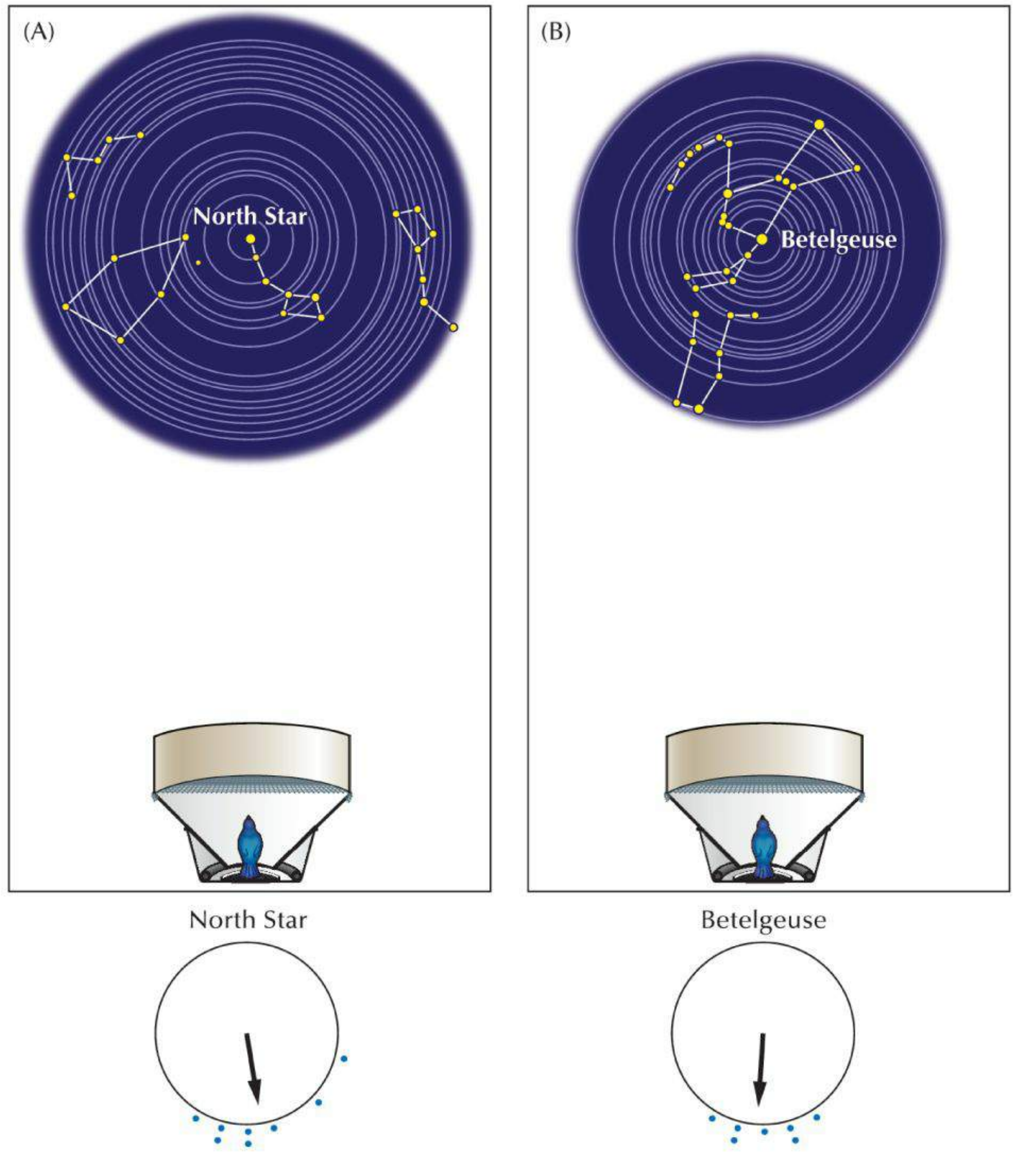
Global navigation is a direct extension of the natural homing abilities of birds. The process of learning how to navigate globally starts early with a young bird’s first explorations and, in some cases, adult leadership. Young cranes and geese undertake their first migrations with their parents in the lead. They learn the route and stopover locations from this experience. In an amazing chapter of the program to rebuild viable populations of the endangered Whooping Crane, William Lishman and his partner Joseph Duff taught young hand-reared cranes (without parents) to follow them in an ultralight plane, colored black and white like an adult crane. Step-by-step, they are establishing a new population that will migrate from central Wisconsin to Florida’s Gulf Coast and back each year.

Aside from visual cues, the magnetic compass serves as the initial and primary basis for orientation by some young birds (Box 10–4). A young pigeon’s ability to use magnetic-compass information develops first, before its ability to use a solar compass. On their first flight, young homing pigeons calibrate the general direction of their outbound journey based on magnetic-field information. Reversal of this direction on the return flight establishes the “home direction” that expands to full sensitivity to the polarity and declination lines of the Earth’s magnetic field. Proof of these steps comes from experiments that interfere with the exposure to natural magnetic fields. A young pigeon does not establish a home direction if it is transported in a distorted magnetic field from its nest on its first trip or if it is made to carry a magnet on its maiden flight.

BOX 10–4

Baby Buntings Learn the Night Sky

Baby Indigo Buntings, hand-reared without seeing the stars, cannot orient when they are first exposed to the night sky. In fact, they must see the sky regularly during the first month of life to be able to choose their migratory direction. The axis of rotation of the night sky, which centers on the North Star, establishes their north–south frame of reference (Emlen 1970; see illustration). They then learn the constellations associated with this axis. If the axis of rotation of a planetarium sky is switched from the North Star to Betelgeuse, the brightest star in the constellation Orion in the southern sky, the baby buntings orient south in line with the new axis of rotation.



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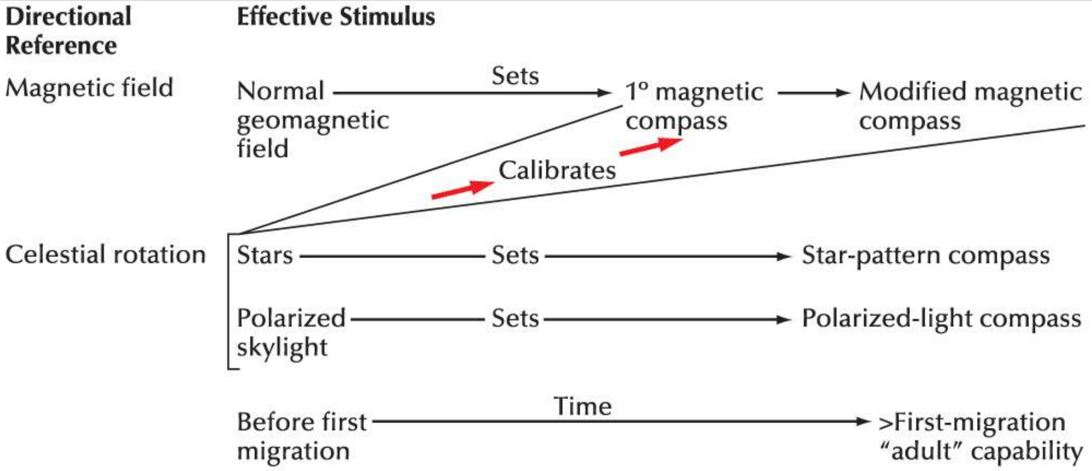
Data from Emlen 1975b

(A) Early visual experience of the natural night sky entrains an Indigo Bunting’s use of the stars for orientation. (B) Buntings raised under a modified night sky that rotated around Betelgeuse instead of the North Star adopted Betelgeuse as the pole star and consistently oriented from it. Each dot represents the direction selected by one young bunting. The vectors (arrows) show the general direction of orientation.

After a home direction has been established through route reversal and use of the magnetic compass, however, a young pigeon adds other clues to its navigation toolbox. The addition of learned compasses, such as the solar compass, then builds the bird's integrated orientation system. Exposure to the sun for less than one hour activates its solar compass. The young bird then calibrates it by reference to the magnetic compass. Refinements, including compensation for the sun's daily movement through the sky, follow with experience (Wiltschko et al. 1983).

The development of the navigation tool kit in migratory species, such as the Savannah Sparrow, follows a different sequence from that in pigeons (Able and Able 1996; Figure 10–21). Pigeons navigate locally, so they do not usually experience major changes in the angles (declination) of the magnetic field. Long-distance migrants encounter major changes in declination, extremely so for those species, such as Bobolinks, that cross the equator to winter in the Southern Hemisphere. In addition, they use celestial information, especially star configurations, as guidance systems. Rather than starting with a well-calibrated magnetic compass and adding other systems to it, as does the pigeon, Savannah Sparrows and other nocturnal migrants first establish their celestial compasses. The axis of rotation of the stars in the night sky has primacy, supplemented by twilight cues, such as polarized light. These cues are of primary importance for the initial calibration of their magnetic compasses. The sparrows, as well as some thrushes, also recalibrate and fine-tune their magnetic compasses regularly as adults at different locations in the course of the annual cycle.



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REPUBLISHED WITH PERMISSION OF THE COMPANY OF BIOLOGISTS, FROM ABLE, K.P., AND M.A. ABLE, "THE FLEXIBLE MIGRATORY ORIENTATION SYSTEM OF THE SAVANNAH SPARROW (PASSERCULUS SANDWICHENSIS.)" *THE JOURNAL OF EXPERIMENTAL BIOLOGY*, 1996, 199: 3–8, FIGURE 1. PERMISSION CONVEYED THROUGH COPYRIGHT CLEARANCE CENTER, INC.

Figure 10–21 Development of navigation systems in the Savannah Sparrow.

REVIEW KEY CONCEPTS

10.1 Migration

Billions of birds migrate every fall and spring to exploit seasonal feeding and nesting opportunities. The migratory habit, a genetic trait, may appear in newly established populations of nonmigratory species or, in contrast, may be lost by colonizing populations of migratory species. Trade-offs between the costs and the benefits of migration determine how far individual birds migrate. Wintering shorebirds, for example, distribute themselves widely in relation to the food availability in coastal wetlands, with apparently no extra cost to migrating long distances to achieve energy savings.

Key Terms: migration, flyways, fallouts

10.2 Connectivity

New tracking technologies connect seasonal bird populations and aid science-based conservation planning. Different migrants of many taxonomic groups and habits add to the complexity of the seasonal population networks. The sex and age classes of these fully migratory species travel different distances to separate wintering grounds. The migration routes of birds around the planet unite into a vast global network that can exchange viruses, such as bird flu and West Nile.

Key Term: differential migration

10.3 Fat, Fuel, and Flight Ranges

The flights of many long-distance migrants require extraordinary physical endurance. Nonstop three- to four-day journeys across the open ocean or desert regions are fueled by reserves of fat. Regular refueling stops are typical of most migrants. Shorebirds, for example, gather in vast numbers at critical en route staging areas. A worldwide network of Important Bird Areas identifies essential nesting, stopover, and wintering sites to be protected as critical habitat for migratory species.

Key Terms: stopover, Important Bird Areas (IBAs)

10.4 Evolution

Evolutionary changes of circannual rhythms adapt population-specific migration behaviors, including durations, compass directions, and distances. These migration behaviors have evolved and been lost repeatedly in different species, lineages, and populations of birds despite apparent complexities of the physiological and behavioral controls. Within a species, increasingly sedentary populations can competitively replace migratory populations (or vice versa) in a few generations.

10.5 Navigation

Birds use different sources of information to navigate while migrating, while commuting between nest sites and feeding grounds, and while flying home after having been displaced by curious ornithologists. They often prefer one source if it is available and use the others when necessary. In addition to using visual landmarks, such as landscapes and buildings, migrants use the sun by day and the stars by night. Birds also use olfactory cues and the Earth’s magnetic field. In addition, an innate magnetic compass serves as the platform for the development of advanced navigation abilities. Nocturnal migrants calibrate their magnetic compasses to local field conditions by using the axis of rotation of the night sky and bands of polarized light at sunset.

Key Terms: navigation, sun-arc hypothesis, geomagnetic fields, cryptochromes, hippocampus

APPLY YOUR KNOWLEDGE

1. Describe those factors that reduce and those that increase the nonstop flight ranges of birds during migration.
2. Contrast the importance of stopover points along a bird's migration route with the observation that birds minimize the number of these stopover refueling stations used during migration.
3. Describe the importance of photoperiod to the preparatory steps to migration.
4. What is Zugunruhe, and what evidence exists to support the statement that Zugunruhe is under endogenous, genetic control?
5. Describe the evidence that birds can use a sun compass navigation system.
6. Describe the evidence that birds can use a star compass navigation system.
7. Identify the various locations that first were considered the sites of geomagnetic field reception. How has this ability to "see" and navigate by Earth's geomagnetic fields been narrowed to cryptochromes in the eye?

8. Describe the navigational systems used during the flights of young birds by comparing geese, pigeons, and Savannah Sparrows.
9. Describe how twilight cues are used to recalibrate a bird’s navigational system during migration.
10. What factors contribute to the advantages and disadvantages of bird migration at night, during the day, or both day and night?

CHAPTER 11 *Social Behavior*

Chris & Monique Fallows/Nature Picture Library

Wandering Albatrosses nest in colonies on remote islands in the southern oceans. Elaborate displays reinforce their lifelong pair bonds.

> Social vertebrates, and particularly birds, are excellent subjects for generating and testing

> Darwinian hypotheses about living with relatives. [EMLEN 1995, P. 8098]

Birds are both predators and prey. Their needs for food and for protection—the most pressing requirements of any living creature—determine where and how they live. These needs also determine whether they are social or asocial, cooperative or competitive. Sometimes, an individual bird should go it alone; at other times, there is safety in numbers. Ultimately, birds must share limited space.

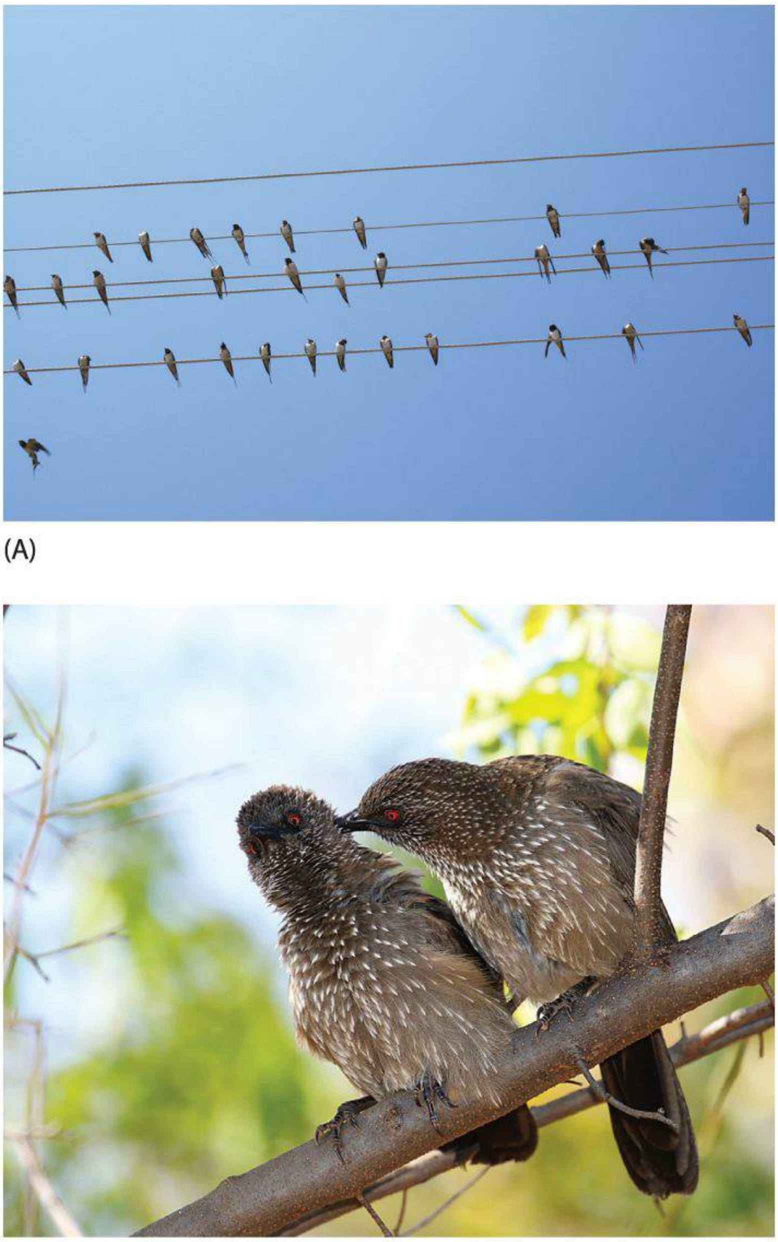
Birds establish and protect their spatial relations; aggressive assertions of status or rights to resources are normal parts of avian social life. Social behaviors of individual birds—territoriality, flocking, and dominance displacements—vary flexibly in relation to the mix of costs and benefits. Territorial birds, in particular, assert personal control over food supplies and mates but rarely achieve exclusive rights. Private spaces aside, birds often opt to be near their competitors in social clusters of territories.

When two birds interact, each has selfish purposes that can foster either hostility or cooperation. Birds can manipulate one another to personal or sometimes mutual benefit. Inherent in all social interactions governed by rules is the threat of cheating by those that would take advantage of the existing system. For many years, students of bird behavior have tended to assume the morality of truthfulness in their interpretations. But avian social communication may not be as straightforward and honest as once supposed. Individual birds serve their own interests in many ways. The social exchange of information, public and private, between rivals and partners as well as between species invites our attention as a unifying concept in ecology and evolution.

This chapter provides an overview of the major features of the social behavior of birds, including the costs and benefits of territoriality, social rank, conspecific attraction, flocking, and coloniality. The first three chapters of Part 4 explore the sexual behaviors and mating strategies of birds. Their sexual relations often do not match their overt social relations.

11.1 Individual Space

Spacing patterns depend on the scale of one’s perspective. When birds fly in flocks, the distances between individual birds within a flock may be small, but the distances between flocks may be large. That said, most birds maintain a small individual space around themselves wherever they go. Swallows, for example, space themselves at regular intervals on a telephone wire (Figure 11–1A). Sparrows and sandpipers feeding in large flocks also maintain small distances between one another; their individual spaces reduce hostile interactions. Individuals of highly social species overcome the individual distances to preen each other, called **allopreening** (Figure 11–1B), or huddle together, sometimes in large groups, to stay warm while roosting overnight (see section 6.5).


(A)

(B)

(A) Bukethun/Shutterstock. (B) Hennie Briedenhann/Shutterstock

Figure 11–1 Birds typically maintain individual space between each other. (A) For example, American Cliff Swallows space themselves at regular intervals on a telephone wire. (B) Some, like this pair of Arrow-marked Babblers, will overcome this separation in order to allopreen or groom each other.

The tendency of individual birds to space themselves promotes uniform dispersion patterns. If birds landed on a field at random, some sites in the field would remain empty and others would receive several birds in succession, resulting in random patterns of association. Individual birds close to one another would move apart and fill the unoccupied spaces. Such regular, or uniform, dispersion patterns are typical of birds that occupy uniform habitats. Killdeers residing in large fields, Sanderlings feeding on the beach, American Robins nesting in suburbia, and American Kestrels wintering along roadsides space themselves in a regular manner. Conspecific attraction, the opposite social force, clusters birds nonrandomly. Thus, Solitary Eagles live in pairs on exclusive expanses of tropical forest in the mountains of South America. At the other extreme, hundreds of Sociable Weavers occupy gigantic communal nests in the Kalahari Desert in southern Africa.

11.2 Territorial Behavior

Territorial behavior is a primary form of aggressive spacing behavior that has intrigued naturalists since Aristotle. H. E. Howard's *Territory in Bird Life* (1920) formally introduced scientific inquiry into the subject. We now understand that **territorial behavior** includes diverse patterns of aggressive behavior with multiple, often overlapping functions. Not easily categorized, territorial behaviors weave together with complex social interactions that change fluidly and adaptively in space and in time.

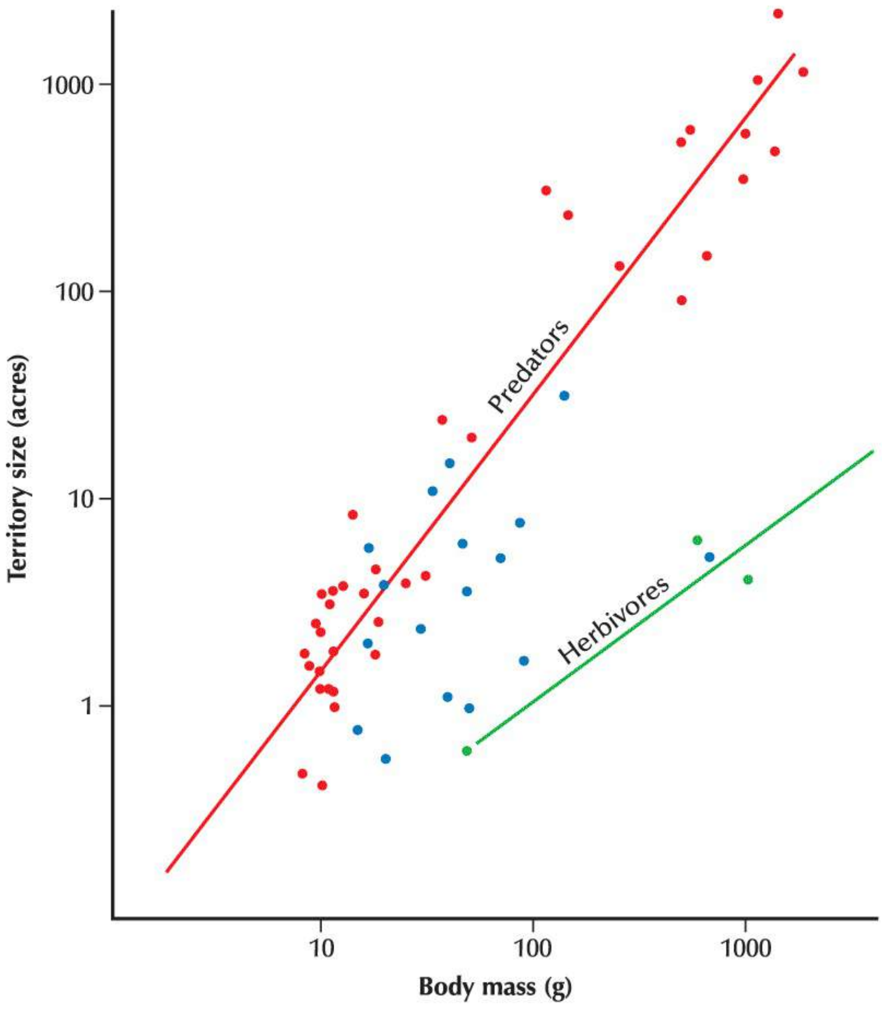
The simplest territories are those with only one type of resource, such as the food territories of hummingbirds and sunbirds in fields of flowers or those of sandpipers on a beach at low tide. At the other extreme are the all-purpose nesting territories of land birds, which serve for display, courtship, paternity, nest seclusion, and feeding. All-purpose territories enable individual birds to reserve essential resources, to reduce predation, and to reduce sexual interference by neighbors.

Birds broadcast their presence and intended control of a territory with loud vocalizations (see Chapter 8) or with nonvocal communication sounds, such as the familiar tree drumming or rapping by woodpeckers. Both males and females may display and defend, sometimes together. Territory residents chase trespassers until they leave, resorting to physical contact as needed. Sometimes these contests for the control of a territory last for hours. Beneath the conspicuous surface of territorial control and ownership exists an inconspicuous underground of subordinate individual birds that will surface and take charge when the owner is absent or dies (section 18.3).

In suitable habitats, territories are usually contiguous areas separated by well-defined though invisible boundaries. Blurring the distinction between territorial spacing and coloniality are intermediate dispersions that reflect the many advantages of social information, mating options, and predator detection that favor clustering of conspecific territories. At one extreme, the dense nest territories of colony-nesting Royal Terns actually pack into a hexagonal configuration resembling the cells in a bee's honeycomb (Buckley and Buckley 1977).

Conspecific attraction is emerging as a major theme in avian behavior and ecology at many levels of sociality. Attraction to conspecifics or even competitors simplifies and speeds up the process of finding and claiming a territory in prime habitat. In one example, playback experiments demonstrated that Black-throated Blue Warblers assess future options by listening to the postbreeding songs of established males (Betts et al. 2008). Public social clues trump vegetation structure in the selection of breeding sites. Different species may also cluster their territories. Philadelphia Vireos and Red-eyed Vireos, for example, defend their territories against each other in prime habitats, facilitated by the smaller Philadelphia's mimicry of the Red-eye's vocalizations (Rice 1978).

The territorial defense of food resources is flexible and dynamic, corresponding to the balance between its costs and its benefits. For nectar-feeding birds, the economics of territorial defense can be measured in terms of the calories invested into defense and the extra calories gained by feeding at protected flowers with more nectar (Box 11–1). Across species, territory size increases directly in relation to body size, energy requirements, and food habits (Figure 11–2). This observation suggests a general importance of food resources to the territorial individual bird. Variations within species are even more revealing. Pomarine Jaegers, for example, defend small breeding territories when lemmings, their principal food, are abundant and defend large territories when lemmings are scarce (Wiley and Lee 2000).



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DATA FROM SCHOENER 1968

Figure 11–2 Territories or home ranges of birds increase directly in relation to body size, energy requirements, and selection of food types. The correlation suggests that territory size is geared to the food and energy requirements of the bird. Predators (red circles) have higher daily energy requirements than do herbivores (green circles), which have correspondingly smaller territories. Blue circles indicate species with mixed diets.

Box 11–1

Territory Defense by Sunbirds Depends on Economics

The costs and benefits of the feeding territories of nectar-feeding birds are unusually straightforward and easily defined. Hummingbirds and their African counterparts, the sunbirds, defend clumps of flowers for several days to several weeks or longer. Golden-winged Sunbirds in Kenya, for example, defend about 1,600 mint flowers, which produce enough nectar each day to satisfy an individual sunbird's energy requirements. Territorial sunbirds benefit by having an assured, adequate food supply. They defend these territories when the energetic benefits exceed the energetic costs of defense (Gill and Wolf 1975, 1979).

A territorial sunbird invests energy at a rate of approximately 12.5 kilojoules per hour chasing intruders. It recovers this investment and more by feeding at nectar-rich flowers on its territory, this feeding time being less than that required at nectar-poor, undefended flowers visited frequently by other sunbirds. Raising the average nectar volume from one to two microliters per flower cuts feeding time in half. The territorial sunbird, therefore, can spend more time sitting than can a nonterritorial sunbird and save energy. In this example, a defense investment of 20 minutes costing 3.7 kilojoules reduces the sunbird's total costs from 32 kilojoules per day to 26 kilojoules per day, a net savings of six kilojoules (Table 11–1). When the projected savings are less than the investment, sunbirds do not defend a feeding territory.

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Golden-winged Sunbird, a species that often defends territories of nectar-rich flowers.

Table 11–1 *Energy Costs of Feeding on Undefended and Defended Flowers for the Golden-Winged Sunbird*

	Undefended Flowers (1 ml Nectar/Flower)			Defended Flowers (2 ml Nectar/Flower)		
Activity	**Time Spent (h)**	**Energy Rate (kJ/h)**	**Energy Spent (kJ)**	**Time Spent (h)**	**Energy Rate (kJ/h)**	**Energy Spent (kJ)**
Foraging	8	4.0	32.0	4	4.0	16.0
Sitting	—	—	—	3.7	1.7	6.3

Defense	—	—	—	0.3	12.5	3.7
Total energy spent			32.0			26.0

Note: Energy saved by feeding on defended flowers: 6.0 kilojoules.

Source: Data from Gill and Wolf (1975).

Birds assert themselves more effectively when they are on familiar ground or on home territories than when they are strangers in a new place. The ability of territorial male Steller’s Jays to win fights, for example, decreases with distance from their nesting areas rather than ceasing abruptly at a territorial boundary (Brown 1975). Territory owners usually win encounters with intruders. For one thing, the owner can use familiar details of the territory to its own advantage during high-speed attacks and chases.

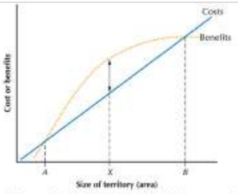
Because territorial owners have an investment to protect, they do not usually give up a fight as easily as a newcomer. Acorn Woodpeckers, for example, vigorously defend their tree granaries against squirrels, jays, and other Acorn Woodpeckers. The granaries hold valuable stores of winter food. In addition, each of the many holes (as many as 11,000 per tree) represents an investment of 30 to 60 minutes of drilling time. Consequently, these woodpeckers defend trees that are riddled with empty holes as well as those with holes that contain acorns (Figure 11–3).

Territorial defense incurs costs as well as benefits (Figure 11–4). Conspicuous display can attract predators. The time and energy

STEVE & DAVE MASLOWSKI/SCIENCE SOURCE

Figure 11–3 The granaries of Acorn Woodpeckers are valuable, defensible resources that contain essential supplies of acorns for the winter.

required to display, to patrol territorial boundaries, and to chase intruders can be a major investment. Territoriality is favored when the resulting benefits outweigh the incurred costs. The central requirement is that adequate resources must be economically defensible (Brown 1964). Two features of resource distribution—temporal variability and spatial variability—determine whether territories are economically defensible. Resources that change rapidly in time invite opportunistic use, not site-specific investment or long-term commitment. Aerial insects whose locations and densities shift frequently, for example, are usually not defensible food resources. Territorial hummingbirds will sit side by side in a bush while they catch passing insects but will chase each other out if one or the other attempts to take nectar from the wrong flower.



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Data from Davies 1978

Figure 11–4 Territories of intermediate sizes (*A* to *B*) are economically defensible because the benefits exceed the costs. The costs of defense increase as territory size increases. The benefits relative to need (orange line) increase rapidly at first but then reach a maximum value when needs are filled, as would be the case when food is in excess. Optimum territory size is at *X*, where the net benefit is greatest.

Sites rich in resources may also be indefensible because they attract hordes of competitors. No gull would attempt to maintain a feeding territory on a garbage dump where thousands of other gulls vie for the same scraps. Similarly, Sanderlings do not defend their feeding territories on California beaches, when prey is either abundant or scarce (Myers et al. 1979; Figure 11–5). Beach space with dense concentrations of prey (isopods) is not defensible because no single Sanderling can keep the hordes of other Sanderlings away. Low prey densities also are not worth defending. Sanderlings, however, vigorously defend beach territories at intermediate prey concentrations. The size of the territories they defend is then related to the required defense effort; increased competition forces smaller territories.

© Doug Wechsler/VIREO

Figure 11–5 Sanderlings may defend exclusive feeding territories or feed in large flocks. Territorial Sanderlings return each winter to defend their sections of a beach.

Birds typically defend territories against others of the same species. Sometimes, they also expel other species. Territorial hummingbirds defend their territories against a variety of nectar-feeding birds. Wintering Northern Mockingbirds defend berry-rich feeding territories against other species, especially those that would eat the berries. Conversely, different species that consort in mixed feeding flocks defend the same territories or home ranges.

Territories may be occupied and defended by a single bird, a mated or cooperating pair of birds, an extended family, or even a group of unrelated individual birds. Small groups of wintering tits and chickadees, for example, defend woodlot territories containing both food and roosting holes. Groups of unrelated Black-capped Chickadees establish common winter territories by late summer (Smith 1991). Group membership, which includes male and female pairs of both resident adults and newly settled first-year birds, is stable throughout the winter. In addition to the protection of food stores for the winter, spring territorial breeding opportunities emerge from the communal winter effort. Group defense of prime territories is also typical of a wide variety of tropical bird species that breed cooperatively.

11.3 Social Rank

Social conflict is a normal part of the daily lives of birds, causing increased concentrations of stress (glucocorticoid) hormones, among other costs (see section 9.3). Dominance and the aggressive reinforcement of social status reduce this conflict. Individual birds that prevail in aggressive encounters become dominant; losers become subordinate. As social ranks are established in new groups of birds, losers cease challenging dominant birds with the result that stable dominance relations lower the frequency and intensity of overt hostility.

Dominant birds use threat displays to assert their status and reserve their access to mates, space, and food. They move without hesitation to a feeder or desirable perch, supplanting subordinates and pecking those that do not yield at their approach. Subordinates are tentative in their actions and frequently adopt submissive display postures. Age, sex, physiology, genetics, and possibly parasite load all affect dominance.

Rank has its privileges, advantages, and, potentially, some costs. High-ranking birds obtain options for access to food, reduced risk of predation, and longer residency; low-ranking birds have less access to good feeding sites and are usually the first to leave. The feeding behavior of White-throated Sparrows in winter, for example, is affected both by their dominance status and by the distance of food from protective cover (Schneider 1984). Dominant birds feed more often near shelter than do subordinates, sacrificing their foraging efficiency but reducing their exposure to predators. Dominant members of species such as the Carolina Chickadee and the Tufted Titmouse stay leaner than subordinate members throughout the winter (Pravosudov et al. 1999). They add just enough fat at dusk to get through the cold night. Subordinate birds carry more fat all day long. The difference between them is that dominant birds can eat when they want, whereas subordinates face a less certain feeding schedule.

Experiments with captive flocks of Blue Tits demonstrated that dominant members were more cautious during periods of danger than were subordinate members. Robert Hegner (1985) flew a model Eurasian Sparrowhawk over his aviary and watched to see which tits were the first to emerge from their hiding places to feed. Low-ranked birds fed first, followed by high-ranked birds. Hegner suggested that high-ranked birds can afford to be cautious because they have the ability to control food sources and thus to ensure adequate foraging, whereas low-ranked birds must take more chances to get to food ahead of their dominant flock mates.

Social status may have a major influence on stress loads and the ability of individual birds to maintain physiological balance, or **homeostasis** (Goymann and Wingfield 2004; see Chapter 6). Deflections from optimal balance cause the release of corticosteroids, stress hormones that enhance performance in the short run but are detrimental if kept at high levels. If an individual bird must fight others to become dominant and to maintain this status, its stress-hormone levels tend to be high. If, on the other hand, dominance status is inherited or due to logical succession, the hormonal costs of being dominant are minor.

Stable group membership facilitates the development of a dominance hierarchy. Most dominance hierarchies in stable bird groups and flocks are linear—or “peck right”—hierarchies, in which each bird clearly ranks above or below a set of others. Social status is directly related to age and sex. Generally, large birds dominate small ones, males dominate females (except during the breeding season), and old birds dominate young ones. Within that framework, social rank increases gradually in relation to time, individual tenure, and changes in group composition.

Generally, birds can distinguish among members of their own species by means of variations in plumage patterns, size, voice, and behavior. The extent of yellow on the bills of Tundra Swans and the variable, harlequin color patterns on the heads of Ruddy Turnstones provide a simple basis for individual recognition (Figure 11–6). Field ornithologists can learn to recognize some individual birds by such differences and more subtle ones—the extent of plumage wear or a missing feather in combination with eye colors or plumage colors typical of certain age and sex classes. Budgerigar parakeets can learn to discriminate among individual members of their own species in photographs (Trillmich 1976).


(A) (B)

(A) © Doug Wechsler/VIREO. (B) Graham Ella/Alamy

Figure 11–6 The harlequin face and neck patterns of Ruddy Turnstones vary among individuals and make them recognizable to each other.

The varied plumage colors of Harris's Sparrows serve as badges of their social status (Rohwer 1982; Figure 11–7). Top-ranked, dominant birds have conspicuous, contrasting black, eumelanin markings on the plumage of the head and neck; low-ranked, subordinate birds have few such markings. Many birds are intermediate in appearance. Such variations facilitate individual recognition among the members of the large flocks that these sparrows typically form during winter.


(A) (B)

(A) Brian E. Kushner/Shutterstock. (B) © R. Crossley/VIREO

Figure 11–7 The White-throated Sparrow has two head color forms that pair assortatively and have different social roles. Both sexes include a striking white-striped morph (A) and a duller tan-striped morph (B), which are controlled genetically by an inversion on the second (autosomal) chromosome.

The evolution of the badge colors ties to the advantages of being dominant versus the advantages of being subordinate. Dominant birds assert the prerogatives of their rank, including access to food. Conversely, subordinates of plain appearance benefit from flock membership, which they can maintain because they do not threaten the dominant birds having visual badges of high status. When dyed with black to look like a dominant bird, subordinates suffer more frequent attacks but do not rise in status because they are not inherently aggressive.

The iconic White-throated Sparrow of northern forests has two head color forms with different social roles (see Figure 11–7). Mated pairs include one of each. White-striped males are more aggressive and inclined to extra-pair copulations than tan-striped ones, which in turn invest more time into mate guarding and parental care. Females of both morphs behave similarly to their male counterparts but with different intensities. See Falls and Kopachena (2010) for details of the genetic, neural, and endocrine control of life-history characteristics of this species of the boreal forests.

Even in the absence of social color badges, birds can infer their social rank relative to others by watching who is dominant to whom. Pinyon Jays of the southwestern United States form large flocks with a clear dominance hierarchy. They monitor interactions among other individual birds and decide their appropriate social rank without direct testing (Paz-y-Mino et al. 2004). Simply summarized, Jay X reasons that, if a new bird, called Jay Y, is dominant to Jay Z, known to be a dominant bird, then Jay X will respect Jay Y's dominance also.

Threat displays, which emphasize the bill and wings as weapons, herald a real attack if the matter is not quickly resolved. Appeasement or submission displays signal the opposite intent, a willingness to yield on the matter, a signal that defuses the conflict and thereby protects the yielding bird from direct attack (Figure 11–8). Graded or variable displays convey information about the intensity of motivation and the probability of a sender's subsequent actions. The high-crest positions assumed by a defensive Steller's Jay indicate that it will probably attack rather than flee its opponent (Figure 11–9). Often, the submissive bird turns its head and bill away from a threatening rival, a movement that reduces the level of provocation and prevents a physical attack. An appeasing avocet, for example, hides its long bill beneath its back feathers and adopts a sleeping posture. Other species fluff their feathers, in contrast with the sleeked postures associated with threat displays.

(A) Branislav Cerven/Shutterstock. (B) Golfandy/Alamy

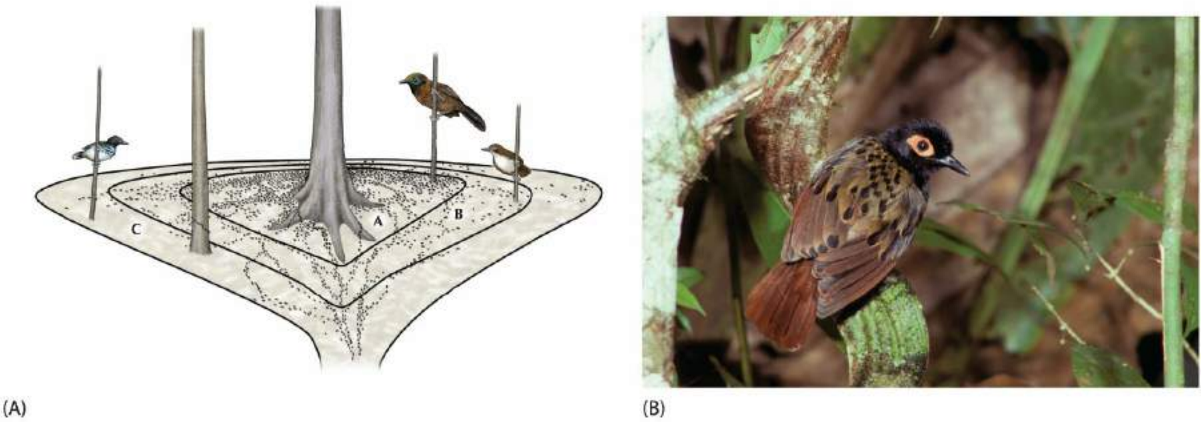
Figure 11–8 Threat display of a Great Tit (A) and submissive posture of a Blue Tit (B).

(A) Art Directors & TRIP/Alamy. (B) © D. & M. Zimmerman/VIREO

Figure 11–9 The positions of the crest of a Steller’s Jay signal the likelihood of (A) attack (high crest) or (B) retreat (low crest).

11.4 Interspecific Aggression, Dominance, and Mimicry

Different species also interact aggressively and show dominance behavior. Usually larger species dominate smaller species. Dominance hierarchies influence ecological roles in mixed-species foraging flocks and visits to bird feeders. Not just a short-term phenomenon, interspecific dominance behavior impacts the ability of unrelated species to coexist. For example, interspecific dominance is a conspicuous behavioral feature of birds that follow raiding parties of army ants in tropical rain forests (Willis and Oniki 1978; Willson 2004; Figure 11–10). Army ant swarms flush large numbers of insects and small reptiles that are usually camouflaged and hard to find. More than 50 species of Neotropical birds are “professional” ant followers; that is, they obtain more than half of their food by foraging in the vicinity of army ant swarms. Frequent flights among attendants, including displacements from prime perches, reinforce a size-dependent dominance hierarchy. Large dominant species, such as the Black-spotted Bare-eye, control the prime zone of the moving ant swarms where prey are most likely to be flushed by the dense, leading columns of ants. Medium-sized and smaller antbird species, such as the Hairy-crested Antbird and White-throated Antbird, are chased from this zone, taking up stations in peripheral, less productive foraging zones. They move toward the center when opportunity arises. Their size differences also allow them to use different perches for specialized access to the ant swarm.



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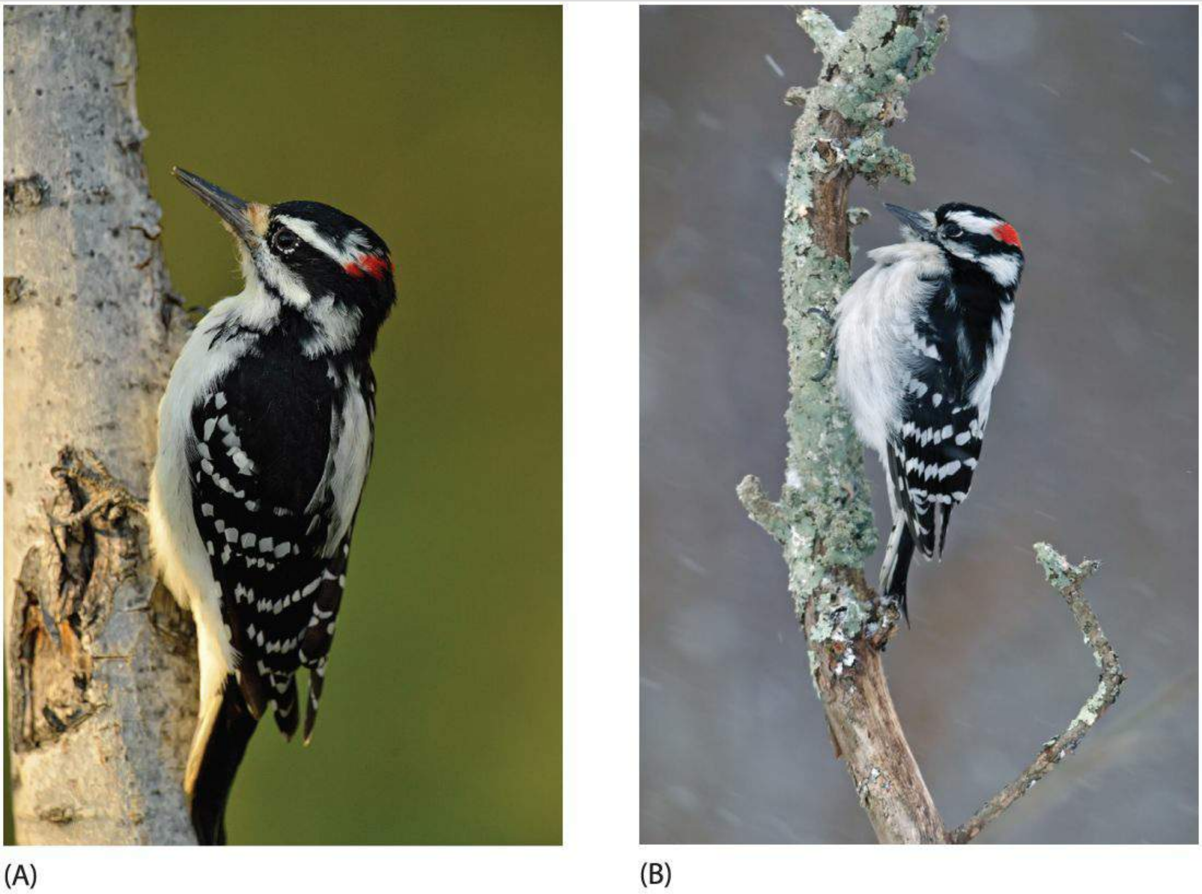
(A) Data from Willis and Oniki 1978. (B) © Doug Wechsler/VIREO

Figure 11–10 The hierarchy of interspecific dominance among birds that follow army ants. (A) Large, dominant species, such as the Ocellated Antbird, control central sites (zone A), where foraging for flushed insects is best; they displace smaller species to outer zones—for example, Bicolored Antbirds to zone B. In turn, the Bicolored Antbirds displace Spotted Antbirds to zone C. Sometimes, a subordinate species can infiltrate the central zone, but only such zone C antbirds as the White-plumed Antbird do this regularly. (B) The Black-spotted Bare-eye dominates control of the prime zone of moving ant swarms in the Amazon rain forests.

Mimicry, or evolutionary convergence in appearance, improves the competitive ability of subordinate species to access resources controlled by dominant species. Convergence of plumage color patterns by unrelated species has long been known. Now it appears that subordinate species may mimic the plumage color patterns of coexisting, unrelated, aggressive dominant species to avoid aggression from the dominant species (Prum 2014). The larger Hairy Woodpecker and smaller, unrelated Downy Woodpecker, for example, are hard to tell apart where their ranges overlap (Figure 11–11). Using these two species as subjects of game theory models, Prum and Samuelson (2012) show how the costs and benefits of convergence in appearance can theoretically evolve to a stable equilibrium including mimicry. Many dozens of similar, coexisting species, including the *Ramphastos* toucans of South America, are candidates for the study of Interspecific Social Dominance Mimicry (ISDM).



(A) Don Johnston/Getty Images. (B) James Zipp/Getty Images

Figure 11–11 The similar but distantly related Hairy Woodpecker (A) and Downy Woodpecker (B) have converged in appearance, and are featured subjects in theoretical models of the evolution of interspecific social dominance mimicry.

Naturalists have long suspected that interspecific mimicry was responsible for the similarities between Old World orioles (Family Oriolidae) and friarbirds (Family Meliphagidae) that coexist on islands in the western Pacific (Wallace 1869; Diamond 1982; Jønsson et al.

2016; Figure 11–12). Orioles compete intensely with the larger, dominant friarbirds for access to ripe fruiting trees. Orioles elsewhere tend to be boldly colored yellow and black. But on the western Pacific islands, they closely match the brown colors of the friarbird species on the same island. Molecular studies of the phylogenetic relationships and evolution of these island species pairs support the ISDM hypothesis. Friarbirds (the model) dispersed to and speciated among the islands before the brown orioles (the mimics) got there. Mimicry by later-arriving orioles facilitated their persistence in the presence of aggressive dominants. Longer histories of co-occurrence and increased differences in size improved the mimicry itself, facilitating stable residency of both orioles and friarbirds on the islands of Wallacea.


(A)

(B)

(A) © Ron Hoff. (B) © Michael K. Poulsen

Figure 11–12 The smaller Black-eared Oriole (A) is a visual and vocal mimic of the larger Black-faced Friarbird (B) on the Moluccan island of Buru.

11.5 Flocks

The large flocks of wintering waterfowl, of migrating shorebirds, and even of roosting blackbirds are spectacles of nature. **Flocks** range in composition from loose, temporary aggregations to organized foraging associations of diverse species. At one extreme are the millions of blackbirds in the United States or the Bramblings in Europe that converge each evening at traditional roost sites. Temporary feeding aggregations of herons and seabirds also are open gatherings of individual birds responding opportunistically to special situations. Multispecies flocks of tropical birds are closed social systems, similar in many ways to much smaller family units. The members of these flocks feed together as a group throughout the year, and they actively exclude new members.

Like territoriality, flock formation is a flexible behavior that includes trade-offs between its benefits and its costs. On the positive side of the ledger, flocking behavior enables cooperative foraging and reduces the risk of predation. Members of a flock are attentive and sensitive to what their flock mates are doing and adjust their own behavior accordingly. A wealth of information is available from one's neighbors. Which ones find food and where? High on the list of costs are increased competition for limited food supplies, increased risk of disease, and increased aggression to maintain individual distances.

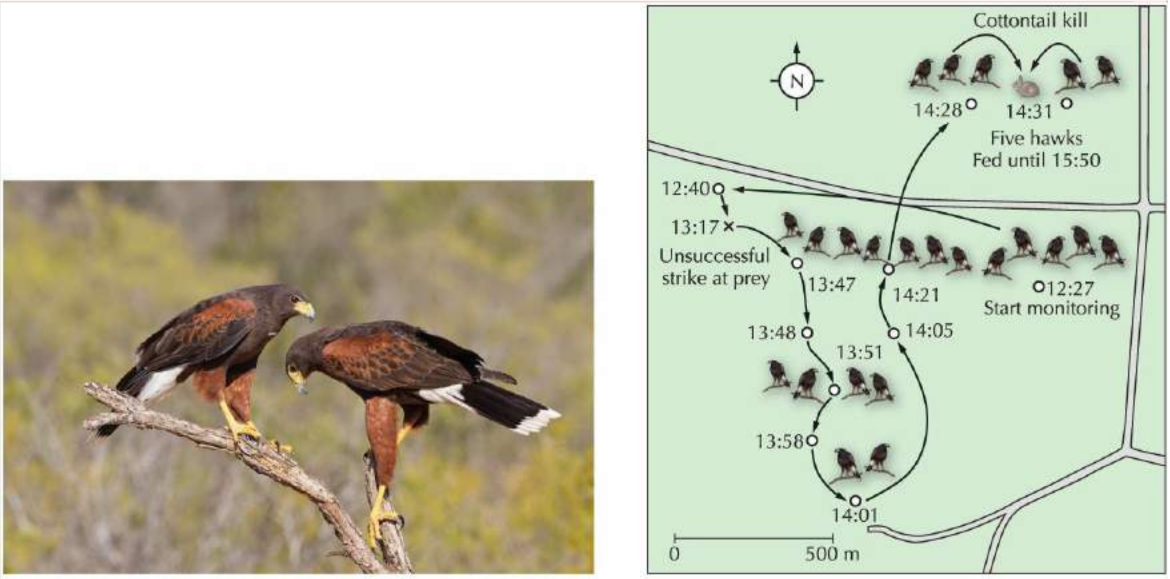
Feeding in Flocks

Casual aggregations of individual birds at rich feeding grounds are fortuitous, but why do unrelated birds form stable foraging partnerships? Some of the advantages are straightforward, practical ones, including cooperative feeding. At one level, flock members may simply benefit from the "beater effect"; prey that is flushed (and missed) by one bird can be grabbed by another. Ground hornbills in Africa, for example, walk in a line across fields to catch insects flushed by one another. Drongos and flycatchers participate in mixed foraging flocks and specialize in prey flushed by others. At a more advanced level, flocks of pelicans deliberately encircle and trap schools of fish in shallow water. At a still more advanced level, predators, from ravens to hawks, hunt cooperatively (Box 11–2).

Box 11–2

Harris's Hawks Hunt in Teams

Family hunting parties of two to six Harris's Hawks cooperate to catch rabbits (Bednarz 1988; see illustration). The hunting party assembles at dawn and then splits into small subgroups that search for prey by moving in a coordinated "leapfrog" fashion through the desert scrub. They then converge on a rabbit that is spotted and kill it with successive, relay strikes by different hawks. When a rabbit hides in thick cover, the group surrounds the area and waits for one or two of its members to deliberately flush the rabbit into the open. All members of the party then feed on the kill. Team hunting improves the probability of catching a rabbit and raises the average amount of energy available to each hawk relative to that available when hunting alone. Team hunting also enables these hawks to kill larger prey than they could by hunting alone. Before this study was undertaken, cooperative hunting and sharing of prey had been documented only for large social mammals, such as lions.



(A)

(B)

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(A) Roberta Olenick/Getty Images. (B) Data from Bednarz 1988

(A) Harris's Hawks, highly social raptors that employ cooperative hunting strategies. (B) Sequence of movements of Harris's Hawks that culminated in the capture of a rabbit. Although all five hawks in the group remained in view, Jim Bednarz and his assistants specifically monitored a subunit that included hawk number 995, which wore a radio. Perched hawks in this illustration indicate the number of hawks that joined the subunit at each location. Subunit size remained unchanged from the preceding location if no hawks are pictured.

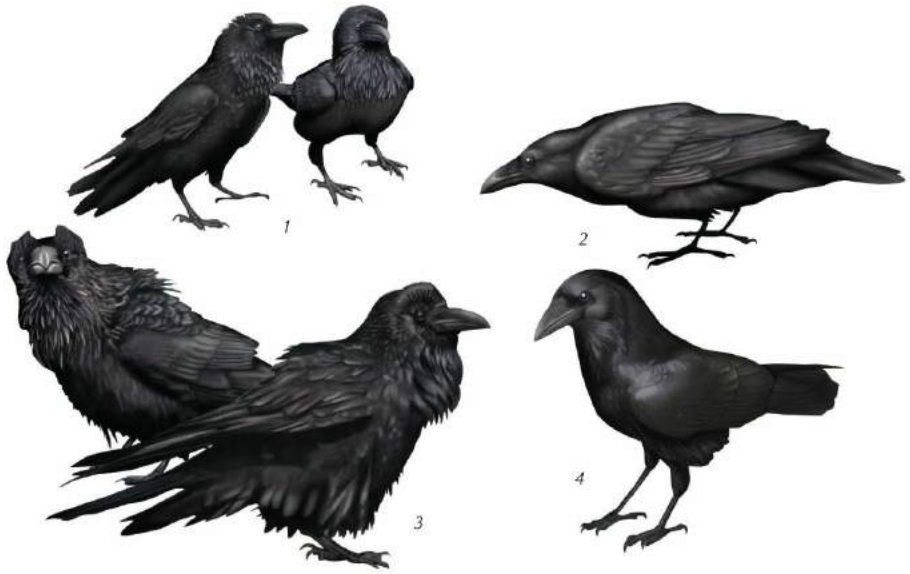
The advantages of social foraging fall into two main categories: information sharing and producer-scrounger (Giraldeau and Caraco 2000). Sharing successes in finding food defines information-sharing models. All birds in the flock search for food, and then they benefit from a discovery by one of them, as do subadult ravens. This behavior is common among social animals of all kinds (Giraldeau and Beauchamp 1999). Group foraging by pigeons and titmice helps them find food because members can join successful individual birds at rich clumps or concentrate their search efforts nearby (Krebs 1973). Groups of four titmice in captivity found more hidden food together than alone.

They watched one another's successes and modified the intensity and direction of their searches accordingly.

Information sharing, however, leads to selfish behaviors and cheating. Dominant birds can usurp the sites discovered by subordinate members of the flock or pilfer hidden food. Some birds may not look for food themselves but rely on others to find it. The exploitation of actively searching birds defines **producer-scrounger models.** Some birds (scroungers) don't look for new food patches themselves but instead wait for others (producers) to find food and then eat some of it. Competition increases at small food patches and with the number of scroungers trying to take advantage of the discovery. Flocks of Scaly-breasted Munias typically include both producers and scroungers. Producer munias have definite strategies that match predictions (Beauchamp and Giraldeau 1997). They abandon discovered food more frequently once scroungers arrive when it is easy to discover another patch of food. They also move on predictably when more scroungers are present or when the patch of food is small.

Large numbers of some bird species congregate for the night in communal roosts, especially during the nonbreeding seasons. In addition to benefits such as reduced predation, increased foraging efficiency, and reduced energy expenditures for thermoregulation (Beauchamp 1999), communal roosts serve as social information centers. For example, Northern Ravens follow their roost mates to find food on the day after discovery of a carcass discovery (Marzluff et al. 1996; Marzluff and Heinrich 2001). Naïve ravens released experimentally into a roost followed roost mates to their feeding sites the next morning. Conversely, three of 20 ravens released at a carcass led roost mates to it the next day. The same individual birds switched leader and follower roles, depending on their knowledge of where food was. Such information exchange increases foraging efficiency and leads to more intricate social interactions, including dominance relations and mate choice, in the complex societies of these intelligent birds.

Northern Ravens depend on carcasses of moose or other large animals to survive the winter. Resident adults usurp and defend these valuable finds for themselves (Heinrich and Marzluff 1995; Figure 11–13). They can defend a carcass successfully against up to nine subadult ravens. So young ravens must outmaneuver or overwhelm dominant or territorial adults to gain access to defended food sources. To do this, a wandering subadult actively recruits other subadults. It does so by using a loud vocalization, called the "yell," and by leading others from communal roosts to the food, described above. Typically, the subadult circles a newfound carcass but does not feed. It flies off and returns the next day with a "gang" of 40 other young ravens that proceed to overwhelm the adult defenses. In the course of a week, the gang grows to 100 or more ravens drawn to the noise or to their well-fed roost mates. What appears to be altruistic behavior—sharing limited food resources with unrelated ravens—is really in a young raven's self-interest. It gets access to the carcass that it spotted and participates in a wide-ranging, all-winter network of carcass discovery and social availability.



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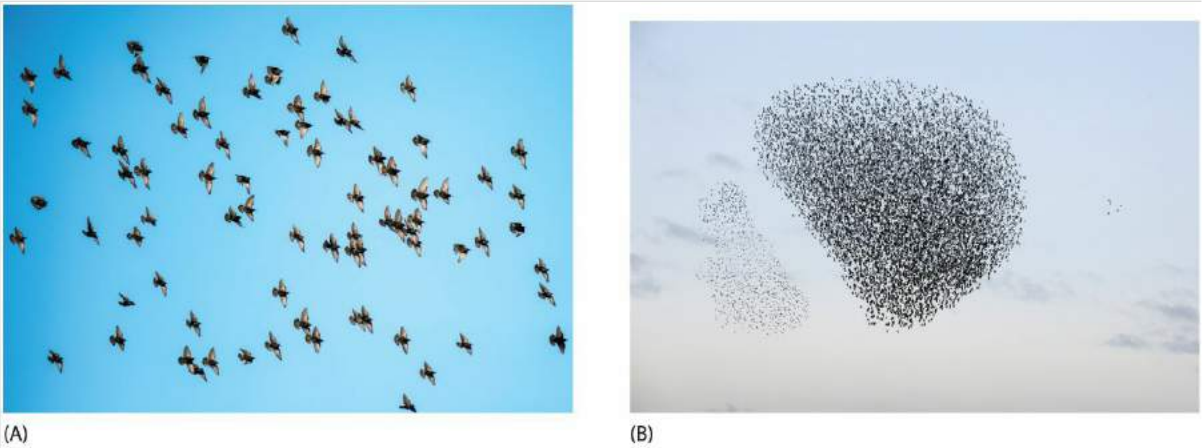
DATA FROM HEINRICH AND MARZLUFF 1995

Figure 11–13 Postures and feather positions portray a Northern Raven's social status. A vagrant at an adult-protected carcass (1) keeps its head up and the feathers on its head fluffed out. A raven first approaching food (2) lowers its head. When juveniles swamp a carcass, a resident adult performs a dominance display (3) that includes erect posture, raised bill, raised earlike feathers, and fluffed-out throat and leg feathers. A raven at an uncontested food source (4) holds its head up and keeps its feathers smooth across its head.

Safety in Flocks

Joining a flock theoretically decreases the risk of being caught and eaten because there is safety in numbers. A bird's chances of being a victim decrease as the number of potential victims in the flock increases, and they decrease even further for birds near the center of the flock (Hamilton 1971; Figure 11–14). Field observations support this logic. The hunting success of a Merlin, for example, varied according to the size of sandpiper flocks that it attacked (Page and Whitacre 1975). It fared poorly with medium-sized sandpiper flocks but did well with isolated birds and with large flocks, which were less able to maintain a tight formation.



(A) FotoRequest/Shutterstock. (B) Franke de Jong/Shutterstock

Figure 11–14 Common Starlings, which normally fly in (A) loose flock formations, form (B) tight formations when threatened by a hawk.

Predator detection improves in flocks; greater individual security is the result. Ostriches, for example, stick their heads up randomly to look for lions that may be stalking them; at any given time, at least one in the flock functions as a lookout (Bertram 1980). Group vigilance increases with covey size of the Northern Bobwhite, but big quail coveys are not necessarily best (Box 11–3).

Box 11–3

Optimal Size of a Quail Covey

Northern Bobwhites feed, roost, and travel in groups called coveys in the fall and winter. The coveys hold tight when approached by a predator, including a hunting dog that points them until its master hunter catches up. The coveys then explode as if on cue, causing poor shots by novice quail hunters.

Covey sizes in Kansas range from two to 22 quail (Williams et al.

2003). Larger coveys exhibit reduced individual vigilance, increased group vigilance, faster detection of predators, and more time spent in exposed feeding areas. Individual survival is lower in small coveys than in large coveys. However, optimal covey size is only 11 quail. Large coveys also have low individual survival because of increased competition for food and thus lower body weights as well as more movement and exposure to predators. The intermediate covey sizes achieve the best individual survival because of the combination of low group movement, improved foraging efficiency, and better individual predator detection.

Flock members warn one another of danger so that they can hide or flee at the same time. Ducks signal one another with head bobs to flush together at the approach of a predator. Alarm calls serve to alert other members of a social group to possible danger. Giving an alarm call would seem advantageous to all but the one that revealed its position by calling. Warning calls thus seem to be heroic or altruistic acts, but they carry benefits for the caller as well if others in the flock are genetic relatives, such as siblings, parents, or offspring. Each flock member can also count on a certain degree of reciprocity. Most important, by calling loudly, the potential victim robs a predator of the element of surprise and thereby reduces the likelihood of attack. By warning others in the flock, the vigilant sounder of an alarm reduces its own danger as it alerts kin and neighbors (Box 11–4).

Box 11–4

Wanted: Experienced Parrot Flocks for Conservation

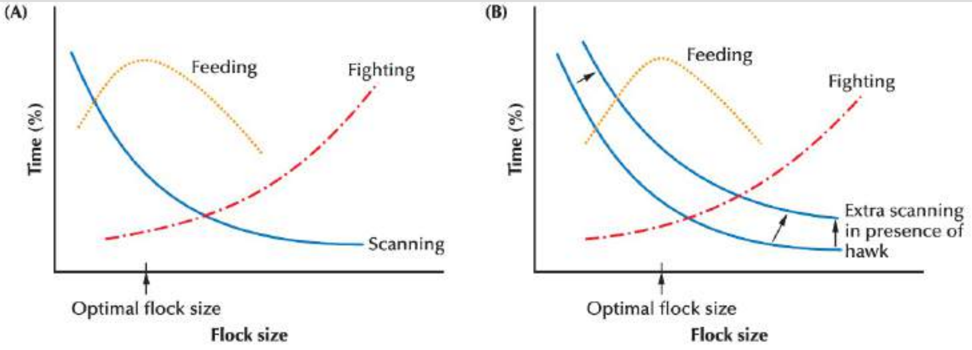
The only two parrots native to the United States disappeared 50 years ago.

Subsistence hunting and habitat degradation exterminated their populations. One of them, the Carolina Parakeet of the eastern United States, is surely extinct, but declining numbers of the other species, the larger Thick-billed Parrot, persist in high mountain refuges in western Mexico. Noel Snyder and his colleagues have undertaken an ambitious conservation program to restore Thick-billed Parrots into the rugged Chiracahua Mountains of southeastern Arizona, where they once lived (Snyder et al. 1999). They used the captive-bred offspring of confiscated Thick-billed Parrots from the illegal pet trade. Their initial efforts were often thwarted because the young parrots lacked predator-avoidance training by experienced flock mates.

Experienced wild Thick-billed Parrots protect themselves from hawks through their wary, vigilant social behavior and through their ability to outfly a pursuer. Northern Goshawks, which are common in the Arizona mountains, found inexperienced, captive-bred parrots to be easy prey because they did not scan the sky for predators, did not freeze or flee when they saw one, and did not react quickly enough to alarm calls of experienced wild birds. The captive-bred birds seemed fearless despite the fact that they had seen raptors in action from their cages.

Study of their behavior revealed that strong socialization with experienced flock mates is required to learn essential survival skills. The captive-bred birds also require lots of exercise to attain the condition required to keep up with wild flocks and to fly faster than a pursuing hawk. Further, flock mates teach one another to identify pine cones as food sources and how to extract the seeds from them. Finally, well-socialized parrots develop an essential sense of security. Without the sense of security that comes from joining other parrots to feed, pairs of adults seem unwilling to undertake the risks of breeding. The future success of such parrot-conservation programs will depend on the training and gradual release of socially mature flocks of birds that work together to find food and avoid predators.

By relying in part on such mutual protection, each individual bird in a flock can actually be less vigilant—that is, spend less time looking for predators as well as more time feeding—than when alone. The time saved by each bird in a flock because of decreased vigilance, however, is offset by aggressive interactions, which increase in frequency with group size (Caraco 1979). The amount of time available for feeding should, therefore, be greatest in flocks of intermediate size. Moreover, optimum group size should increase when predators are near and when each bird must spend more time in surveillance, which was confirmed by Thomas Caraco and his colleagues (1980) in classic studies of Yellow-eyed Juncos in Arizona. In one experiment, average flock size increased from 3.9 to 7.3 juncos when he flew a tame Harris's Hawk regularly over the feeding grounds (Figure 11–15).



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DATA FROM CARACO ET AL. 1980

Figure 11–15 (A) The optimal flock size theoretically results from a balance between time spent fighting other members of the flock, time spent scanning for predators, and time spent feeding. An intermediate flock size permits the most feeding time. (B) When a predator hawk is present, more time must be spent scanning, and the optimal flock size increases.

When they discover a predator, such as an owl or a snake, birds scold them vocally and sometimes attack them physically. The advantages of mobbing behavior include discouraging or driving away an enemy. In addition, mobbing refines an individual bird's ability to recognize predators, which reduces future risk to self and family. Inexperienced birds quickly associate potential danger with the commotion of mobbing behavior. They then learn to recognize predators by observing the mobbing behavior of their parents or their flock mates. Common Blackbirds of Europe will even learn to attack a detergent bottle if, in experiments, they are tricked into associating the mobbing behavior of others with such an inanimate object (Curio et al. 1978). Species that join mixed-species foraging flocks tend to respond reciprocally to one another's alarm calls and to mob predators cooperatively, possibly sharing their knowledge of potential enemies (McLean and Rhodes 1991).

Mixed-Species Flocks and Social Signals

Flocks are not limited to members of the same species. Rich assemblages of different species form foraging flocks. Flocks of chickadees, titmice, nuthatches, woodpeckers, creepers, and other associates are familiar both in the United States and in Europe, and several species of warblers may join them in the warmer months. Noisy gatherings of antbirds, antwrens, woodpeckers, flycatchers, and honeycreepers surge through the understory and canopy of rain forests of South America. Tropical flocks may include 60 birds of 30 different species, whereas temperate flocks average 10 to 15 birds of six or seven species. Curiously, flock size increases primarily as a result of the addition of new species, not more individual birds of a few species. Furthermore, flock composition changes regularly as the flock moves along, a result of new birds joining and others leaving. Individual birds join the flock as it moves through their territory, only to be replaced by neighbors as the flock moves from one territory to the next.

Flock structure starts with one or more so-called **nuclear species** that attract other species and that lead the flock's movements. They tend to be "sentinel" species that are highly sensitive to predators. Other species, the "followers," join such flocks opportunistically and are subordinate to the nuclear species. In temperate-zone woodlands of North America, for example, titmice and chickadees are nuclear species. Large antbirds and greenlets take this role in lowland tropical forests. In eastern Peru, the Bluish-slate Antshrike and the Dusky-throated Antshrike assemble 30 other species with their loud rallying calls early every morning. In Sri Lanka, the stunning Greater Racquet-tailed Drongo is such a leader (Figure 11–16). In addition to their own vocals, these drongos attract selected followers by mimicking their calls (Goodale and Kotagama 2006). Playback experiments with mimicry vocalizations were twice as effective in the attraction of followers.

Why do birds of diverse species assemble to feed together? In particular, why do subordinate species join the nuclear species? Reduced predator vigilance and increased foraging efficiency are part of the answer. Nongregarious species tend to be more aware of

Kajornyot/Getty Images

Figure 11–16 The Greater Racket-tailed Drongo composes and leads large mixed-species feeding flocks of birds in the forests of Sri Lanka. It attracts selected species to its flock by mimicking their vocalizations.

predators when with large numbers of other species partly due to a “numbers” effect and partly due to more information available in the alarm calls of different species (Goodale and Kotagama 2005). Downy Woodpeckers, for example, sacrifice feeding time for high levels of vigilance when foraging alone (Sullivan 1984a, 1984b). They stop frequently to look for predators, with a distinctive head-cocking behavior. When they feed with large mixed-species flocks, they cock their heads less frequently and feed at higher rates. The woodpeckers monitor the calls of flock mates to assess their numbers and their tendency to be alarmed by possible predators.

Colonies

About 13 percent of bird species, including most seabirds, nest in colonies (Figure 11–17). Colonial nesting evolves in response to a combination of two environmental conditions: (1) a shortage of nesting sites that are safe from predators and (2) abundant or unpredictable food that is distant from safe nest sites (Siegel-Causey and Kharitonov

1990). Colonial nesting has both advantages and disadvantages. First and foremost, individual birds are safer in colonies that are inaccessible to predators, as on small rocky islands. In addition, colonial birds detect predators more quickly than do small groups or pairs and can drive the predators from the vicinity of the nesting area; in one classic example, the effectiveness with which Common Black-headed Gulls mobbed predators increased with the number of participants (Kruuk 1964). Because nests at the edges of breeding colonies are more vulnerable to predators than those in the centers, the preference for advantageous central sites promotes dense centralized packing of nests.

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Figure 11–17 Northern Gannets, an abundant seabird of the North Atlantic, nest in densely packed colonies on oceanic islands.

Coordinated social interactions tend to be weak in the initial evolutionary stages of colony formation, but true colonies provide extra benefits. Synchronized nesting, for example, produces a sudden abundance of eggs and chicks that exceeds the daily needs of local predators. Additionally, colonial neighbors can improve their foraging by watching others. This behavior is especially valuable when the off-site food supplies are restricted or variable in location, as are swarms of aerial insects harvested by swallows or schools of small fish harvested by seabirds. Colonial ospreys not only transfer information about foraging directions but also discriminate among fish species brought back by other colony members (Greene 1987). They respond to the arrival of only a neighbor with a schooling fish species. This information significantly reduces the search times that informed birds need to capture patchily distributed prey species.

The colonies of American Cliff Swallows serve as information centers from which unsuccessful individual birds follow successful neighbors to good feeding sites (Brown and Brown 1995). Cliff swallows that were unable to find food returned to their colony, located a neighbor that was successful, and then followed that neighbor to its food source. All birds in the colony were equally likely to follow or to be followed and thus contributed to the sharing of information that helped to ensure their reproductive success. As a result of their enhanced foraging efficiency, parent swallows in large colonies returned with food for their nestlings more often and brought more food each trip than did parents in small colonies.

Cliff Swallows also monitor the breeding performance of other swallows in nearby colonies to decide where to nest the following year (Brown et al. 2000). Reproductive success at a colony site in southwest Nebraska was correlated from one year to the next. The most successful colonies one year attracted the most immigrants the following year. Reuse of a particular colony in successive years increased with collective reproductive success and average breeder body mass (a measure of individual condition) the previous season.

To support large congregations of birds, suitable colony sites must be near rich, clumped food supplies. Colonies of Pinyon Jays and Red Crossbills settle near seed-rich conifer forests, and Wattled Starlings nest in large colonies near locust outbreaks. The huge colonies of Guanay Cormorants and other seabirds that nest on the coast of Peru depend on the productive cold waters of the Humboldt Current. The combination of abundant food in the Humboldt Current and the vastness of oceanic habitat can support enormous populations of seabirds, which concentrate at the few available nesting locations. The populations crash when their food supplies decline during El Niño years.

Among the costs, colonial nesting leads to increased competition for nest sites and mates, increased cuckoldry, the stealing of nest materials, increased physical interference, higher parasite loads, and more efficient disease transmission. In spite of food abundance, large colonies sometimes exhaust their local food supplies and abandon their nests. Large groups also attract predators, especially raptors, and facilitate the spread of parasites and diseases (Tella 2002). The globular mud nests in large colonies of the American Cliff Swallow, for example, are more likely to be infested by fleas or other bloodsucking parasites than are nests in small colonies (Brown and Brown 1986). Experiments in which some burrows were fumigated showed that these parasites lowered survivorship by as much as 50 percent in large colonies but not significantly in small ones. The swallows inspect and then select parasite-free nests. In large colonies, they tend to build new nests rather than use old, infested ones. On balance, the advantages of colonial nesting clearly outweigh the disadvantages given the many times at which colonial nesting has evolved independently among different groups of birds.

The foundations of the social behavior of birds reviewed in this chapter underlie the full annual cycle of birds, breeding and nonbreeding, and migration and residency as well as the cultural evolution of birds over time. Next, in Part 4 of this book, we focus on reproduction, discussing sex, mates, and breeding systems.

REVIEW KEY CONCEPTS

11.1 Individual Space

The defensibility of a given space, the variability of food resources, and the values of social attraction determine spatial relations of birds. In general, the tendency of individual birds to space themselves evenly promotes uniform dispersion patterns. Conversely, habitat quality and conspecific attractions cluster their distributions nonrandomly.

Key Term: allopreening

11.2 Territorial Behavior

Territorial displays assert a bird’s claim to primary use of an area. The relative costs and benefits of territorial behavior govern its flexible expression. Birds typically defend territories against other of the same species, but sometimes they also expel other species, especially those that compete for food resources. Conversely, some species that consort in mixed feeding flocks defend shared territories or home ranges.

Key Term: territorial behavior

11.3 Social Rank

Dominance structures the relations among individual birds in flocks, a system that reduces strife. Age, sex, physiology, genetics, and possibly parasite load all affect dominance. Social rank tends to increase gradually with age, individual tenure, and changes in group composition. Differences in plumage color serve as badges of social status.

Key Term: homeostasis

11.4 Interspecific Aggression, Dominance, and Mimicry

Interspecific dominance hierarchies influence the coexistence of unrelated species in shared territories. Mimicry, or evolutionary convergence in appearance, improves the competitive ability of subordinate species to access resources controlled by dominant species.

Key Term: mimicry

11.5 Flocks

Flocks may be loose and opportunistic aggregations or highly structured social systems with closed memberships. Flock members benefit from one another's vigilance for danger and the finding of scarce food. Mixed-species flocks increase the benefits of mutual protection without the costs of sharing space or food with competing members of the same species. Many bird species congregate in large numbers to nest in colonies or to roost communally. Reduced predation risk in safe places, by virtue of large numbers and through group defense, is one of the primary benefits. Birds also monitor each other's reproductive success in order to expedite next year's choice of prime breeding territories or colony sites.

Key Terms: flock, producer-scrounger model, nuclear species

APPLY YOUR KNOWLEDGE

1. Describe and explain the correlations between territory size and food abundance.

2. Describe temporal and spatial resource variability and resource defensive behavior.
3. Compare competition for territories and social rank structure as behaviors that partition resources.
4. How is a bird’s social rank determined as dominant or subordinate?
5. Describe the feeding behaviors of dominant and subordinate birds.
6. Compare the advantages and the disadvantages of flocking behavior between conspecifics and between members of mixed flocks.
7. Compare the structures of territories and the individual space within colonies. What factors favor colony nesting?
8. Describe the advantages and disadvantages of colonial nesting. Which of these appear to be the most important factors in support of colony nesting?
9. How does colonial nesting increase reproductive fitness through more successful foraging of colony members?

PART IV *Reproduction*

Red Junglefowl [bouybin/Shutterstock.com]

CHAPTER 12 *Bird Sex*

PAUL REEVES PHOTOGRAPHY/SHUTTERSTOCK.COM

Drake Mallards copulate with hens using an elongated penis that mediates underwater intromission. Waterfowl are one of the few groups of birds that have such sex organs.

12.9 Clutch Size

> I think, that, if required, on pain of death, to name instantly the most perfect thing in the universe, I should risk my fate on a bird’s egg. [T. W. HIGGINSON 1863, P. 297]

A bird’s egg is one of the most complex and highly differentiated reproductive cells achieved in the evolution of animal sexuality. The many sizes, shapes, tints, and textures of birds’ eggs fascinated the earliest ornithologists and inspired naturalists to collect them (Figure 12–1). Interest in the avian egg also helped to develop ornithology as a comparative science. Nineteenth-century ornithologists published enormous monographs illustrating the eggs of British and African birds, and serious students of **oology**—the study of eggs—undertook detailed studies of the microscopic structure of eggshells and embryos.

JOHN READER/SCIENCE SOURCE

Figure 12–1 The eggs of birds vary 2,000-fold in size (ostrich versus hummingbird), in shape from round to pointed, and in color from pure white to bright blue, often camouflaged with dark pigment.

This chapter reviews the fundamentals of sexual reproduction in birds, including their sex organs, or gonads; their sex chromosomes; their ova and sperm; copulation and fertilization; and the production of a fully formed egg in the oviduct. Included are descriptions of avian sexuality from the usual "cloacal kiss" to unusual genitalia. Then follows a detailed review of the structure and functions of the fully complete external egg that costs the female much to produce and, having been laid, demands continued parental care. Subsequent chapters examine the nests and incubation behavior of birds (Chapter 15) and the development of young birds, along with the challenges of parental care (Chapter 16).

12.1 The Sexes

Birds are strictly bisexual animals, with separate male and female organisms. Hermaphroditism—both sexes in one individual organism—is a familiar condition among reptiles, fish, insects, and plants but is virtually unknown in birds. Birds also do not change sex with age, as some members of other animal species may do. Rather, the sexes of birds are determined for life at fertilization. Different gene activities and hormone balances govern separate sexual roles and life-history strategies. In addition, contests take place between the sperm of different males for fertilization, and females can manipulate egg quality through different doses of testosterone.

Gonads and Chromosomes

The males and females of some species of birds are dramatically different in coloration or size, usually as the result of sexual selection (Chapter 13). The sexes of many other bird species, from flycatchers to penguins, are indistinguishable externally. Unlike mammals and many reptiles, birds typically lack external genitalia. The **gonads**—paired testes in the male and usually a single ovary in the female—are located deep inside the body cavity on the surface of the kidneys (Figure 12–2). These sex organs produce gametes and secrete sex hormones.

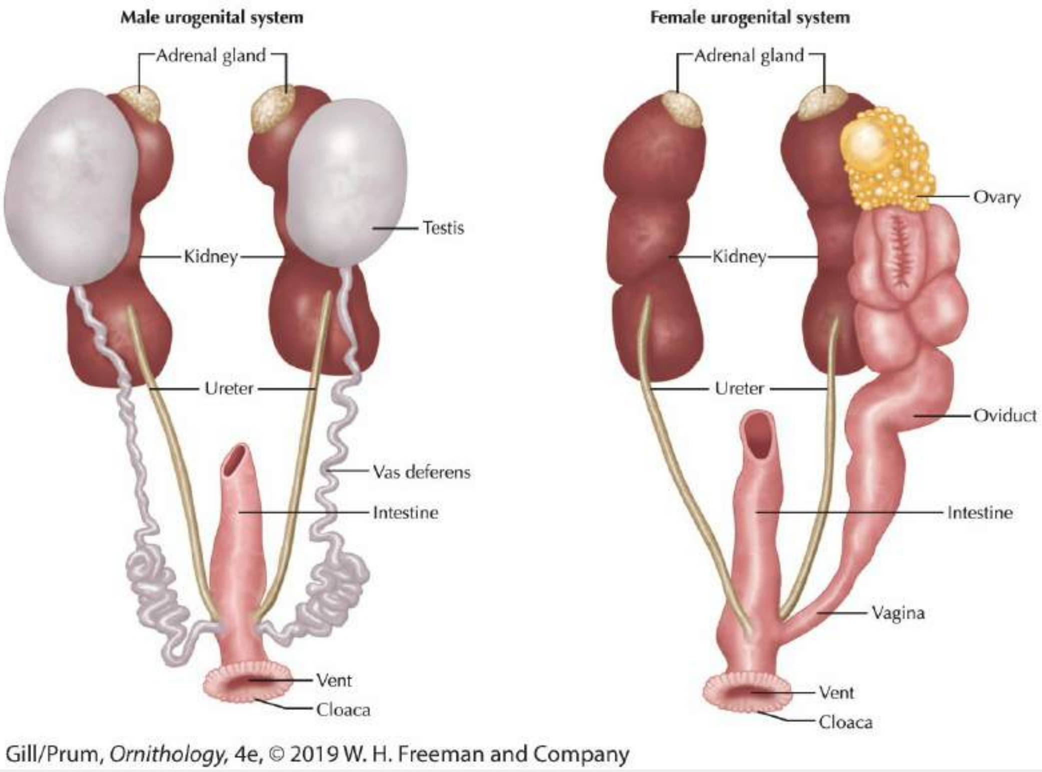

Figure 12–2 Avian reproductive systems (bold terms show reproductive structures). (*Left*) Testes and the vas deferens of the male urogenital system. (*Right*) Ovary, oviduct, and vagina of the female urogenital system.

In crocodiles, turtles, and most lizards and snakes, sex determination is temperature dependent. Like mammals, however, birds have evolved distinct sex chromosomes (Figure 12–3). The avian **sex chromosomes W and Z** evolved independently of mammalian sex chromosomes from a pair of autosomal chromosomes (Fridolfsson et al. 1998). They differ from the mammalian X and Y sex chromosomes in genetic structure as well as in origin. Female birds, rather than males, are the **heterogametic** sex, that is the sex with different sex chromosomes (ZW). Male birds are **homogametic,** and have two Z chromosomes (ZZ). Patterns of inheritance of sex-linked traits correspond to these chromosomal identities. Like the Y chromosome in mammals, the avian W chromosome is greatly reduced and has many fewer genes than the Z. Interestingly, in paleognathes, the W is not reduced, and the two sex chromosomes are the same in size.

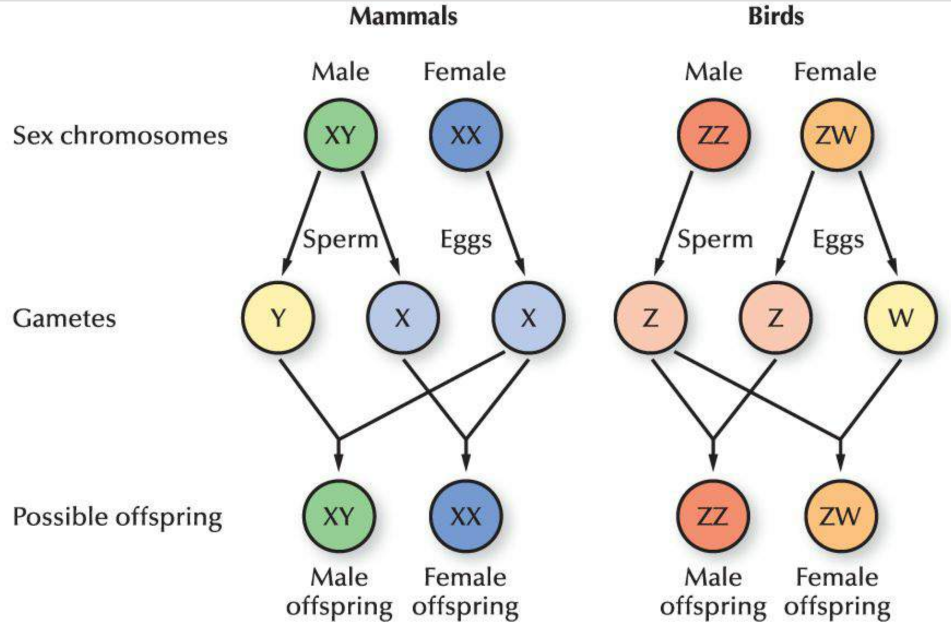

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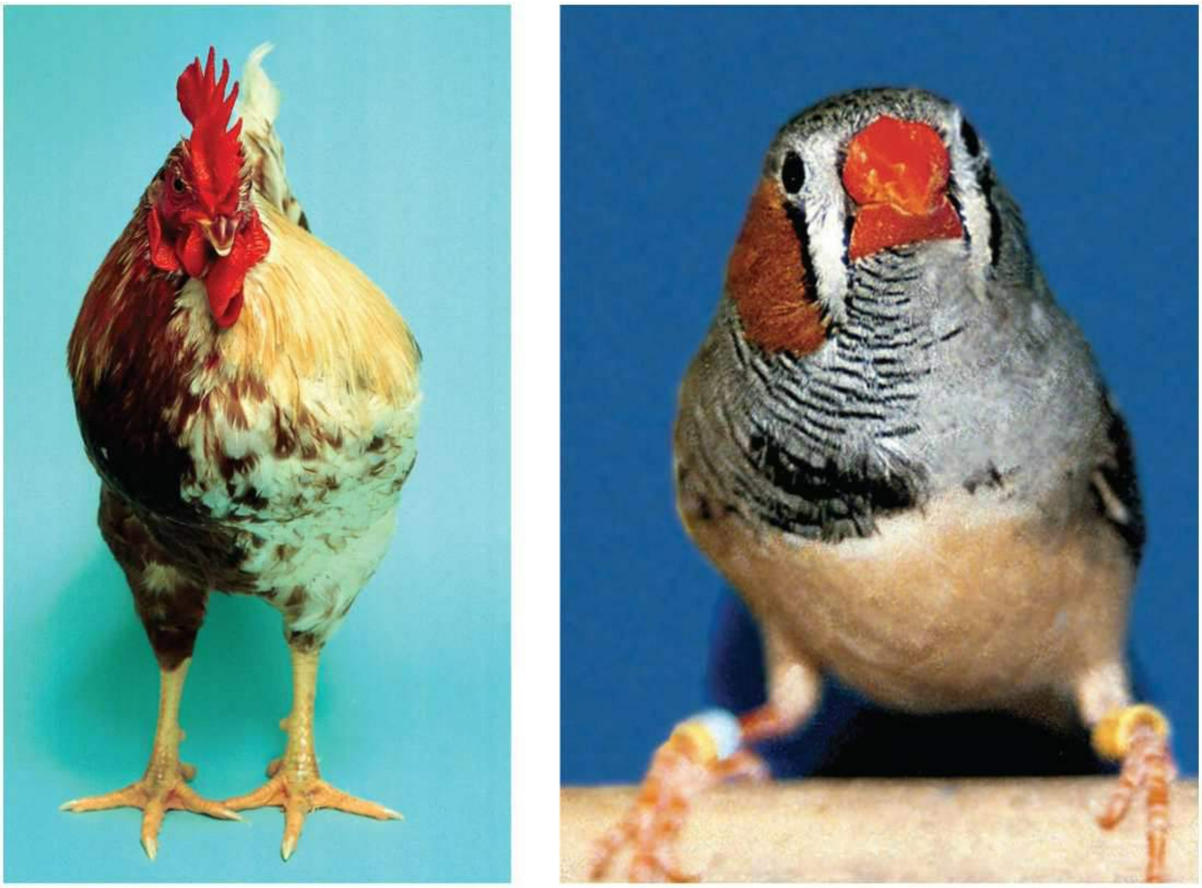
Figure 12–3 Sex chromosomes. Birds and mammals differ in the bases of sex determination. Their sex chromosomes are of different origins and hence are given the letters Z and W in birds rather than X and Y as in mammals. Male birds are the sex with two of the same sex chromosomes (ZZ), and female birds are the sex with one of each (ZW), the converse of mammals.

Geneticists don’t yet know how the W and Z sex chromosome of birds interact to determine sexual identities (Ellegren 2002). In mammals, genes on the Y chromosome trigger the development of males. One (dominant) gene inactivates part of the X chromosome. Another gene, called *SRY*, starts the development of the testes and, in turn, sexual differences in the brain.

Occasionally, subsequent to an aberration in the first (mitotic) division of the fertilized ovum, half of a bird embryo becomes female, ZW, and the other half becomes male, ZZ (Figure 12–4). Called **bilateral gynandromorphs,** these birds have a testis on one side of the body and an ovary on the other. Externally, they have male and female plumages on the corresponding right and left sides of the body, with a sharp division down the center. Bilateral gynandromorphs have been reported among a wide variety of bird species, including an Orchard Oriole, a Black-throated Blue Warbler, Evening Grosbeaks, American Kestrels, House Sparrows, Zebra Finch, and chicken (Patten 1993). Nothing is known about the breeding activities of such birds in the wild.



(A) (B)

(A) Photo courtesy of Dr. Michael Clinton, The Roslin Institute, The University of Edinburgh, Roslin, Scotland, UK. (B) Neural, not gonadal, origin of brain sex differences in a gynandromorphic finch. Agate RJ, Grisham W, Wade J, Mann S, Wingfield J, Schanen C, Palotie A, Arnold AP. Proc Natl Acad Sci U S A. 2003 Apr 15;100(8):4873–8. Copyright (2003) National Academy of Sciences, U.S.A.

Figure 12–4 Rare individual birds are male on one side and female on the other as a result of an aberration in the first cell division of the fertilized egg. These oddities are called bilateral gynandromorphs. (A) Domestic Chicken. (B) Zebra Finch.

Sexual differences in both avian and mammalian brains are thought to be controlled by hormones from the gonads. Studies of a bilateral gynandromorph Zebra Finch revealed that genes on sex chromosomes also act directly on the neural circuitry of the brain (Agate et al. 2003). The Zebra Finch was male on the right side of its body and female on the left side of its body. Despite the infusion of male and female hormones into both sides of its brain, enlarged male song circuitry developed only on the right side of its brain. The enlarged circuitry was a direct response to gene activity in cells that were ZZ (male). A double dose of one protein (TrkB) known to mediate neural development is likely to be implicated (Chen et al. 2005).

Sex Hormones

The brain regulates the secretion of sex hormones through the hypothalamus and, in turn, the pituitary gland (see Figure 9–7). Two hormones secreted by the anterior pituitary control the gonads: follicle-stimulating hormone regulates gamete formation, and luteinizing hormone regulates hormone secretion by the testes and the maturation of follicles in the ovary. The gonads themselves secrete two principal steroid sex hormones—**testosterone** and **estrogen**—that directly activate gamete production.

The action of the principal sex hormones on specific receptors in the brain also induces reproductive behaviors. These behaviors include aggression, courtship, nest building, and parental care. Although testosterone is well known as the male hormone and estrogen as the female hormone, both hormones are present in males and females. The proportions of the two hormones and the ways in which body tissues react to each of them cause male or female attributes.

Testosterone and estrogen affect sexual distinctions in plumage, body size, and vocalizations. For example, testosterone causes the bills of Common Starlings to turn bright yellow in the breeding season, whereas estrogen causes the red bills of female Red-billed Queleas to turn yellow in the breeding season. Testosterone also promotes the growth of the red head ornaments—wattles and combs—of roosters and the bill ornaments of breeding auklets.

Males acquire their breeding plumage as a result of increased amounts of testosterone in their blood. The experimental injection of testosterone triggers the growth of colorful feathers in either sex. Conversely, castration prevents Ruffs from acquiring their fancy neck feathers. Phalaropes offer another such case. They are unusual sandpipers in that the bright-plumaged females defend breeding territories and the less colorful males assume the duties of incubation and parental care. Female phalaropes normally have higher concentrations of testosterone than do males, whose maximum levels of testosterone remain below the threshold required to produce colorful feathers. In a similar case, males of some breeds of chickens have femalelike feathers because the cellular chemistry in the skin actively converts testosterone into estrogen. When castrated, they grow male feathers. The injection of testosterone into these castrated males causes them to revert to the female type of plumage (George et al. 1981).

The elaboration of secondary sex traits by steroid hormones has costs. In particular, testosterone tends to reduce the immune response in birds and to make them more susceptible to disease or parasitic infection. Experimental elevation of testosterone suppresses antibody production or cell-mediated immunity in Dark-eyed Juncos and House Sparrows (Evans et al. 2000; Casto et al. 2001). The prolonged elevations of testosterone in polygynous male songbirds may exact a substantial cost. Still uncertain, however, is whether testosterone directly suppresses the immune system or whether it does so by increasing levels of corticosteroid stress hormones, which, in turn, suppress disease resistance as well as some aspects of reproduction (see Chapter 9).

12.2 Ovary and Ovum

The avian ovary resembles a small cluster of grapes. Most birds have only one ovary, the left one, and one associated oviduct. Two functional ovaries are typical of many raptors and of kiwis. They are also occasionally present in pigeons, gulls, and some passerines.

In early development of the embryo, primordial germ cells migrate to the site where the gonads will develop. More of these germ cells settle on the left side than on the right, leading to an unpaired left ovary in most female birds and a testis on the left side that tends to be larger than the one on the right side in males.

The primordial germ cells first generate what is called **medullary tissue.** It becomes the primary tissue of the testes and a secondary tissue of the ovary. Ovarian medullary tissue normally becomes more active with age in females. In extreme cases, the increased activity causes overt masculinization of older females. For example, with age, somber female Golden Pheasants acquire the spectacular plumage of males as a result of this phenomenon.

A second phase of cell proliferation creates the **cortex,** the principal tissue of the ovary. Primary **oocytes**—the cells that give rise to ova—are already present in the cortex of a hatchling bird, but distinct ova do not appear until the bird is older. Each maturing ovum resides within a follicle. At maturity, the microscopic ovarian granules of the immature bird increase in size 10 to 15 times. The total number of primary oocytes in a wild bird is at least 500, and often there are several thousand, many more than are actually used to produce functional eggs.

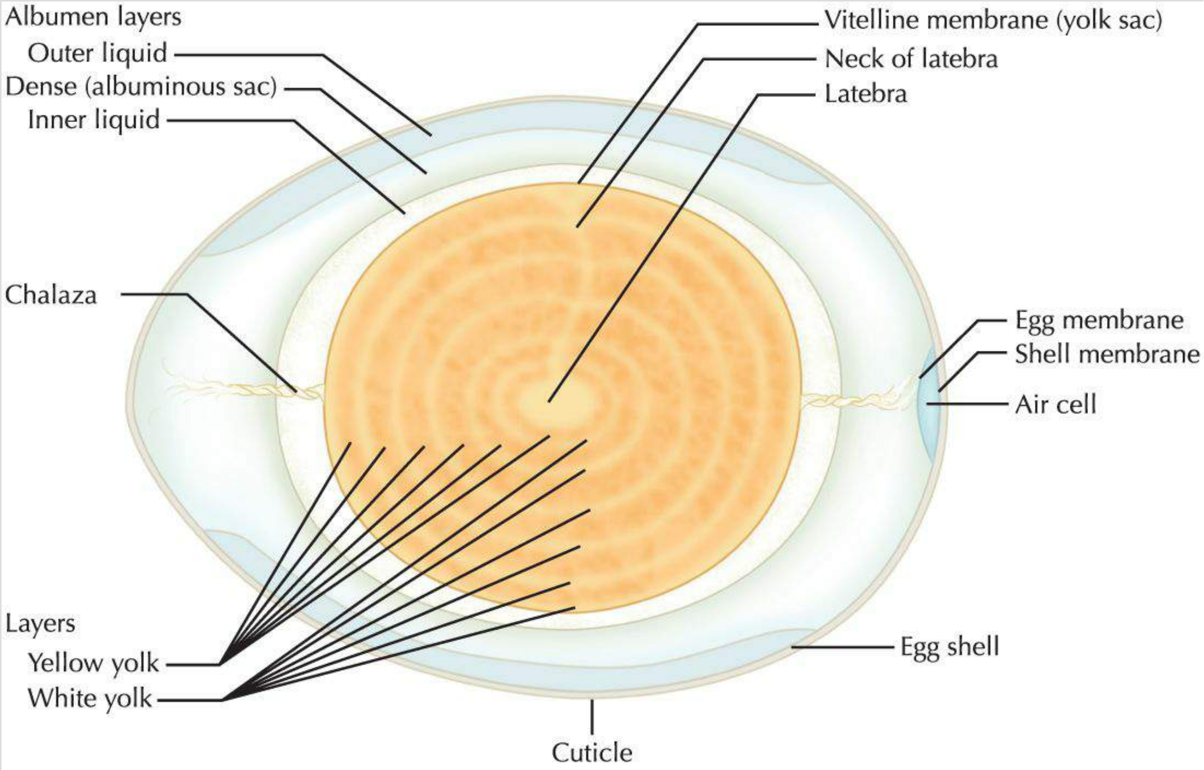
Maturation of the Ovum

The ovum is the mature female reproductive cell that can divide to give rise to an embryo after fertilization by the counterpart male cell: the sperm. The development of a mature ovum into an egg includes two different yet interdependent processes: (1) the formation and deposition of yolk layers and (2) the differentiation, growth, and maturation of the germ cell itself. The infusion of yolk, the deposition of egg white (or **albumen**), and the shell layers all contribute to the growth and conversion of the ovum into a fully provisioned egg. The yolk is added to the ovum before ovulation. The rest of the components of the egg are added as the egg passes through the oviduct.

The period of yolk formation, or **follicular maturation** of the ovum, lasts from four to five days in passerine birds; from six to eight days in larger birds, such as ducks and pigeons; and as long as 16 days in some penguins. The ovum swells to its functional size, more than 1,000 times its original microscopic volume.

Yolks vary in color from pale yellow or light cream to dark orange red or even brilliant orange. Within a species, such variations are partly due to diet. Hens that eat red peppers rich in carotenoid pigments, for example, lay eggs with red yolks instead of the normal yellow yolks (Fox 1976).

The yolk is not homogeneous (Figure 12–5). Rather, it comprises alternating layers of yellow yolk in large globules (0.025–0.15 mm in diameter) and white yolk in smaller globules (0.004–0.075 mm in diameter). The layers correspond to daytime (yellow) and nighttime (white) yolk deposition. These layers can be counted like a tree’s growth rings to determine the time required for yolk formation (Roudybush et al. 1979). The center of the yolk, or **central latebra,** is composed of a fluid, white substance called **vitellin,** which extends to the periphery through a distinct, narrow passage. A thin vitelline membrane encases the yolk, separating it from the albumen to be added later.



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DATA FROM ROMANOFF AND ROMANOFF 1949

Figure 12–5 Structure of a freshly laid hen’s egg. Note alternating layers of white yolk and yellow yolk. The components of egg structure are discussed throughout this chapter.

Most of the nutrients and energy supplies in the completed egg are added before ovulation. Females also transfer hormone and health functions to their offspring through the egg contents (Box 12–1). They put substantial amounts of immune factors, including carotenoids, immunoglobins, and lysozymes, into the egg yolk (Saino et al. 2002a, 2002b). These factors improve the immune systems and the fitness of developing embryos and chicks after hatching. Bright yellow and orange yolks are rich in carotenoids. **Carotenoids** are not just pigments that add color to the yolk and to feathers; they are also precursors of vitamin A. They protect DNA and lipid molecules from oxidative damage (like antioxidants in our diets), and they enhance immune functions (Surai et al. 2001). Higher carotenoid concentrations in the yolk of Barn Swallow eggs, for example, increase T-cell-mediated immune function in their nestlings (Saino et al. 2003).

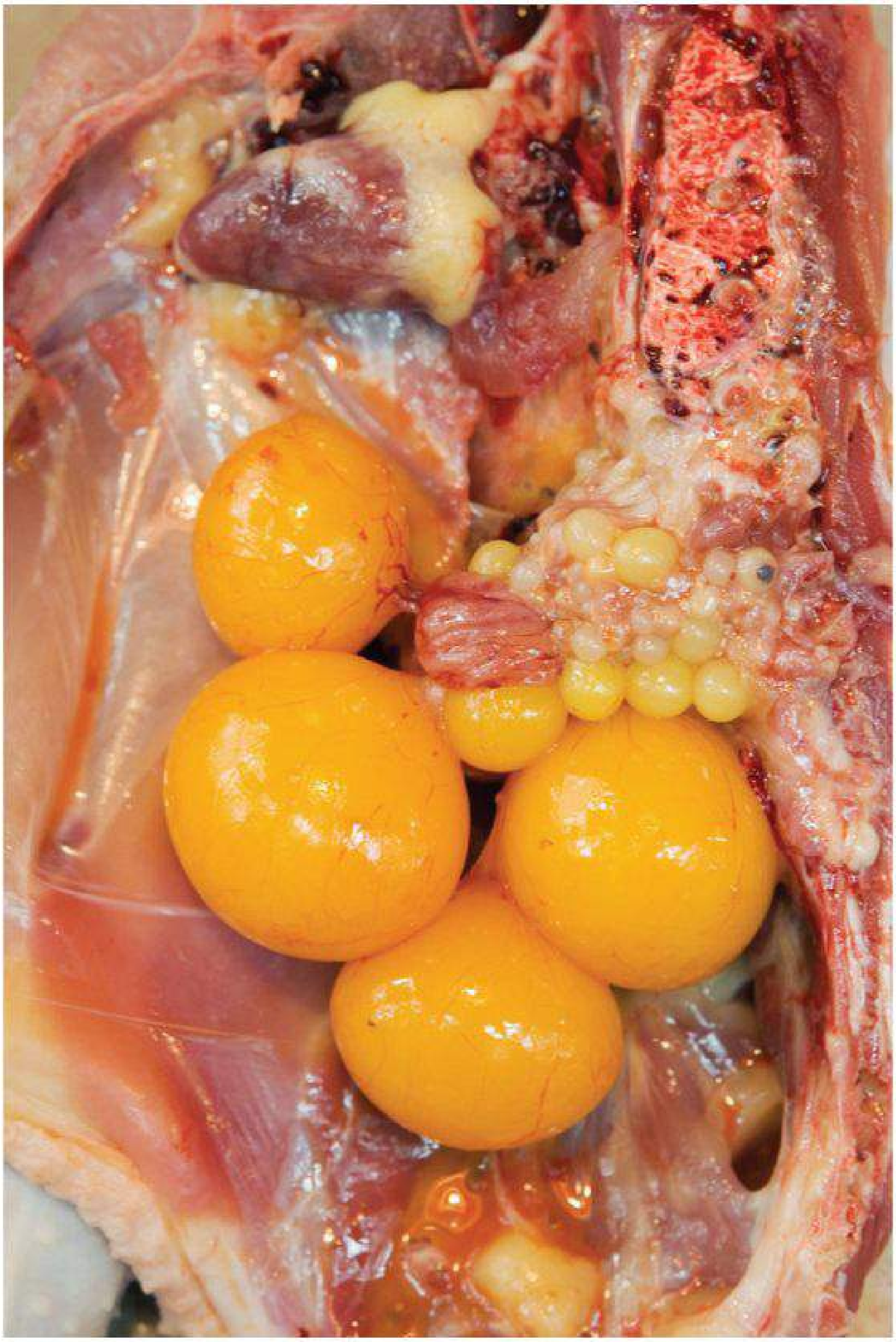
BOX 12–1

Manipulating Egg Quality and Brood Mates

Female birds vary the provisions that they add to eggs in a clutch and thereby control their quality and the offspring that hatch from them (Gil 2003; Groothuis et al. 2005). For example, they adjust the amount of testosterone that they add to the egg yolk. Some ova get more than others. Additional testosterone changes the behavior of the nestlings, with some cost in reduced immunity to disease and parasites.

In the original study of this phenomenon by Hubert Schwabl (1993), female canaries added more testosterone to each successive egg in the clutch. The social rank and aggressiveness of the nestlings increased accordingly, helping to equalize last-hatched nestlings in the competition for food deliveries. Conversely, White Storks and Cattle Egrets short the dose of testosterone in the last egg of a clutch; the Cattle Egret does so by half (Schwabl et al. 1997; Sasvari et al. 1999). These species practice brood reduction (Chapter 16). The last chick to hatch is a weakling that often does not survive, especially in years of low food availability.

Swollen with yolk and nutrients, the full-sized ovum is ready to be transferred to the oviduct and to pass through it. Only a few ova actually make it to this stage. Many follicles, called atretic follicles, stop developing in the early stages of maturation and are resorbed (Figure 12–6).



PHOTICK/JAMES HARDY/GETTY IMAGES

Figure 12–6 The ovary of a sexually mature chicken showing large, mature follicles and resorbed, or atretic, follicles (small, yellow ones in the center).

Ovulation

In ovulation, the egg is released from the ovary. The follicle enclosing the mature ovum ruptures at the stigma—a layer of smooth muscle fibers. The enlarged ovum pops out and falls into the ovarian pocket—an irregular cavity formed around the ovary by the surrounding organs.

Entry into the oviduct is not simply a matter of chance. The open upper end of the oviduct, called the **infundibulum,** actively pulses back and forth toward the new ovum, partly engulfing it and then releasing it for as long as half an hour before finally taking it in. Finally, inside the infundibulum, the ovum is ready for fertilization.

Parthenogenesis, the development of unfertilized eggs, is a regular event in some reptiles but is an extremely rare phenomenon known only in domestic birds. Some unfertilized eggs develop normally in domestic turkeys. Between 32 and 49 percent of infertile eggs may begin so-called parthenogenetic development, but their embryos usually die (Johnson 2000). All surviving parthenogenetic turkey chicks are males (because they have the duplicated ZZ sex-chromosome combination) and have a full diploid set of chromosomes. They may even be sexually competent. However, the exclusive survival of homogametic male offspring from heterogametic, parthenogenic females has likely constrained the evolution of parthenogenesis in birds.

Sex of Offspring

A female's condition affects the quality of her eggs, which, in turn, causes embryos to differ in their growth and their survival. Differences in the survival of the embryos favor one sex or the other and thus the relative numbers of males and females that hatch, called the **primary**

sex ratio (Arnold et al. 2003). Females in poor condition tend to produce eggs with female embryos (Royle et al. 2001).

Selecting the sex of their offspring is an important strategy available to parents, at least in theory. Previously, only wasps and bees were known to control directly the production of male versus female offspring. Birds apparently can do so, too. For example, female Blue Tits paired with males that have intense ultraviolet coloration produce mostly male young (Box 13–1). They do so at ovulation by means unknown but not by absorbing or aborting female eggs (Sheldon et al. 1999).

Advances in technology for the early sexing of bird nestlings have catalyzed a burst of field studies of brood sex ratios in birds (Hasselquist and Kempenaers 2002).

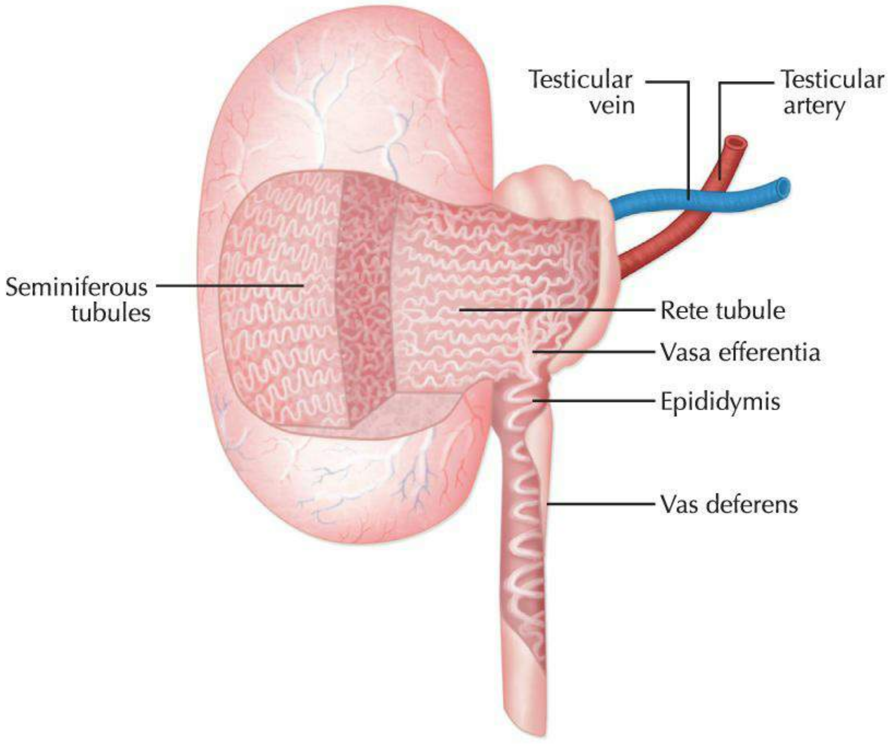
The cooperatively breeding Seychelles Warbler favors female offspring through the selective release or production of female ova (Komdeur et al. 2002; Box 14–4). In this species, daughters from preceding broods help parents raise the young on high-quality territories, which increases their parents' reproductive success. Thus, daughters are the valued sex when conditions are good. Sons, the dispersing sex, garner new territories when conditions are poor and when help by daughters is not advantageous. Adult female warblers switch production of the sexes as predicted (Komdeur et al. 1997). Of the offspring of breeding pairs on low-quality territories without helpers, 77 percent were sons, whereas of the offspring of pairs on high-quality territories without helpers (and therefore in need of daughters), only 13 percent were sons. Breeding pairs transplanted from low-quality territories to empty high-quality territories switched to producing female eggs instead of male eggs. Females do this by changing the sex of their eggs when ovulated, again by means unknown.

12.3 Testes and Sperm

The testes of most mammals reside in external sacs, or scrota, away from internal body heat because sperm are sensitive to high temperatures. The two **testes** of birds are housed, instead, inside the abdominal cavity at body temperature. To compensate for the extra body heat, the formation and development of sperm take place primarily at night, when body temperature is slightly lower. New sperm are then stored in swollen seminal vesicles. Apparently, avian sperm have evolved some physiological mechanism for surviving at high body temperatures that mammals lack.

The testes of birds are internal, bean-shaped organs that are attached to the dorsal body wall at the anterior ends of the kidneys. They usually are cream colored but are dark gray or even blackish in some species. Initially only a few millimeters long in small birds, they swell rapidly at the beginning of the breeding season, often reaching from 400 to 500 times their inactive mass. The testes of a mature Japanese Quail, for example, increase three orders of magnitude in size from eight to 3,000 milligrams in just three weeks. Fertility in domestic geese is directly related to the weight of their mature testes (Szumowski and Theret 1965).

The thick, outer fibrous sheath of the testis encases a dense mass of tiny, convoluted tubes, called **seminiferous tubules.** Lining the tubules are active germinal epithelia that produce sperm. Both Sertoli cells, which line the tubules, and Leydig cells, which are packed between the tubules, secrete the sex hormone testosterone. These cells undergo well-defined seasonal cycles in the accumulation of lipid and cholesterol used in the development and formation of sperm. Cells of the germinal epithelia transform into mature sperm in synchronous waves down the tubule. The entire length of a seminiferous tubule produces sperm at the same time in strongly seasonal breeders, such as Arctic shorebirds. Mature sperm quickly leave the testis through a series of other thin tubules—rete tubules, vasa efferentia, epididymis, and vas deferens (Figure 12–7).



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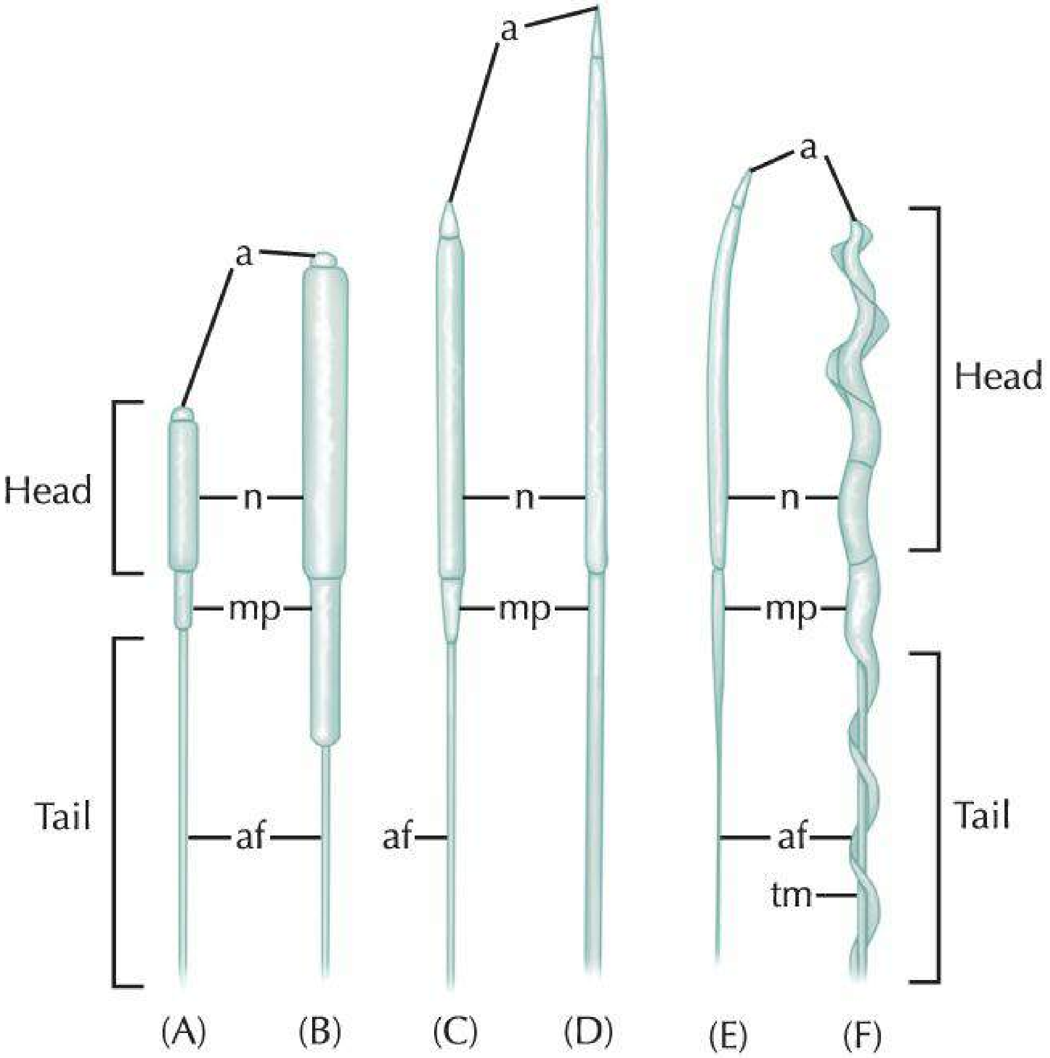
DATA FROM MARSHALL 1961

Figure 12–7 Internal anatomy of the avian testis.

A typical bird sperm consists of three sections, as in other vertebrates (Figure 12–8). The head (acrosome and nucleus) contains the genetic material. The midpiece provides metabolic power. The tail (axial filament and tail membrane) propels the sperm forward.



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DATA FROM MCFARLANE 1963

Figure 12–8 Structural differences in spermatoa characterize the orders of birds: (A) Collared Trogon (Trogoniformes), (B) Great Black-backed Gull (Charadriiformes), (C) Common Eider (Anseriformes), (D) Blue Ground Dove (Columbiformes), (E) Domestic Chicken (Galliformes), and (F) Yellow-rumped Warbler (Passeriformes). Abbreviations: a, acrosome; af, axial filament; mp, midpiece; n, nucleus; tm, tail membrane.

Distinctive sperm structures characterize different groups of birds and some species. Nonpasserine sperm are generally long and straight like those of mammals. Passerine sperm are distinct, with a spiral head and a long, helical tail membrane (Figure 12–8F). Instead of swimming by beating the flagella-like tail, they spin. The relative proportions and lengths of the sections are inherited traits that vary among male Zebra Finches (Birkhead et al. 2003).

The seminal vesicles are the expanded bases of the two ductus deferentia, which swell with accumulated semen awaiting discharge. They are responsible for the conspicuous cloacal protuberances of breeding male passerine birds. In mammals, the seminal vesicles and accessory glands, such as the prostate, add nutritious ingredients to the semen. In birds, the seminal vesicles supply few nutrients, and the other glands are absent (Kirby and Froman 2000).

12.4 Genitalia and Copulation

The evolution and function of avian genitalia is now a topic of interest after a history of neglect. Most birds lack a penis, which is a universal feature of the reproductive anatomy of reptiles and mammals. Only two basal clades of birds—the ratites (Paleognathae), and the land fowl and waterfowl (Galloanseridae)—typically retain this organ (Montgomerie and Briskie 2007; Figure 12–9).

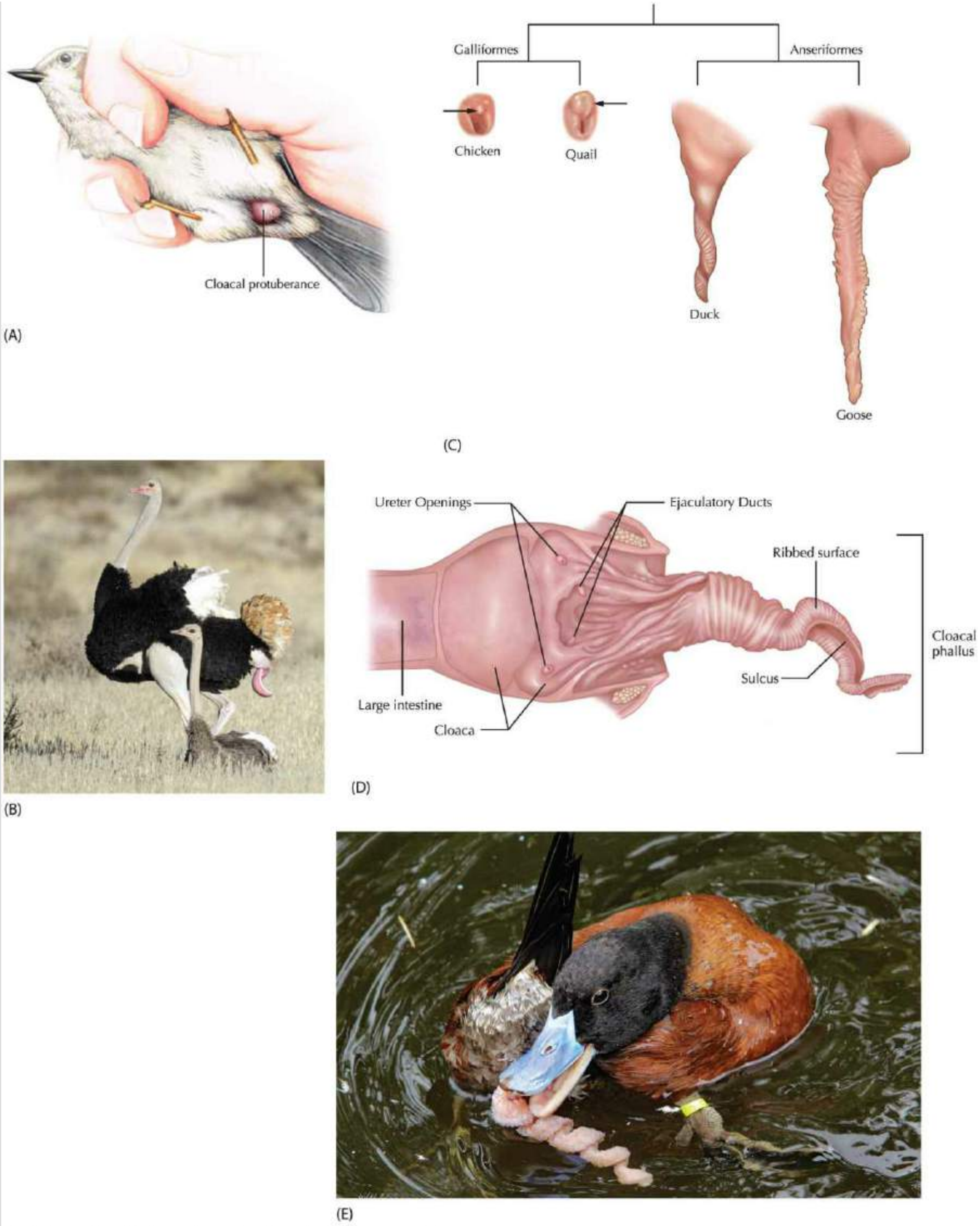

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Figure 12–9 Phallic organs of male birds. (A) Cloacal protuberance of a male Dunnock. (B) Penis display of an ostrich. (C) The cloacal phallus of a duck and a goose compared to reduced ones of a chicken and quail. (D) Diagram of the cloacal phallus of a domestic duck. (E) The Lake Duck of South America sports the longest known penis (42.5 centimeters) of any bird.

The avian **penis** is a special modification of the ventral wall of the cloaca, the cavity at the end of the digestive tract that releases both excretory and genital products. The initial nodule grows in parallel in male and female embryos. Then *Bmp4* genes stop further development of the analogue of a clitoris in female embryos (Herrera et al. 2015). Mutations of these same development genes control the evolutionary loss and gain and the elaboration of the avian penis. Avian penises are homologous with those of mammals and reptiles, but they differ in the physiology of their erections. The erectile mechanism of birds is based on lymphatic fluids instead of vascular blood pressures (Brennan and Prum 2011).

Penises were lost multiple times in avian evolution. The fully extended, bright red penis of an ostrich may be 20 centimeters long, but some tinamous have virtually lost this organ. Phylogenetic analysis reveals that the penis was lost multiple times within birds, in the tinamous, the Galliformes, and in Neoaves—the ancestor of most birds. Within the Galloanseridae, chickens, turkeys, and their relatives have little nonintromittent penises, whereas some ducks have extraordinary counterclockwise-spiraling organs over 40 centimeters long.

High-speed video of the 20-centimeter penis of a Muscovy Duck revealed that the explosive lymph-powered erection averaged 0.36 seconds and achieved a maximum velocity of 1.6 meters per second (Brennan et al. 2010). Ejaculation takes place immediately.

The Ruddy Duck and its close relative, the Lake Duck of South

America, have extraordinary penises (McCracken 2000). The spiny penis of the Lake Duck is the greater of the two, extending 20 to 42 centimeters long, almost the length of the duck's own body and rivaling that of an ostrich (Figure 12–9E). This organ stays coiled inside the body until activated explosively.

The elaborations of duck penises, like those of the Lake Duck, are positively correlated with the frequency of forced extra-pair copulations (Brennan et al. 2007, 2009). So are recently discovered complexities of genital morphology of female ducks. In multiple lineages of waterfowl in which the frequency of forced extra-pair copulations is high, particular vaginal elaborations coevolved with male penis length: (1) dead end sacs and (2) clockwise coils. These structures help the female to thwart intromission by the opposite, counterclockwise-spiraling male phallus during forced copulations. When female waterfowl solicit copulation with a characteristic display posture, these vaginal structures do not inhibit intromission. The coevolution of male and female genitalia is an antagonistic sexual arms race that proceeds through sexual conflict over paternity.

Lacking a penis, most birds mate via brief cloacal contact, often described as a "**cloacal kiss.**" Standing or treading precariously on a female's back, a male twists his tail under hers, and she, in turn, twists into a receptive position (Figure 12–10). The male may slip off while trying to maintain contact for the few seconds required. The mating ritual of an ostrich is a dramatic event: intromission and ejaculation last a full minute. Some species, like the Aquatic Warbler, take much longer (Box 12–2). Flying swifts do it quickly in midair.

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Data from Birkhead and Møller 1992

Figure 12–10 Copulation in birds. (A) Northern Goshawks average from 500 to 600 copulations per clutch. (B) Spotted Sandpipers copulate frequently within 1 minute when they are reunited after separation. (C) The female Greater

Flamingo’s head stays underwater during copulations. (D) The male Dunnock pecks at the female’s cloaca before copulation, inducing the female to eject sperm from previous copulations.

BOX 12–2

Prolonged Copulation

Some mammals, including minks—the aquatic weasel with dense fur used for coats—are notorious for their lengthy copulations that last for hours. The prolonged copulation of the Aquatic Warbler also is extraordinary compared with that of other birds (Schulze-Hagen et al. 1995). This species has the highest-known level of multiple paternity per brood of any bird species. Rather than the normal one to two seconds, copulation in this species lasts 25 minutes. The male and female lie together on the ground, male atop the female, holding on to her head feathers with his bill. The male inseminates the female repeatedly just before and after egg laying. This behavior ensures that his sperm will be positioned to fertilize the next ovum released from the ovary. Such attention is required to win a share of the intense competition for paternity.

Enlarged cloacal protuberances in some passerine birds function as copulatory organs (see Figure 12–9A). The size of the protuberance varies among species with the intensity of sperm competition. The cloacal protuberance of the male Bearded Reedling of Europe everts during copulation into a large red phallus-like structure (Briskie 1998; Sax and Hoi 1998). Unlike those of other species, this protuberance does not store sperm. It serves solely as a copulatory organ. The size of the organ indicates a male’s reproductive status. It waxes and wanes through the fertility cycle of its mates.

Buffalo weavers are the only other passerine birds known to have a phallus-like organ that is present in both males and females but is twice as long (16 mm) in males. Extra-pair paternity and sperm competition are intense in this colonial species. Located anterior to the cloaca, the phallus-like organ is not inserted during copulation but serves, instead, as a unique stimulatory organ (Winterbottom et al. 2001). Endurance—24 mountings of 30 seconds long over 11 minutes—leads to a male “orgasm” that is a prerequisite to ejaculation. How enhanced male stimulation affects female behavior and why females also have this genital structure are yet unexplained.

12.5 Fertilization and Sperm Competition

Sperm are transferred when each partner's cloaca everts. Tiny papillae protruding into the cloaca from the posterior walls of the male's sperm sacs come into contact with the opening of the female's oviduct. Ejaculation follows. In chickens, average concentrations of sperm are 3.5 million per cubic millimeter of semen. A single ejaculation passes from 1.7 billion to 3.5 billion sperm (with records ranging from 7 billion to 8.2 billion by roosters). The concentration of sperm, however, drops rapidly after three or four ejaculations. A minimum of about 100 million sperm is required for the proper fertilization of hens (Kirby and Froman 2000).

Avian sperm swim directly to the upper end of the oviduct, where they may encounter the ripe ovum. They can reach the infundibulum in less than 30 minutes. But then there is only a narrow window of opportunity for fertilization. The ovum quickly adds protective barriers against fertilization by more than one sperm.

Female birds of many species have special sperm-storage tubules (Birkhead 1995; Figure 12–11). The primary storage tubules are located at the junction of the uterus and vagina of the oviduct above the cloaca. Secondary, short-term storage tubules are sited at the infundibulum itself. The number of tubules varies greatly among species—from 500 to 20,000. Large birds have more tubules. The tubules can hold the sperm for weeks, albeit with some passive loss in viability, and then release sperm at a constant rate shortly before ovulation. Last sperm in are the first ones out.

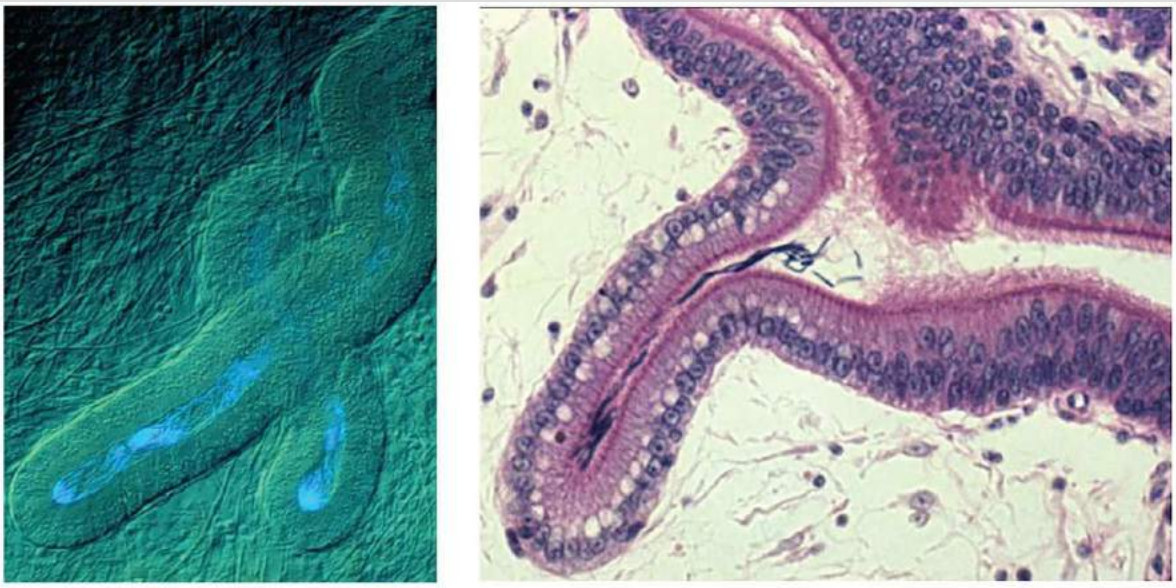


IMAGE COURTESY OF MURRAY BAKST, US DEPT AGRICULTURE

Figure 12–11 Photographs showing the sausagelike sperm-storage tubules of a turkey at two levels of magnification.

Normally, eggs are fertilized within a few days of copulation, but some sperm remain viable for weeks. Domestic chickens and turkeys, in particular, can produce fertile eggs from 30 to 72 days after copulation. For most birds, the probability of laying fertile eggs decreases rapidly from one to two weeks after copulation. Some unpaired birds mate on migration and continue onward carrying stored sperm. In one set of studies, the presence of viable cloacal sperm during spring migration revealed that at least 25 percent of the females of North American migrant passerines copulate long before they reach the breeding grounds (Quay 1989).

In many species, female birds tend to mate with more than one male, even if socially monogamous. For this reason, the sperm of different males may be in the storage tubules or in the oviduct at the same time. If so, they compete to fertilize the ova released from the ovary. Such so-called sperm competition is prevalent among animals. It is an important element of sexual selection. Male adaptations to sperm competition include large testes, large sperm stores, long sperm, the guarding of mates, and frequent copulations (Birkhead 1998; Pitcher et al. 2005; Box 12–3). Females, however, control the pace, timing, and probability of paternity.

BOX 12–3

Sperm Competition among Smith's Longspurs

The Smith's Longspur, a bunting of the subarctic tundra, offers an extreme example of intense sperm competition backed by enormous testes (Briskie 1993). High copulation rates help to displace the sperm of other males. Each female pairs and copulates frequently with two or three males for a single clutch of eggs. Males do not defend territories; instead, they pair and copulate with two or more females and compete for copulations and paternity of the offspring. They practice **polygynandry.** During the peak week in June, females solicit copulations an average of seven times per hour and are mounted by their mates three times per hour. An average of 365 copulations precedes each clutch of eggs laid. The male that copulates most on the day of ovulation usually fertilizes that ovum. It does so by diluting or displacing ejaculates of rival males, thereby putting its own sperm in position when a new ovum is released. The huge testes of the Smith's Longspur—twice the size of those of the related but monogamous Lapland Longspur—support its frequent copulations and supply its many ejaculates.

Mating order and, to a lesser extent, the interval between copulations determine which male wins paternity of offspring (Birkhead 1998). Last male sperm precedence is the rule, especially if sequential copulations are separated by more than four hours. Relative numbers of sperm determine the probability of fertilization by a particular male's sperm. After insemination, sperm are passively lost from the female's storage tubules at a constant rate for days or weeks. For this reason, the interval between two inseminations increases the probability that the second one will be better represented by more sperm in the oviduct. On the other hand, females actively eject most new sperm when they defecate after copulation. This act is part of the mating ritual in some species. In another polyandrous species subject to extreme sperm competition, the male Dunnock pecks at the exposed cloaca of the receptive female just before they copulate (see Figure 12–10D). In response, the female ejects a droplet of the sperm from a previous copulation (Davies 1983).

Last male sperm precedence is also responsible for most extra-pair fertilizations in monogamous species (Birkhead 1998). Despite frequent copulations with a mate, the sperm of extra-pair males prevail for two reasons. First, females solicit extra-pair copulations when they are about to ovulate and so achieve optimal timing. Second, males tend to participate in extra-pair liaisons after they have completed siring their own broods and when they copulate less frequently with their mates. Because they are "rested," they achieve higher densities of sperm in larger ejaculates.

12.6 The Complete Egg

Fertilization transforms an ovum into an embryo, which then begins its passage through the oviduct to complete the formation of the cleidoic egg. Before accompanying the egg on its formative passage, we should examine the major features of the completed egg (see Figure 12–5).

The avian egg is closed, or **cleidoic**—the type of egg that freed the reptiles from the aquatic mode of life of their amphibian ancestors. It contains all the nutrients and water required by the embryo for its early development. The embryo inside the egg is not isolated from the external environment. Its survival requires an active exchange of oxygen, carbon dioxide, and water vapor through the shell membranes. Its growth and well-being depend on the egg's provisions and on its temperature. Its chances of hatching depend on the ability of the parents to regulate the egg's immediate environment within narrow limits.

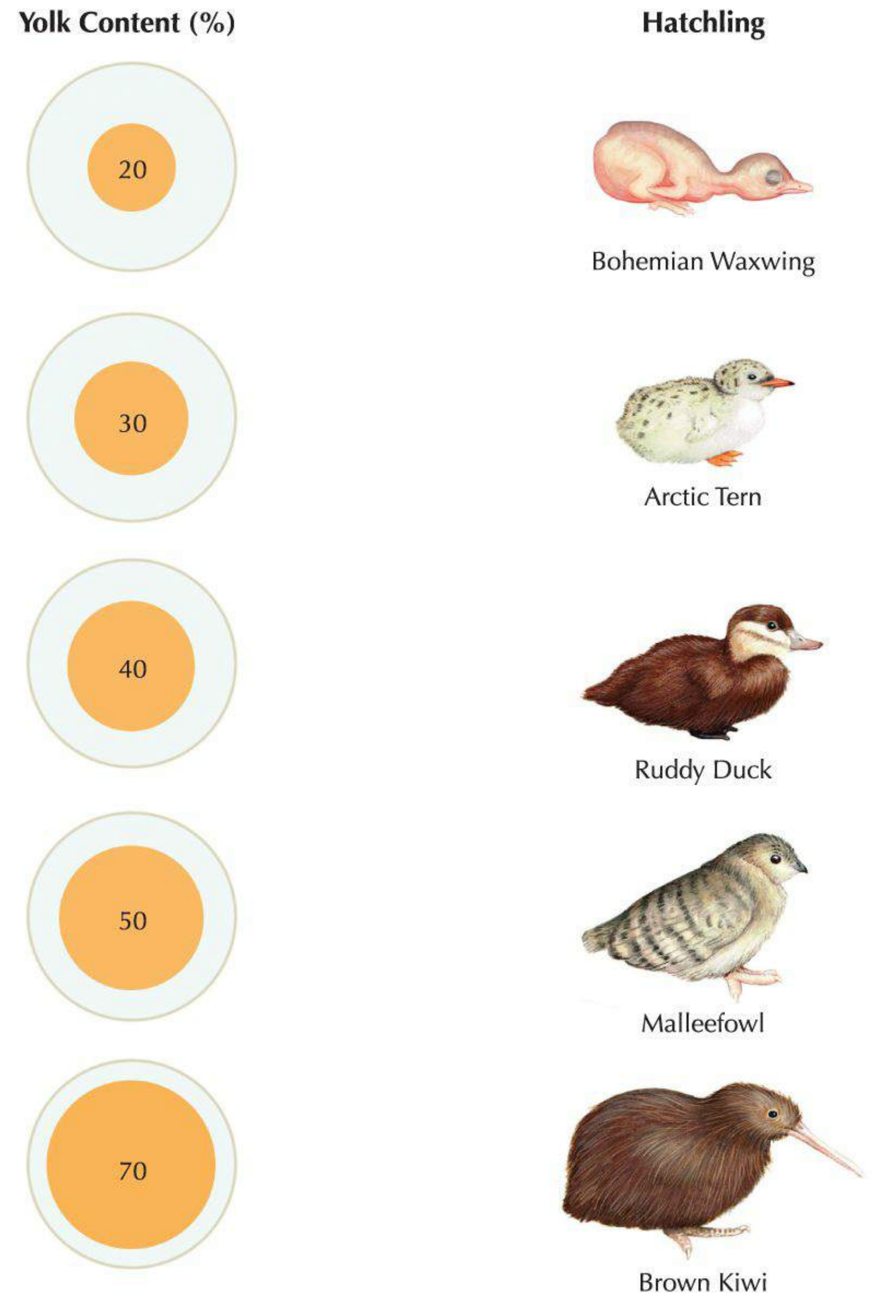
Cleidoic eggs evolved from the naked, amniotic eggs of ancestral reptiles, presumably in response to predation by soil invertebrates and microbes (Packard and Packard 1980). The flexible shell membranes of primitive reptilian eggs were water permeable, but the harder, calcified eggshells that evolved in the dinosaur ancestors of birds are less so. While the increased calcification of the avian eggshell provided better protection for eggs, it prohibits absorption of water essential to the encased embryo. The calcified cleidoic eggs evolved to include water within the closed system in the form of albumen (the egg white).

The albumen consists primarily of water (90 percent) and protein

(10 percent). Besides being the embryo’s water supply, the albumen is an elastic, shock-absorbing cushion that protects the embryo when the egg is moved or jolted. It insulates and buffers the embryo from sudden changes in air temperature and slows the cooling rate when the parent is not incubating. Albumen constitutes from 50 to 71 percent of the total weight of the egg.

In addition to the albumen, the freshly laid avian egg contains the yolk, which is an energy-rich food supply for the embryo. Lipids constitute from 21 to 36 percent of the yolk, and proteins make up another 16 to 22 percent. The rest is primarily water. The yolk sac, or vitelline membrane, functions as the early analogue of a stomach and intestines. This sac is ultimately absorbed into the embryo’s body cavity. The yolk initially cradles the tiny embryo in a small pocket.

Bird eggs vary greatly in composition, especially in the amount of yolk that they contain relative to their size (Sotherland and Rahn 1987). Most clearly, yolk increases from a low of about 15 percent in the eggs of gannets (Sulidae) to a high of 69 percent in the eggs of kiwis. The water content of the egg decreases as the yolk content increases. Increasing yolk content correlates with the chicks’ maturity at hatching, ranging from helpless (altricial mode of development) to mobile and sometimes independent (precocial; Figure 12–12). Chapter 16 looks at these different modes of development, including different rates of growth of the embryos in the eggs and the implications for the early life of birds and care by their parents.



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DATA FROM SOTHERLAND AND RAHN 1987

Figure 12–12 Differences in the relative amount of yolk in the eggs of different birds. Typical hatchlings are (*from top to bottom*) Bohemian Waxwing (altricial), Arctic Tern (semiprecocial), Ruddy Duck (precocial), Malleefowl (precocial), and Brown Kiwi (precocial).

Eggshells

Above all, the hard eggshell provides structural support and protects the egg from soil invertebrates and microbial infection. The external shell layers shield the embryo, conserve food and water, and facilitate the respiratory exchange of gases. Eggshells vary in thickness from paper thin in small land birds to as much as 2.7 millimeters thick in ostriches. They are strong enough to withstand the weight of an incubating adult but delicate enough to allow the chicks to break out. The shell usually constitutes from 11 to 15 percent of an egg's total weight—as much as 28 percent in extreme cases.

Among the most endearing qualities of birds' eggs are the varied and often intricate colors of their shells (see Figure 12–1). Only birds lay eggs with pigment-colored shells. Most eggs laid in open nest sites are exquisitely colored and patterned. Shaded ground colors, superficial blotches, and fine specklings or scrawls provide camouflage, helping to blend the smooth contours of an egg into its background.

The eggs of some ground-nesting species, such as nightjars, are conspicuously white. In these exceptional cases, the well-camouflaged incubating parent shields the eggs from the eyes of potential predators. The eggs of hole- or burrow-nesting species tend to be dull white. The need for camouflage is minimal in such nest sites. Enhanced visibility of the white eggs in the dark interior of the nest cavity may reduce accidental breakage by the parents. The whitish eggs of grebes are camouflaged by brownish stains from mud and rotting nest vegetation.

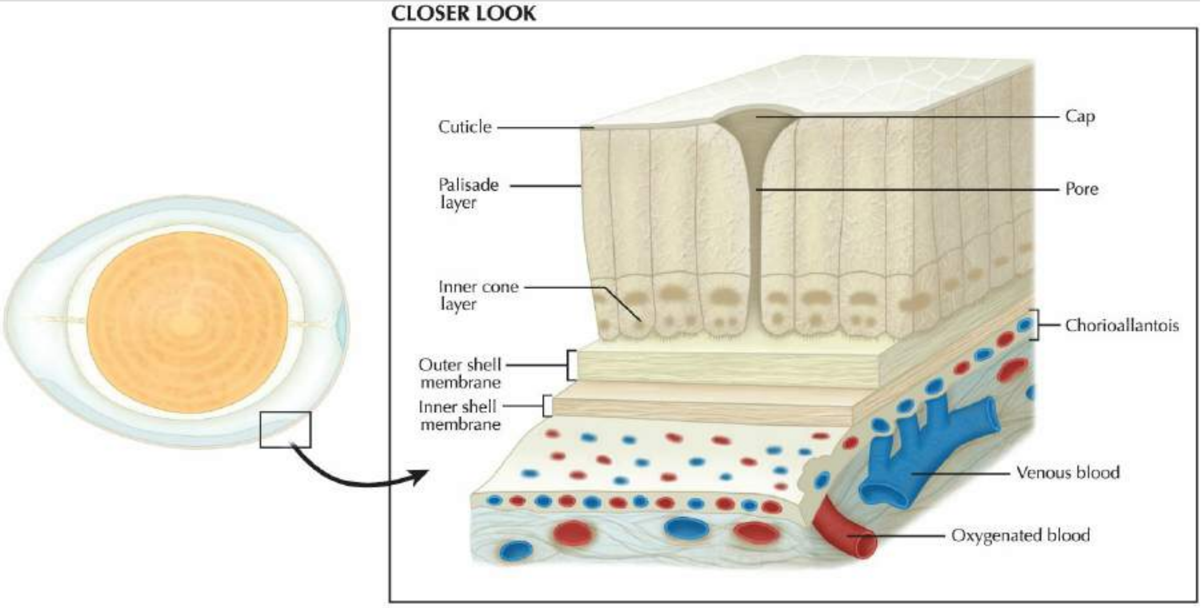
A variety of birds, such as American Robins, lay bright blue eggs.

The brightest blue eggs of all are those of the Great Tinamou of Central and South America. The function of blue coloration is still not known (Underwood and Sealy 2002). Remember that most mammalian predators don’t see color and that birds themselves don’t see colors exactly as we do.

Besides providing camouflage, brown speckling may strengthen the eggshell (Gosler et al. 2005). The amount of speckling on the eggs of Great Tits, caused by the addition of protoporphyrin pigments, varies with the thickness of the eggshell. Darker spots mark thinner and more permeable parts of the eggshell itself. The intensity of brown speckling also varies among locations according to the availability of the calcium needed by birds to produce the eggshells. Eggs produced in locations with reduced calcium are both thinner and more intensely speckled. Andrew Gosler and his colleagues suggested that the protoporphyrin pigments responsible for the brown speckles make the thinner eggs less brittle by lubricating the crystalline microstructure of the eggshell.

Different shell textures characterize the various families of birds. Accentuating the bright blues, greens, and violets of tinamou eggs is their polished, enamel-like texture. The eggs of ibises and megapodes, in contrast, have dull, chalky textures, whereas duck eggs are oily and waterproof. The eggs of cassowaries are heavily pitted, and the dark, pigment-scrawled eggs of jacanas appear lacquered. The astonishing eggs of the Guira Cuckoo have a blue background with a superficial pattern of raised ridges made of brilliantly white vaterite, a distinct crystalline form of calcium carbonate.

Eggshell textures are the result of a porous microstructure that regulates the passage of water vapor, respiratory gases, and microorganisms between the inside of the egg and the external world. The eggshell is permeated by thousands of microscopic pores (Figure 12–13). An ordinary hen’s egg has more than 7,500 pores, mostly at the blunt end of the egg.



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Data from Rahn et al. 1979

Figure 12–13 Pore canals allow gas exchange through the eggshell. Oxygen enters the eggs through pores in the cuticle and passes through columns of crystals to the permeable shell membranes. Carbon dioxide and water vapor escape to the outside environment through these same pores. Blood vessels in the capillary bed of the chorioallantois link the developing embryo to the gas-exchange pathway.

The shells of most avian eggs have simple, straight pore canals that widen slightly toward the openings on the exterior surface. The eggshell pores of swans and ratites, however, branch from their origins near the shell membrane into a more complex network (Tyler and

Simkiss 1959). Covering the exterior openings of the pore canals of all avian eggshells except those of pigeons and doves are tiny plugs or caps that may act as pressure-sensitive valves.

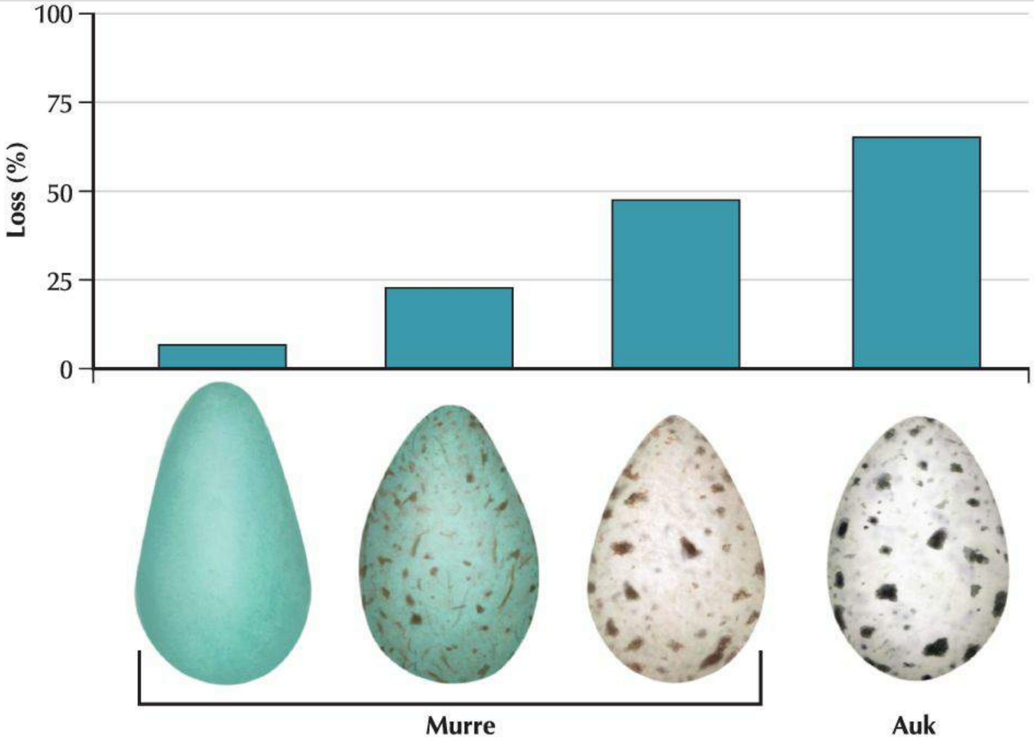
The structure of eggshells could limit the altitudinal or geographical distributions of birds (Carey 1991). Rates of potential water loss are high in dry habitats, where relative humidity is low, or at high altitudes, where barometric pressures are low. Such water loss would limit the hatchability of eggs without some adjustment in pore density or length. Domestic chickens change their eggshell microstructure with altitude (Rahn et al. 1982). There is also some compensation for altitude in the eggs of swallows (Carey 1980). The degree to which eggshell microstructures vary as a form of environmental adaptation invites new research.

Egg Sizes and Shapes

Modern bird eggs vary in size from the tiny (0.2 gram) pea-sized eggs of hummingbirds to the enormous two-gallon eggs of the extinct elephant birds (Aepyornithidae) of Madagascar. Although egg size increases with body mass, small birds lay much larger eggs relative to their body mass than do big birds. Most birds lay eggs ranging from 11 percent to only 2 percent of body mass, with some dramatic exceptions. Kiwis lay unusually large eggs. The Brown Kiwi lays two, sometimes three, 500-gram eggs, each of which is 25 percent of the female’s own mass. It lays these enormous eggs at four-week intervals (Figure 13–1). Occasionally, birds lay dwarf, or runt, eggs that are less than half the size of their normal eggs. Most of these eggs lack a yolk and result from aberrant stimulation of the oviduct by an object, such as a blood clot.

The term “egg shaped” brings to mind a rounded structure, longer than it is wide and slightly more pointed at one end than at the other. The familiar hen’s egg is an example. Some factors influence the shapes of the eggs of domestic hens, but sex is not one of them. Males do not come from pointed eggs, nor do females come from more rounded ones, as Aristotle once suggested and popular wisdom would have it. Eggs vary from the nearly spherical eggs of petrels, turacos, owls, and kingfishers to the pointed (pyriform—literally “pear shaped”) eggs of plovers and murres. Between these shapes are the ellipsoidal, or biconical, eggs of grebes, pelicans, and bitterns.

What determines egg shapes? They are a compromise between structural advantages, clutch volume, and egg content. Spherical eggs maximize shell strength, the conservation of heat, and the conservation of shell materials because they maximize volume relative to shell surface. Pointed eggs—for example, those typically laid by shorebirds—further enhance the volume or content of large eggs within the limits set by the area that an incubating parent can cover with its body. The pointed eggs of murres and other cliff-nesting birds have an additional advantage: they roll only in a tight arc, lessening their chance of falling from nest ledges (Figure 12–14).



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Data from Tschanz et al. 1969, Drent 1975

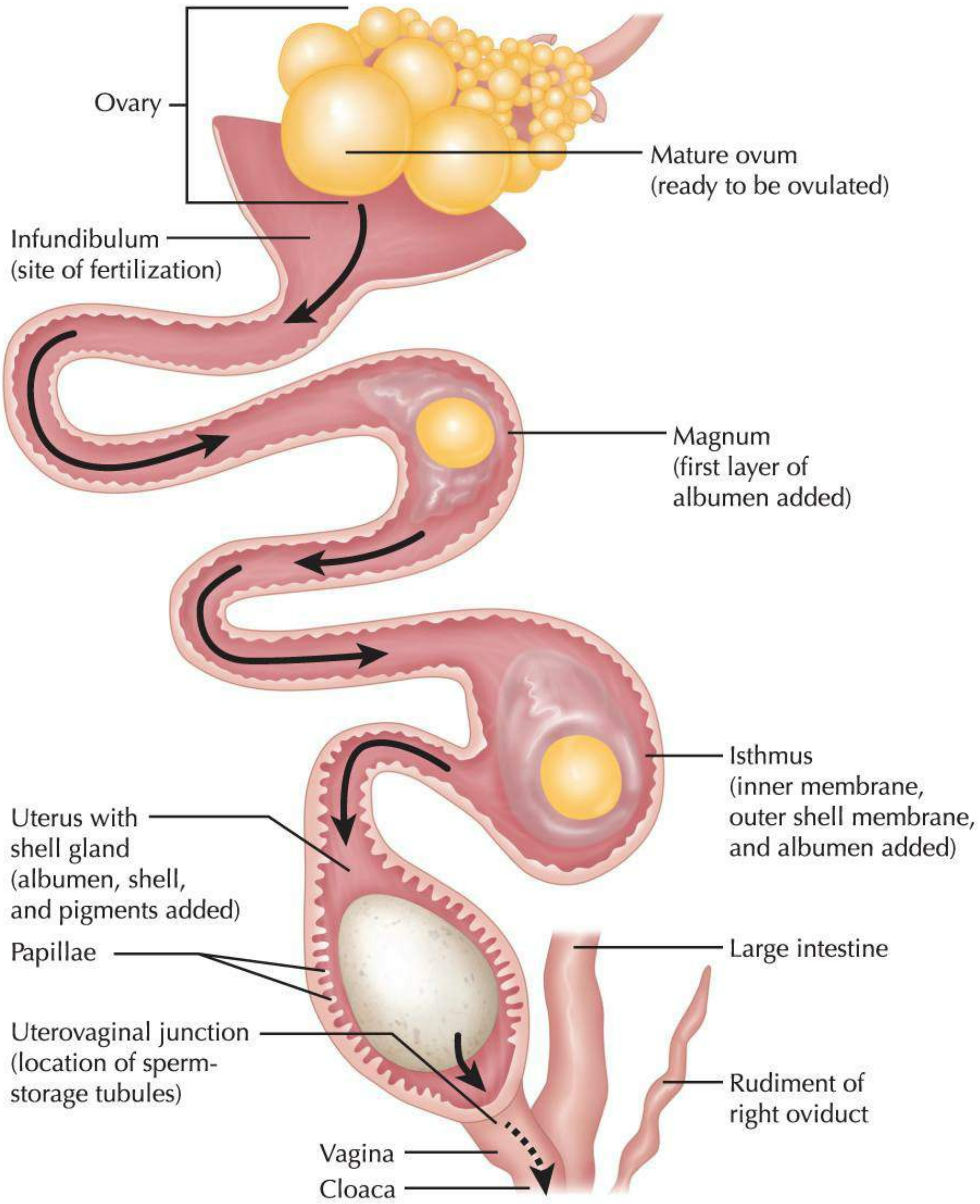
Figure 12–14 Pointed eggs, such as those of the Common Murre, are less likely to roll off a cliff ledge than are the more rounded eggs of auks, such as Razorbills. Data presented here are from 400 trial experiments in which eggs of each type were pushed gently on a nesting ledge.

12.7 Egg Formation in the Oviduct

A freshly laid egg consists of (1) the ovum, if unfertilized, or an embryo, if fertilized; (2) a full supply of food to nourish the embryo; and (3) protective layers to safeguard the internal environment. These components are assembled in an orderly way in the egg’s trip down the oviduct.

The egg’s passage through the oviduct usually takes about 24 hours but may require a week. After only a brief stay in the infundibulum (20 minutes), the egg of a chicken enters the main length of the oviduct, where it remains for three to four hours, progressing at a rate of 2.3 millimeters per minute, as if on an assembly-line conveyor belt. The albumen is added in this period. The membranes of egg and shell are added next in a one-hour passage through the isthmus section of the oviduct at a rate of about 1.4 millimeters per minute. Shell formation in the uterus then takes from 19 to 20 hours.

The oviduct is a long, convoluted tube with elastic walls able to accommodate the egg as it enlarges (Figure 12–15). Peristaltic contractions of smooth-muscle layers propel the egg from the infundibulum to the vagina. A glandular epithelial lining successively adds the albumen, shell membranes, and pigmentation in distinct anatomical sections of the reproductive tract.



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Data from Evans and Heiser 2004

Figure 12–15 Formation of the complete egg in the oviduct, starting with the release of a mature ovum into the infundibulum. Layers of albumen and the shell membranes are added as the egg proceeds down the oviduct. The shell gland of the uterus adds pigments as a final stop. Sperm-storage tubules are located at the uterovaginal junction of the oviduct.

As a first step, the anterior section of the oviduct, called the **magnum,** adds four layers of albumen. The yolk rotates gently in response to the slight spiral arrangement of the cellular ridges that line the oviduct’s interior. Twisted strands of albumen, called **chalazae,** form as the yolk rotates (see Figure 12–5). They act as small built-in springs that help stabilize the yolk position and keep the embryo on the dorsal side of the finished egg.

Covered with albumen, the egg enters the isthmus of the oviduct, which surrounds the albumen first with an inner membrane and then with an outer shell membrane. This pliable and tough outer membrane is usually firmly attached to the shell itself. It is riddled with tiny pores that allow the passage of gases and liquids by osmosis and diffusion. Small amounts of pigments added to the shell membrane may impart a pinkish hue.

The final stage of egg production is the addition of a hard shell. It consists mostly of calcium carbonate ($CaCO_3$) in the form of calcite crystals. The shell is added in the uterus section of the oviduct. Eggshells are made of inorganic calcium and magnesium salts (carbonates and phosphates) embedded in a network of delicate, collagen-like fibers (Johnson 2000).

Two distinct layers make up the shell microstructure: (1) an inner cone layer with basal protuberances that adhere to the shell membrane and (2) a palisade layer that makes up most of the shell material (see Figure 12–13). Crystalline calcite is the principal construction material. This inorganic salt will gradually be taken from the shell and used as calcium for bone growth by the embryo.

Covering the outer surface of the eggshell is the **cuticle,** a thin, proteinaceous froth of air bubbles that blocks invasion by microorganisms. The chemical elements that make up eggshells are extremely stable. For example, with proper calibration for past temperatures, fossil ostrich eggshells can be used to estimate the ages of archaeological sites as old as 1 million years (Brooks et al. 1990).

Magnesium and phosphate are minor components of the shell structure, but even slight variations in their concentrations affect the strength and thickness of the shell, altering the delicate balance of gas and water exchange required by the embryo. Magnesium is usually concentrated in a very thin layer of the inner shell, where it plays a role in the reclamation of eggshell salts by the embryo.

Pesticides also affect shell thickness, causing serious declines in raptors, waterbirds, and others high on the food chain. Pesticides, such as DDT and DDE (a breakdown product of DDT), affect normal eggshell formation by increasing magnesium and phosphate levels—with fatal consequences. For example, the normal level of magnesium in Common Tern eggshells is 1.54 percent, and the normal phosphate level is 0.25 percent. Exposure to DDT and DDE increases these concentrations to 2.1 percent and more than 0.6 percent, respectively, causing denting and developmental failure (Fox 1976). An even higher phosphate level (0.86 percent) has been associated with dead embryos.

In the 1960s, these pesticides were responsible for the widespread eggshell thinning and reproductive failure of Brown Pelicans (Figure 18–18), many species of raptors, and penguins. Many eggs were so thin that the weight of the incubating parent crushed them. Reduced pesticide use has led to improved eggshells and rebounds of endangered species.

At the end of the egg's journey through the oviduct, the shell gland adds shell colors, first as pigments deposited in the course of shell formation—the ground color—and later as superficial markings in the cuticle, the thin transparent coating of protein molecules that covers the entire shell. The shell pigments are porphyrins (see Chapter 4), which derive from the hematin of old blood cells that have been broken down in the liver and transformed into bile pigments.

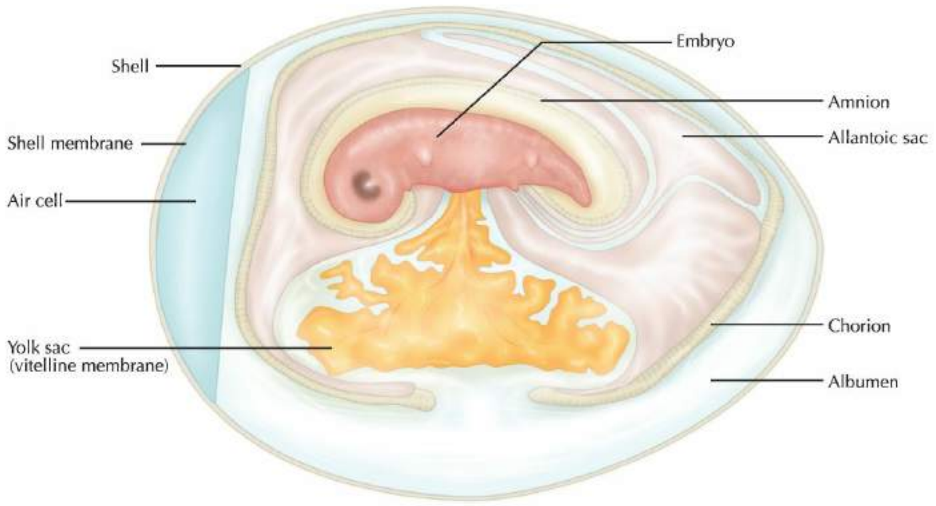
No bird retains and nurtures a fertilized egg inside its body and bears live young. All birds lay a shelled egg for external incubation—a trait called **oviparity.** The high body temperatures (40°–42°C) of birds preclude the retention of eggs inside the body cavity and mandate the rapid expulsion of the fertilized egg to cooler temperatures outside the body, followed by external incubation in nests.

Birds eject the finished egg voluntarily with their powerful vaginal musculature. The large size of most eggs precludes the retention of more than a single egg. Larger retained clutches would increase the energy cost of flight and make females more vulnerable to predators. Most birds lay their eggs early in the morning, probably to avoid the risks that daytime activity could pose to a bird carrying a heavy, fragile egg in its oviduct.

Nonavian reptiles lay all their eggs at once, whereas birds (with one ovary) lay their eggs serially one a day or over a series of days. Theropod dinosaurs, including the ancestors of birds, had two ovaries that produced eggs two at a time to build a clutch serially (Sato et al. 2005; Varricchio and Jackson 2016). Most passerines, ducks and some geese, hens, woodpeckers, rollers, small shorebirds, and small grebes lay an egg a day. Ratites, penguins, and large raptors take from three to five days, and boobies and hornbills take as many as seven days. At the other extreme, mound builders require from four to eight days to produce one of their huge eggs that will hatch precocious young (see section 15.4).

12.8 The Embryo

Three extraembryonic membranes support the life and growth of the avian embryo (Figure 12–16). The **amnion** surrounds only the embryo, which floats in a contained environment of water and salts. The **chorion** is a protective membrane that surrounds all the embryonic structures. The **allantoic sac** functions in both respiration and excretion. This sac increases in size as development proceeds. A growing network of fine capillaries keeps it well supplied with blood. Pressed tightly against the chorion and the shell membranes, the resulting “chorioallantois” is the site of export of carbon dioxide produced by the embryo and import of oxygen from the outside world (see Figure 12–13). The allantois also acts as a sewer for the storage of toxic nitrogenous wastes.



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DATA FROM BELLAIRS 1960

Figure 12–16 The developing embryo and the extraembryonic membranes.

The avian egg provides a secure, self-contained environment for embryonic development. It also imposes restrictions on the kind of nitrogenous waste that the embryo can produce. Ammonia is not a suitable waste product because the embryo, confined in its shell, cannot excrete it. Unexcreted ammonia would rapidly reach toxic concentrations. Nor is urea, a water-soluble compound, acceptable. The egg lacks the space required to store large volumes of this dilute waste. Birds, both embryonic and adult, have an excellent solution to their waste-disposal problem. Uric acid is a nonsoluble form of nitrogenous waste that can be deposited safely as tiny crystals inside the allantois. It is not toxic, and it does not require large volumes of water to flush it from the adult system.

Diffusion through the shell membranes allows the exchange of water vapor and gases, which are vital to embryonic life. Eggs breathe passively. No active, regulated exchange is known, nor is it required to account for the known rates of exchange of gas and water vapor. The density of pores is an exquisite compromise between the high densities that would facilitate rapid gas exchange and the low densities that would minimize water loss.

The dynamics of gas exchange change as incubation progresses. The eggshell thins progressively as calcium is removed from it and incorporated into the embryonic skeleton. This thinning increases the rate of gas exchange at a time of increasing respiration by the growing embryo. The permeability of the shell membranes to oxygen also increases as they dry out, and oxygen moves inward more rapidly as the growing embryo draws increasing amounts of oxygen from the chorioallantois.

12.9 Clutch Size

The number of eggs that a bird lays in one set, called the **clutch,** is subject each season to the availability of energy and other resources. Each egg requires a substantial investment of energy and nutrition. The production of a full clutch within a short time interval is a major feat that can strain a female's daily energy budget. Food shortages can reduce or stall egg production and thus affect clutch size. Optimal clutch sizes are also subject to long-term trade-offs that affect lifetime reproduction success (Chapter 17).

Generally speaking, the amount of energy transferred to the egg varies from 4.2 kilojoules per gram in passerine birds to as much as 8.4 kilojoules per gram in the fat-rich eggs of waterfowl. The efficiency of energy transfer is only about 20 percent. A laying female passerine bird, for example, must eat five kilojoules of food for every kilojoule that is transferred to her eggs. Estimates of the daily costs of egg production range from 45 to 60 percent of basal metabolic rate for passerines, from 80 to 130 percent for shorebirds and fowl-like birds, and to more than 200 percent for waterfowl (Carey 1996). How ornithologists should best measure the direct costs of egg production is an ongoing debate (Williams 2005), but all agree that these costs are significant.

Egg production also requires sources of protein and of minerals, such as potassium and calcium. Poor supplies of these nutrients may limit egg production, especially in birds that eat fruit and seeds. Providing females with extra protein causes egg size, clutch size, or both to increase in many species. The importance of calcium for eggshell production was noted earlier.

The greatest costs of egg formation are incurred during the period of yolk production. The peak daily energy expenditure for total egg production depends on the amount of overlap in the growth cycles of separate ova and on the number of follicles growing simultaneously. For a Fiordland Penguin, for example, the peak occurs on day 20 as it adds albumen to the first egg at the same time as it adds the last of the yolk to the second egg (Grau 1982).

The resources required for egg production come from stored reserves supplemented by increased daily intake. Species such as waterfowl, which draw heavily on stored energy and nutrient reserves to produce their large, expensive eggs, are called **capital breeders.** Wood Ducks, for example, lay large clutches of about 12 richly provisioned (and, therefore, energy-expensive) eggs at a total metabolic cost of 6,000 kilojoules (Drobney 1980). A hen's fat reserves provide most of this energy (88 percent). The protein content of the eggs, however, comes from invertebrates eaten by the hen during the laying period, which requires an additional investment of energy from her fat reserves. The use of stored reserves for egg production by passerine birds is not yet well studied (Williams 2005).

Other birds are **income breeders.** These species ingest, on a daily basis, the resources that they need for egg production. Brown-headed Cowbirds are income breeders. They do not use stored reserves despite their great egg production—approximately an egg a day for more than a month. Instead, they obtain the nutrients for egg production directly from the diet (Ankney and Scott 1980).

Arctic shorebirds also are income breeders. Ornithologists once assumed that female Arctic shorebirds carried most of the resources that they would need for egg production when they migrated north. They supposedly built up these reserves at their refueling stopovers en route to the breeding grounds. Analyses of carbon isotopes, however, showed it not to be the case (Klaassen et al. 2001). The carbon-isotope signatures of eggs and natal down of the hatchlings match those of the Arctic tundra, demonstrating the direct transfer of resources ingested after arrival in the Arctic.

Laying females draw some of the calcium needed for eggshells from their own bone tissues. They also supplement that source with extra calcium intake. Rodent teeth and small bones on the forest floor are important sources of calcium for egg production. So are snails, wood lice, and millipedes (Bure and Weldinger 2003). These essential natural sources of calcium are declining in some forests because of acid rain, which dissolves the calcium in the litter on which land snails, for example, depend for their shells (Graveland et al. 1994). Declines in the abundance of land snails then cause poor reproduction by forest birds. Experimental supplements of calcium can reverse reproductive decline by improving egg volume, eggshell thickness, the onset of breeding, and chick health (Mänd et al. 2000).

Other costs of egg production may not be resource based and are more subtle and mostly speculative. For example, decreases in breast muscle and increases in body weight during the egg-laying period may impair a female’s ability to fly and hence her ability to avoid predators (Veasey et al. 2001). Female Blue Tits are 14 percent heavier and fly 20 percent more slowly during the egg-laying period than they do after the eggs hatch, but males stay the same (Kullberg et al. 2002). Another potential cost may stem from the elevated levels of estradiol hormone associated with egg laying. This hormone inhibits the production of red blood cells and reduces the red-blood-cell count of laying females, potentially impairing their ability to fly and their general aerobic performance (Williams 2005).

Non–resource-based costs of egg production may be more important than resource-based costs (Ketterson and Nolan 1999; Williams 2005). Reproductive hormones have a broad effect on the body, affecting immunocompetence, organ size, and the protection of blood vessels and nerves. Minimizing such costs in the short term by limiting reproductive investment potentially increases longevity and lifetime reproductive success. Linking these short-term constraints to long-term costs and benefits remains a major challenge for students of avian life-history strategies.

REVIEW KEY CONCEPTS

12.1 The Sexes

Female birds have two different sex chromosomes (ZW), whereas males have two similar sex chromosomes (ZZ). Two hormones secreted by the anterior pituitary control the gonads and in turn secondary sexual characteristics. Follicle-stimulating hormone (FSH) regulates gamete formation. Luteinizing hormone (LH) regulates hormone secretion by the testes and the maturation of follicles in the ovary.

Key Terms: oology, gonads, sex chromosomes W and Z, heterogametic, homogametic, bilateral gynandromorphs, testosterone, estrogen

12.2 Ovary and Ovum

Just a few of the many primary oocytes in the ovary are released as ova and fully provisioned first with lipids and nutrients. Female birds can control the sex of offspring at ovulation by means unknown but not by absorbing or aborting female eggs.

Key Terms: medullary tissue, cortex, oocytes, albumen, follicular maturation, central latebra, vitellin, carotenoids, infundibulum, parthenogenesis, primary sex ratio

12.3 Testes and Sperm

The testes of birds are housed inside the abdominal cavity at body temperature, not in external scrota as in most mammals. Sperm develop primarily at night when the bird’s body temperature is slightly lower.

Key Terms: testes, seminiferous tubules

12.4 Genitalia and Copulation

Most birds lack external genitalia. Ratites, waterfowl and some land fowl, however, have penises, some of which are extraordinary organs evolved by sexual selection and sexual conflict. Copulation in other birds normally entails only brief cloacal contact.

Key Terms: penis, cloacal kiss

12.5 Fertilization and Sperm Competition

Female birds of many species store viable sperm for weeks in special storage tubules. Females use the storage tubules to mediate competition among sperms received from different males.

Key Term: polygynandry

12.6 The Complete Egg

The avian egg is one of the most complex reproductive cells achieved in the evolution of animal sexuality. The avian eggshell evolved to protect the embryo from soil invertebrates and microbes.

Key Term: cleidoic

12.7 Egg Formation in the Oviduct

After fertilization, the egg with its tiny embryo passes through different regions of the oviduct that add albumen, membranes, and a hard shell made of calcium carbonate. Females transfer to their eggs immune factors and steroid hormones in variable doses that affect the quality and competitive ability of their offspring.

Key Terms: magnum, chalazae, cuticle, oviparity

12.8 The Embryo

Three extraembryonic membranes support the life and growth of the avian embryo: the amnion, the chorion, and the allantoic sac. Pores in the microstructure of the eggshell permit gas exchange and minimize water loss through the eggshell.

Key Terms: amnion, chorion, allantoic sac

12.9 Clutch Size

Major investments of energy and nutrients drawn from reserves or daily consumption can limit clutch sizes and female health. Declining sources of supplementary calcium, such as snail shells or rodent teeth, can impair reproductive performance.

Key Terms: clutch, capital breeders, income breeders

APPLY YOUR KNOWLEDGE

1. Describe the features of the female bird’s reproductive tract and egg production that minimizes the negative impact on a female’s ability to fly.
2. Explain the interplay between brain and gonads through the production of hormones that regulate the reproductive cycle.

3. Describe the genetic mechanism of sex determination in birds compared to that of mammals. Under what conditions is it advantageous to produce more female young and to produce more male young? How can females control the ratio of male to female eggs?
4. Compare and contrast copulation in passerines and ducks. What adaptations of a male's sperm and reproductive organs enhance reproductive competition and fitness? What adaptations have females evolved to enhance control over paternity?
5. Explain why it is more likely that the last male to copulate with a female is the more likely father of a female's offspring.
6. Describe the cleidoic egg with a calcified shell. Which features of the egg (a) protect the embryo, (b) supply water, (c) exchange gases, and (d) store waste?
7. Describe the sequence of egg formation from the time of fertilization to the time of egg laying.
8. How do pesticides and acid rain compromise the production of a viable egg?
9. Compare and contrast the different strategies of capital breeder and income breeder females that meet the resource demands of producing a clutch of eggs.

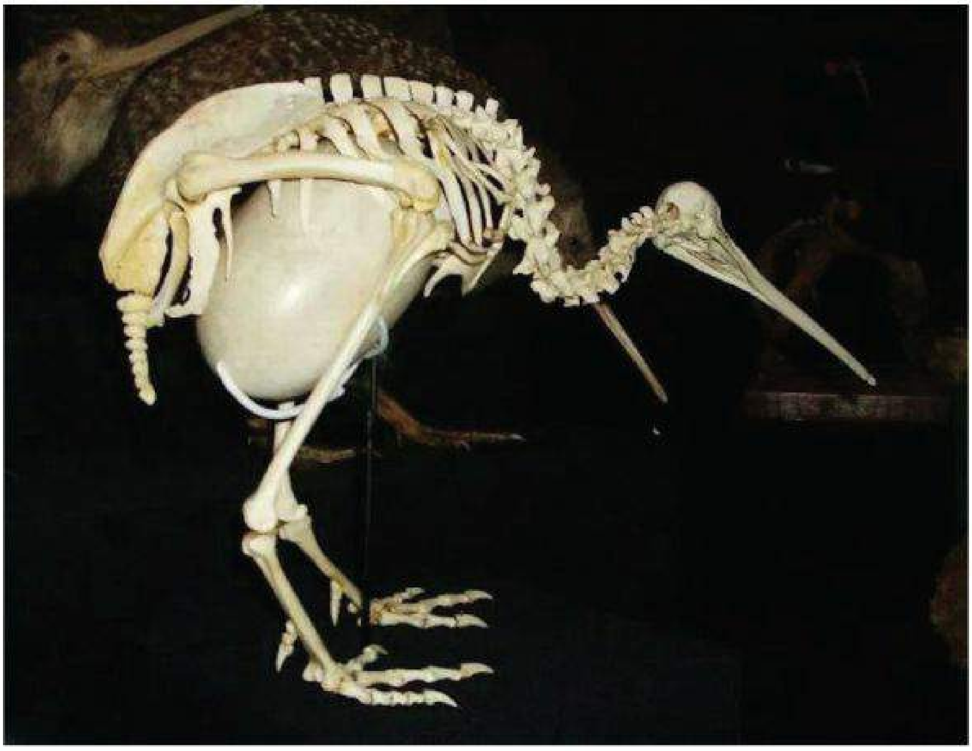
CHAPTER 13 *Sexual Selection*

Tim Laman

Birds-of-paradise present elaborate mating displays of fancy plumages that evolved from female preferences.

> The lek is nature's version of a singles bar.
> [Sherman 1999, p. 119]

The eggs of the flightless Brown Kiwi are huge, each 25 percent of a female kiwi’s body size (Figure 13–1). They are an extreme example of a female bird’s reproductive investment. In contrast, male kiwis and other birds invest differently, producing vast numbers of tiny sperm, capable of fertilizing many such eggs.



MUSEUM OF NEW ZEALAND TE PAPA TONGAREWA

Figure 13–1 The Brown Kiwi produces an enormous egg relative to its body size. This species provides an extreme example of the great investment of reproductive energy that female birds put into egg production.

The different investments that males and females make into their gametes drive different options for maximizing individual reproductive success, including their mating opportunities and how best to invest in quality of offspring. Most birds form a social pair bond with a bird of the opposite sex. They raise their offspring together because both parents are needed to provide adequate care. But beneath the veneer of cooperation lie major conflicts of interest and hidden agendas. Males balance the options of mating with extra females against caring for their own young.

Conversely, females may improve the quality of their offspring through extra-pair copulations with high-quality males. DNA fingerprinting analyses reveal chicks fathered by neighbors in many broods. Adding further uncertainty to the genetic identity of chicks in a single nest is the possibility of brood parasitism by other females, resulting in nestlings unrelated to either parent.

This chapter starts with a look at the attributes that affect birds' reproductive success. Front and center are the challenges of mate choice. Pair formation requires a critical assessment of potential mates, especially by females, which evaluate traits that may indicate a male's genetic quality. Females can use elaborate male courtship displays and plumages to assess male condition, but these displays and plumages may also help males achieve dominance and access to females. Featured examples include species that display on communal display grounds known as leks, such as manakins and Ruffs, as well as bowerbirds and their artistic crafts. The chapter concludes with an overview of monogamy (one male to one female), the most common avian mating system, with emphasis on the role of the extra-pair copulations that sire a substantial fraction of offspring in many species of songbirds. Alternative breeding systems—polygyny (one male to multiple females), polyandry (one female to multiple males), promiscuity, brood parasitism, and cooperative breeding—are the province of Chapter 14.

13.1 Mate Choice and Sexual Selection

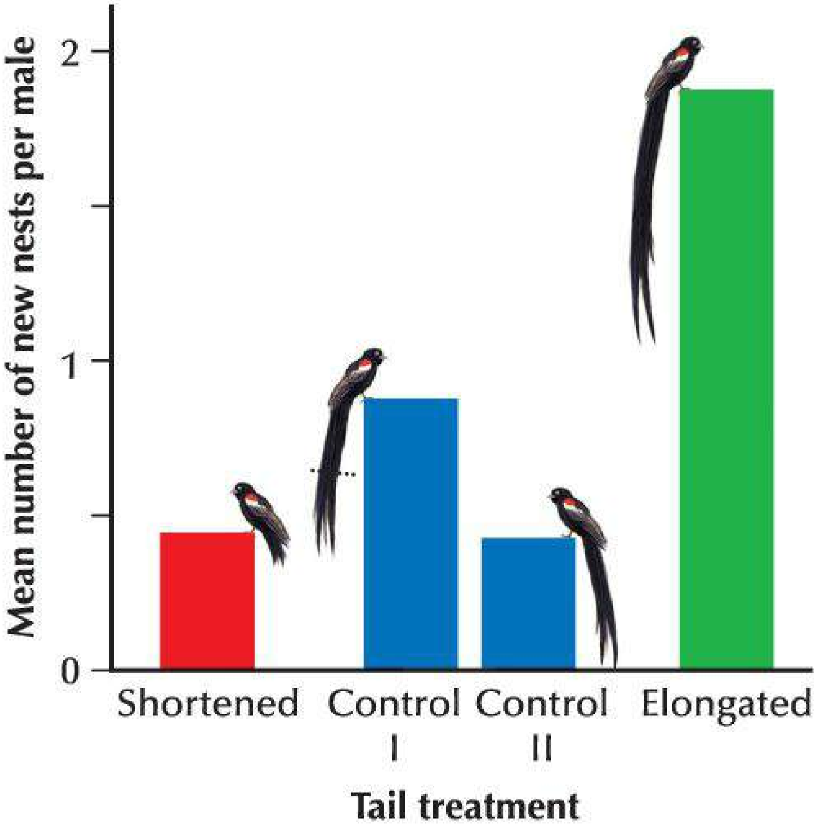
Striking sexual differences in plumage (and size) are typical of many birds. Darwin concluded that exaggerated sexual differences, such as the “tail” of a peacock or displays of the birds-of-paradise, evolve within species over numerous generations as a result of what he called **sexual selection**—namely, differences in mating or fertilization success that arise from contests among males for mates and female preferences for particular males (Figure 13–2). The latter—female mate choice—tends to drive the evolution of elaborate sexual ornaments such as display and song, and males vie with each other to be chosen. As differential reproductive success increases, so do the display features of preferred males, such as large size, fancy plumage, intricate songs, and striking displays. The resulting evolutionary process of sexual selection leads to differences between the sexes in size and ornamentation, called **sexual dimorphism.** Darwin’s insights into the evolutionary role of sexual selection are now largely confirmed, but the roles of female choice, competition among males, and resources other than mates intertwine in ways even more intricate than Darwin proposed.

(A) blickwinkel/Alamy. (B) Tim Laman/Getty Images. (C) Tim Laman/National Geographic Creative. (D) Tim Laman

Figure 13–2 Elaborate plumages and displays of male birds-of-paradise: (A) Lesser Bird-of-paradise, (B) Magnificent Bird-of-paradise, (C) Superb Bird-of-paradise, and (D) Magnificent Riflebird.

Consider the male Long-tailed Widowbird of Africa, which is jet black with bright red epaulettes such as those of the familiar Red-winged Blackbird of North America. This widowbird defends marshland territories in the highlands of Kenya. True to its name, the male Long-tailed Widowbird has an enormous tail, as much as half a meter long. Sexual selection favors the long tail of the male because it enables female widowbirds to spot him from afar. Humans can spot a displaying Long-tailed Widowbird from more than a kilometer away.

In a classic experiment, Malte Andersson increased the tail lengths of some male widowbirds by 25 centimeters and decreased the tail lengths of others by that same amount (Figure 13–3). Males with “super” tails attracted more females to nest on their territories than did males with shorter tails or tails of normal length. These experimental manipulations, however, did not affect a male’s ability to hold his territory. Female preference for an exaggerated trait, rather than male competition, drives sexual selection in Long-tailed Widowbirds. But, we should ask, what advantages, if any, accompany the preference for a long-tailed male?



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DATA FROM ANDERSSON 1982

Figure 13–3 Female Long-tailed Widowbirds prefer males with long tails. In this experiment, the tails of some males were shortened, and the tails of others were extended. Control I males had their tails cut off and then restored, and Control II males had unaltered tails. The ability of males to attract females to their territories directly correlated with their tail length.

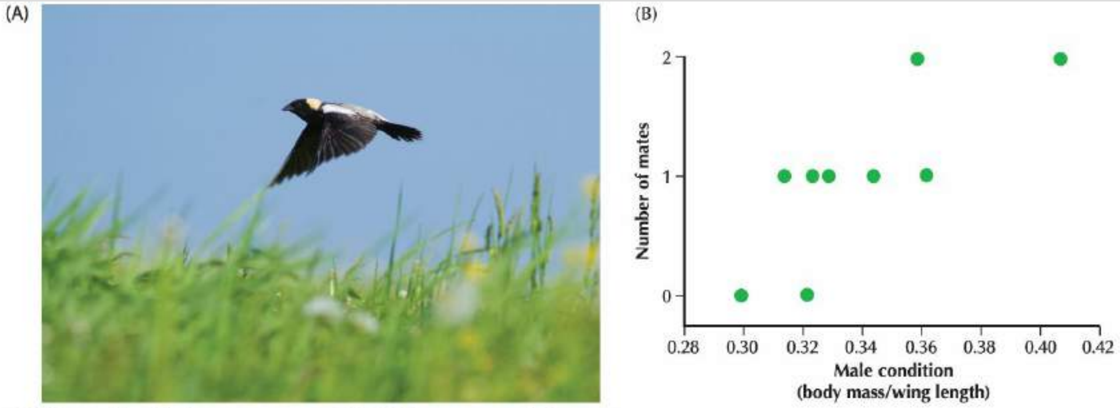
Studies of birds guide research on the mating systems of animals of all kinds. Three general hypotheses explore why females choose males with more elaborate plumage or displays. They are called the “good genes,” the “direct benefits,” and the “arbitrary choice and runaway selection” hypotheses, respectively. The good genes hypothesis proposes that exaggerated male plumage and courtship displays truthfully signal genetic or physiological superiority. This hypothesis assumes that females recognize the superior males and select them to sire offspring. What aspects of genetic or physiological superiority might exaggerated courtship displays serve to index? One possibility would be a male’s superior survival skill. For example, the enormous tail of a widowbird or a peacock might actually be a handicap during flight or escape. So would be bright colors that might attract predators. Males that survive to display such handicaps would have superior stamina or abilities to escape predators. Evolution would tend to favor bigger and bolder badges of this so-called handicap superiority if females preferred to mate with the males that bore such badges.

The direct benefits hypothesis proposes that sexual ornaments communicate a potential mate’s ability to provide resources or protections that enhance the female’s survivorship or her fecundity. Unlike the good genes mechanism, the female and her offspring do not benefit genetically; instead, they benefit materially from resources such as higher-quality territories, protection from predation, or lower risk of sexually transmitted diseases.

Challenging both the good genes and direct benefit hypotheses is the possibility that sexual ornamentation evolves through arbitrary choice and runaway selection for aesthetically pleasing ornaments (Prokop et al. 2012; Prum 2017). Darwin himself previewed the concept of aesthetic evolution, including the evolution of traits that are merely attractive and provide no adaptive benefit to individuals who prefer them. This hypothesis stresses a process of ornament and display elaboration based on coevolved female preferences for fancier males—or "fashion icons" (Ridley 1992). Sexy males, it is presumed, will have sexy sons that are more popular than others, driving both the evolution of genes for the ornament and genes for the preference. Once the process of favoring slightly more elaborate displays or plumages begins, only natural selection on mating preferences for good genes or direct benefits can prevent further elaboration from happening. The process of imprinting in young birds could foster adult preferences for new and fancier ornamentation (Chapter 16).

Choice of Superior Mates

Assessment of prospective partners is a vital aspect of the early stages of courtship and pair formation. The ornaments and displays favored and maintained by sexual selection would be those that reliably reflect superior conditions of certain males, enabling females to select the best possible mates. For example, House Finch females prefer brightly colored males, which have better survival rates and are better family providers (see Box 4–4). The familiar flight displays of male Bobolinks over lush fields may advertise their condition. Females favor males that can display longer. Such males have larger fat reserves and consequently fledge more young than their neighbors do (Mather and Robertson 1992; Figure 13–4). Experiments confirmed this female preference: males with clipped wings had shorter flight displays (3.5 seconds) than those of control males (5.8 seconds) and acquired significantly fewer mates (average = 0.67) than did control males (average = 1.0).



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(A) © Mary Read/naturepl.com. (B) Data from Mather and Robertson 1992

Figure 13–4 Honest advertising. (A) Female Bobolinks prefer males in good condition with longer flight displays. (B) The average number of females that (unaltered) males attracted increased with their relative condition, defined in terms of their total body mass relative to wing length.

One application of the good genes hypothesis proposes that ornamented plumage provides an index to a male’s health, particularly his resistance to pathogens and parasites (Hamilton and Zuk 1982). Females could detect disease-prone males by the lower quality of their display plumage or by their reduced display stamina. Among their many effects, parasites reduce the sheen of ultraviolet coloration of bird feathers. The iridescent blue plumage of male Satin Bowerbirds, for example, has a peak in the ultraviolet (Doucet and Montgomerie

2003). The visual intensity of this peak predicts the male’s level of infection by blood parasites because ultraviolet color decreases with increasing infection. Ultraviolet signals also are important for mate choice in bluebirds (see section 4.4), Blue Tits (Box 13–1), and many other species as well (Siitari et al. 2002).

Box 13–1

Blue Tits Choose Mates in the Ultraviolet

Male and female Blue Tits look almost the same to the human eye but not to each other (Andersson et al. 1998; Hunt et al. 1998). The plumage of both sexes includes strong ultraviolet (UV) reflectance, which makes the birds more conspicuous to each other against the background colors of the woods in which they live. Males also have a brilliant purple crown patch that we cannot see. The males display their UV crown patch prominently during courtship, especially in the early morning light. Consistent with the process of sexual selection, females prefer males with the brightest crown patches. Females also pair assortatively: those with the brightest UV reflectance in their own plumage pair with the most brightly colored males.

The intensity of the crown patch color indicates a male’s viability, predicting its survival to the next breeding season (Sheldon et al. 1999). In addition, males that are genetically more heterozygous (at protein loci) have brighter crown patches than those of males with less genetic variability (Foerster et al. 2003). Even more startling, female Blue Tits increase the proportion of male offspring in their broods in proportion to the UV reflectance of their mates. They skew the sex ratio of their young to favor the best males. Experimental masking of the crown patch of their mates erases the bias toward male offspring.

ROB CHRISTIAANS/SHUTTERSTOCK

Male Blue Tits have a brilliant blue crown patch visible with substantial ultraviolet reflectance. Females prefer males with the brightest crown patches.

Other evidence for the use of a bird's appearance as an index to its health comes from studies of Red Junglefowl, which are the ancestors of domestic chickens. Marlene Zuk and her colleagues (1990a, 1990b) first established that hens of the Red Junglefowl mated more quickly with roosters bearing large, fleshy, red combs on their heads. The hens may use comb size as an index to the health of a potential mate. Comb size is strongly affected by the level of blood testosterone, which, in turn, affects the bird's physical condition. Intestinal nematode worms reduce comb size with the result that hens prefer roosters without worms over infected ones.

Parasites also affect the quality of male ornaments that serve as the basis for female choice in Barn Swallows. The long, forked tail streamers of the familiar Barn Swallow may be a male’s most important ornament (Møller 1994; Evans 1998). Streamers have important aerodynamic functions, including the reduction of flight costs. In addition, the streamers are subject to sexual selection. Male swallows attract females by singing and displaying their outermost tail feathers, which are larger than those of females. Tail length serves as an index to a male’s load of ectoparasites, particularly bloodsucking mites, which reduce weight, tail-feather length, the survival of nestlings, and the reuse of nests. Unmated males have more parasites than mated males, and mated pairs exhibit similar parasite loads; that is, males and females with the lowest parasite loads tend to pair with each other. Female swallows mate more readily with males that have longer tails. Often these males are older because tail length increases with age, but females still prefer same-aged males with the longest tails. Once paired, females also prefer longer-tailed, unmated males as partners for extra-pair copulations. Balancing the attractiveness of males with long tail streamers, then, is their reduced ability to guard their mates from other males (Smith et al. 1991). Thus, their females mate more often with other males.

The large sizes and conspicuous plumages favored in reproductive displays may be liabilities in other regards. Large size itself requires greater energy expenditure. There is some evidence that large male Red-winged Blackbirds are at a disadvantage because they must sacrifice display time for feeding. Among species of North American blackbirds, males that are much larger than females tend to suffer greater mortality as nestlings (Searcy and Yasukawa 1983). Similarly, because they grow twice as fast as females to reach their full adult size by the end of their first summer, male Western Capercaillies, a huge species of Eurasian grouse, are more vulnerable than females to starvation when food is scarce (Wegge 1980).

Territory Quality

Sexual selection is manifest in the initial stages of competition among males for a breeding territory and female choice of the best territories. Red-winged Blackbirds exhibit striking sexual dimorphism and large variation in their sexual success (Yasukawa and Searcy 1995). Males establish and defend large territories; those with high water levels and good nest cover improve a female’s nesting success. So the best territories attract as many as 15 females (Figure 13–5). A female’s nesting success is not reduced by the presence of other females and may actually improve because of a lower risk of predation.

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Figure 13–5 A territorial male Red-winged Blackbird in aggressive display posture.

Male Red-winged Blackbirds are jet black with bright red and yellow shoulder patches, or “epaulettes.” Females are smaller and plainer, streaked brown. The male’s red epaulettes are essential to winning in competition with other males for quality territories. Males on which the red is experimentally dyed black suffer more frequent challenges and usually lose their territories, although those that are not challenged still attract mates. The epaulettes may have evolved in relation to male–male competition, not to female choice. The male in control of a quality territory often is not the father of a female's offspring. Females seek sexual partners off of the territory in which they nest; 48 percent or more of nestlings are sired by a male neighbor, not by the female's mate (Yasukawa and Searcy 1995). Females nesting in the territories of vasectomized males still lay clutches containing fertile eggs. In addition, females that consort with neighbors produce more young than do females that are faithful to their mates.

13.2 Lek Displays and Dynamics

The display grounds of promiscuous birds vary from solitary courts to communal display grounds, or **leks.** A lek is an aggregation of male display territories that include no other resources for reproduction other than opportunities to mate. At one extreme, Great Argus males in Malaysia hold forth on isolated deep-forest courts (Figure 13–6). At the other extreme, dozens of Black Grouse face off on the moors of northern Eurasia. Andean Cock-of-the-Rock males (Figure 13–7) gather like glowing red ornaments in the subcanopy of montane cloud forests of South America, and Sage Grouse strut on the open plains of the western United States (see Figure 3–10). Such avian displays have provided inspiration for human cultures. The Jivaro Indians of South America draw on the Andean Cock-of-the-Rock in a sensual dance ceremony. Blackfoot Indians of the western United States are inspired by the foot stomping, bowing, and strutting of the Sage Grouse while wearing costumes matching the grouse's spread pointed tail.

(A) Arterra Picture Library/Alamy. (B) © Juan Carlos Munoz/naturepl.com

Figure 13–6 The mating grounds of promiscuous birds include (A) communal leks of Black Grouse and (B) isolated display courts of the Great Argus.

PAPILIO/ALAMY

Figure 13–7 A male Andean Cock-of-the-Rock, a brightly colored lek species of the tropical forests of South America.

The strength of sexual selection by female choice reaches extremes in these species. In the Sage Grouse of western North America, one or two preferred males consummate 54 to 86 percent of all matings that take place on their leks (Schroeder et al. 1999). One male Lesser Bird-of-Paradise displaying on a lek with six other males made 24 of the 25 observed copulations (Beehler 1983).

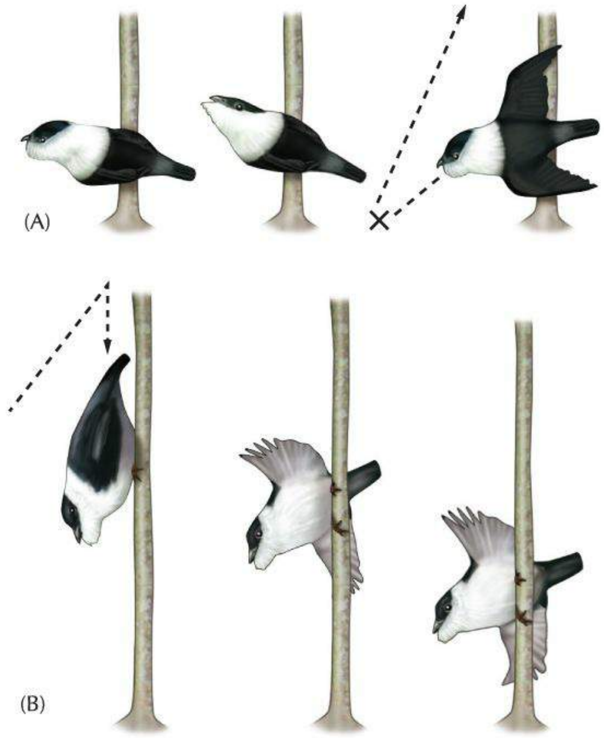
Why should promiscuous males gather in leks in which a few dominant birds mate most frequently? The potential costs are substantial. Among them is predictable failure to consummate copulation because of disruption by competitors.

Field studies of different species support three primary models for the evolution of leks (Sherman 1999). They are (1) the **“hot spot” model**—males gather at sites where they are most likely to encounter roaming females; (2) the **“hotshot” model**—males gather around experienced, attractive, or dominant males to increase their chances of being noticed within large aggregations; and (3) the **female preference model**—females prefer to visit large clusters of males over small clusters or solitary males. In the first two models, good positioning for a male more than offsets the costs of competition within the lek, especially if a male is dominant or has a chance of attaining dominant status. In the third model, the grouping of males allows the female to make safer and more efficient comparisons than is possible with scattered males.

Female comparisons of male displays are a key ingredient of leks. It has long been hypothesized that by mating with a dominant male, a female may obtain for her offspring the good genes responsible for the male’s superior traits. The dominance hierarchy, in effect, selects among males and thus simplifies the selection of a good male. In the

Sage Grouse, successful males are (1) socially dominant birds that (2) hold central positions on the lek and (3) are more active and visually or vocally attractive or both than are unsuccessful males (Schroeder et al. 1999). Preferred males also may be in better health: female Sage Grouse prefer males that are free of lice and avian malaria (Johnson and Boyce 1991; Spurrier et al. 1991). Females may be able to identify males with louse infestations by the red blood spots on their yellow air sacs, which the males inflate while strutting.

Tiny forest birds of the New World tropics, called manakins (Pipridae), also display in leks that contain no nesting resources (Figure 13–8). They form no lasting pair bonds. Instead, female manakins choose their preferred mate to fertilize their eggs and then build their nests and raise their young elsewhere by themselves. Some of the 50 species of manakins perform circuslike, whirling displays or strut up and down fallen logs. In the clustering of males on leks, young, inexperienced males gather near older or successful males. In this way, the young males gradually achieve a controlling position in the system.



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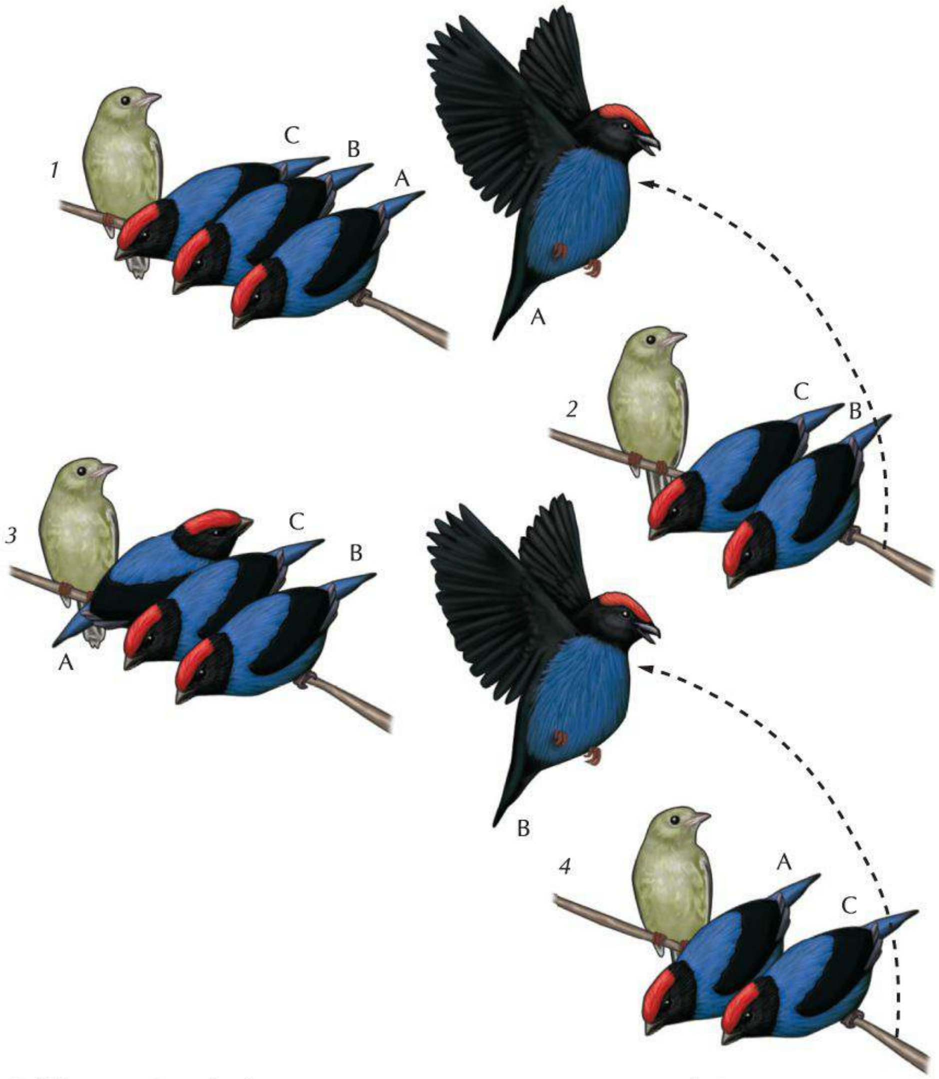
DATA FROM SNOW 1976

Figure 13–8 Displays of the White-bearded Manakin. (A) The grunt jump display starts when the male leaps down headfirst from its perch, turns in the air to land on its feet for a split second, and then with a “grunt” noise rockets back up to a higher perch, all in one-third of a second. (B) The male may then follow with the “slide-down-the-pole” display of short, rapid steps down the perch for a foot or so to the bottom of the upright just for a moment.

Extreme cases of such associations are seen in *Chiroxiphia* manakins, such as the Long-tailed Manakin, which display cooperatively on their lek court (McDonald 2010). Cooperative group displays are required to attract and excite females. Males on the lek chant their *Toledo* call in a coordinated duet almost nonstop during the breeding season, up to 1 million times a season. Females monitor and evaluate the *Toledo* calls of males throughout the local rain forest.

They visit the male pairs with predictably high *Toledo* output and well-performed cooperative dances. The alpha and beta males (up to 15 additional males in some species) line up on a single branch and perform their amazing team display (Figure 13–9). The performance becomes more and more frenzied and suddenly stops. The female stays if the complex dance is done well; if not, she leaves. Subordinate males then drop out in orderly fashion. The alpha male then does a brief precopulatory display and mounts the female. Alpha males get almost all (95 percent) of the matings with interested females, the highest variance in male mating success known for vertebrates.



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DATA FROM SICK 1967

Figure 13–9 Cooperative courtship display of the Blue Manakin. Males line up in a vibrating mass and leap over one another in rapid succession before a waiting female, which may then copulate with the oldest, dominant male.

Young male Long-tailed Manakins, which have no chance of being chosen, exhibit delayed maturity with distinctive subadult plumage colors. They join cooperative displays to become connected to a larger network. They also move around to different display grounds to form alliances that improve their status in the social queue. The best predictor of the future sexual success of a young male is his centrality and connectedness to the male social network. Sexual success is not about dominance but about the quality of male social relationships (McDonald 2007). This takes time. To become a successful alpha male in five to eight years, they must start to connect early; slow starters lose.

Males in cooperative *Chiroxiphia* display partnerships are not more closely related than average (McDonald and Potts 1994). However, kinship relationships among lekking males have been documented (by using microsatellite DNA comparisons) for several species, most notably Black Grouse, peacocks, and Wild Turkey. Black Grouse males on the same lek are more closely related to one another than to males on other leks, possibly the result of wintering together in extended family gatherings. In peacocks, related males tend to display near one another, even when they have been raised separately to prevent prior knowledge of one another (Petrie et al. 1998). How they favor kin is not known for sure.

In Wild Turkeys, several males routinely court females, but only one of them actually mates with a willing female (Figure 13–10). The original work of Watts and Stokes (1971) suggested that males in the coalition were brothers, but 24 years passed before this relationship was confirmed by Alan Krakauer (2005) with the use of molecular, microsatellite techniques. The microsatellite genotypes of dominant and subordinate members of a coalition were close to the expected value for full siblings. The dominant male of a coalition achieves more matings and produces more offspring than do solo males that are not part of a coalition. By virtue of their brothers' better performance, subordinate males in a coalition achieve a greater net genetic contribution to the next generation than they would have achieved on their own as solitary males.

All Canada Photos/Alamy

Figure 13–10 Kinship and reproductive success in Wild Turkey coalitions. Strutting male Wild Turkeys cooperate in courting a hen. Only the dominant male in a coalition of brothers actually mates with the hen. The remaining siblings benefit by virtue of being kin when some of the genes that these siblings have in common with their brother are passed on to the next generation.

The known kinships and improved reproductive success of the turkey coalitions meet two of the three criteria of Hamilton's (1964) theory of "inclusive fitness through kin selection." According to this theory, a bird can also promote its own genes by helping kin, which will share some of the same genes. Turkey coalitions also meet the third criterion of this theory—namely, that genetic benefits of helping outweigh the costs of helping compared with trying to breed independently. The cost of helping is basically the sacrifice of reproductive output if alone, which is equivalent to that of the solitary males included in the study, calculated as 0.9 offspring per male. By helping a brother, a subordinate turkey produces the equivalent of 2.6 offspring, for a net benefit of 1.7 offspring.

Ruffs and Reeves

The Ruff is a large sandpiper with an extraordinary social structure (Figure 13–11). Females, which are called Reeves, are “normal” sandpiper brown in color. Males, however, have elaborate breeding plumages—buff, chestnut, black, white, barred—that are as variable as the coat colors of domestic cats. The lek mating system of the Ruff harbors a set of three alternative mating strategies, known elsewhere only in isopods, fishes, and lizards (Jukema and Piersma 2006). Two of the Ruff’s strategies are well known; the third is a recent discovery.

BLICKWINKEL/ALAMY

Figure 13–11 The Ruff is an unusual species with individually variable male plumage. Three social classes of males associate on the display territories of the lek. Here, a dark-ruffed independent male stands over a subordinate white-ruffed satellite male. Males that mimic females, called faeders, are a recently discovered third genetic morph that mates with other males as well as with females.

Briefly, here is how it works. Within the first type of mating strategy, the more prevalent dark-plumaged, territorial males (**independents**) defend small clustered lek mating courts against other residents. Within the second well-understood strategy, light-plumaged, nonterritorial males (**satellites**) track wandering females and, more importantly, are recruited as partners onto the court of a territorial male. Females show a preference for courts with more than one male, so the satellite male helps the territorial male. Satellite males also obtain an average of 15 percent of the matings. Their low-cost, lower-benefit strategy, combined with greater longevity, achieves a lifetime reproductive success equivalent to that of the territorial males and ensures the persistence of the two different reproductive strategies in the population (Widemo 1998).

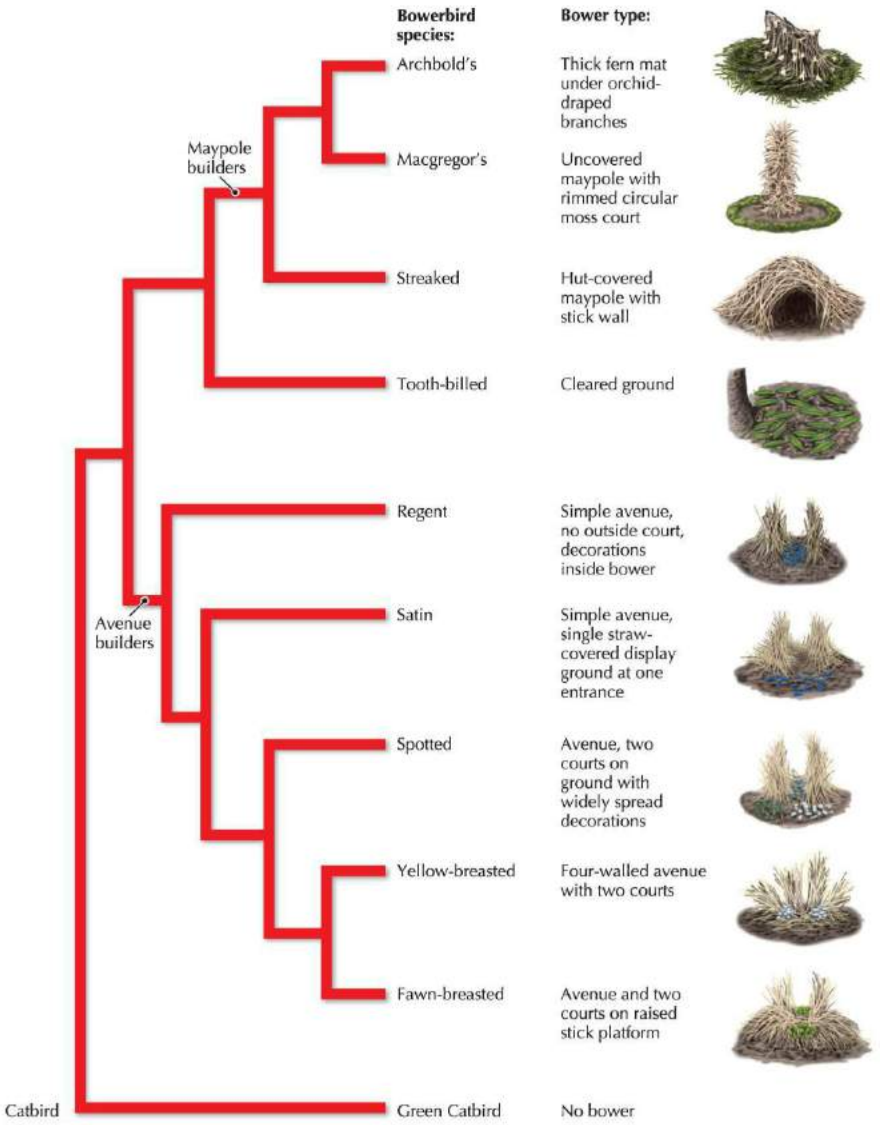
The genetic basis of the color difference between independent and satellite males is well documented (Lank et al. 1999; Ekblom et al. 2012). Controlling the dichotomy (dark versus light plumage) is a simple (autosomal) genetic polymorphism. All territorial males are homozygous recessive, whereas almost all satellite males are heterozygous. Females have the same genes and hence the same plumage color capacities as those of males, but they are not normally expressed. David Lank and his colleagues confirmed this by implanting testosterone under the skin of Reeves and transforming them into Ruffs, with fancy plumage and male behaviors as well. Removal of the hormone transplant returned these individuals into normally breeding females.

The uneasy alliances between territorial and satellite males persist and lead to the stable social polymorphism because Reeves visit pairs of Ruffs more often (on a per capita basis) than they visit solo territorial males. Territorial males tolerate satellite males because more female visits offset the costs of losing some matings to satellite males. More broadly, Reeves visit multiple leks and favor larger aggregations of males on leks. More than half of the females mate with more than one male and have clutches fertilized by more than one male. The frequency of multiple paternity for this species is the highest known for any lekking bird species (Lank et al. 2002).

But this is only part of the story. Newly discovered is a third, cryptic morph of female-like male Ruffs (**faeders**), which sneak around a lek (Jukema and Piersma 2006). These are males that mimic females in plumage color and that have double-sized testes. They are much smaller than other males and slightly larger than females but refrain from the dramatic courtship displays of the other males. Faeders associate with females on male territories, where they can disrupt female mate choice by intervening to solicit copulations from a territorial male. However, they also gain opportunities to copulate with females and pass on the alleles for the faeder appearance and behavior. Faeder males have been wrongly scored by researchers prior to the discovery of the female mimics. The dynamics of their mating strategies are now under investigation.

The Crafts of Bowerbirds

Bowerbirds are large songbirds found in New Guinea and Australia. They have solitary display courts on which they construct and decorate elaborate stick or grass structures, called **bowers,** which provide platforms for both courtship and copulation (Figure 13–12). Understanding the evolution of bowers has advanced greatly since the initial hypothesis that bowers were just elaborate nests used for ritualized courtship. This hypothesis was rejected in favor of the premise that the structures display male social status and health (Borgia et al. 1985). Both bower quality and plumage color have been hypothesized to signal the quality of male Satin Bowerbirds. Measures of bower quality, for example, predict both ectoparasite load and body size of the attending male. Ongoing research, however, reveals that female choice drives the evolution of bowers. Bowers protect females from aggressive males and facilitate controlled assessments of male quality. The bowers and their decorations are under strong sexual selection as extensions of display morphology (Patricelli et al. 2003; Madden and Balmford 2004).



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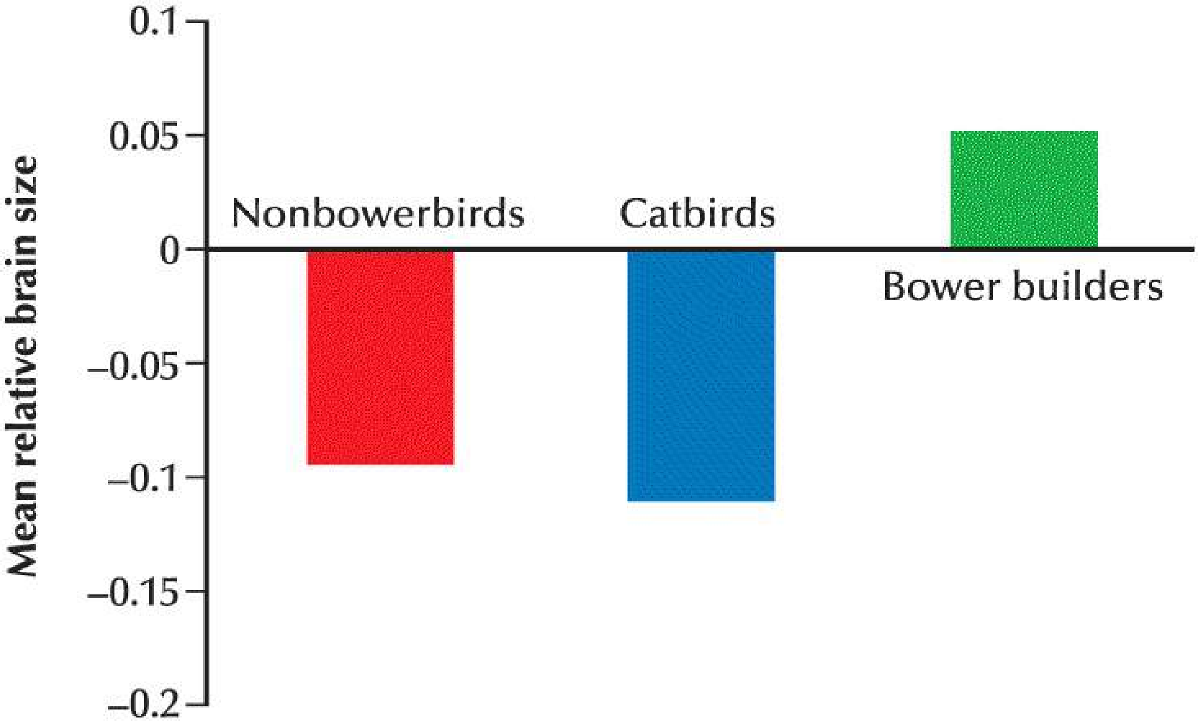
Data from Madden 2001

Figure 13–12 Cladogram of bower evolution. Phylogeny of the species is constructed from sequences of mitochondrial DNA. The catbirds, represented here by the Green Catbird, are basal in the phylogeny and do not build bowers.

Male bowerbirds build bowers of two general kinds: maypole bowers and avenue bowers. Maypole bowers consist of sticks built around a central sapling, or maypole, with a circular runway around it. Avenue bowers have two parallel walls with a narrow passage in between for the visiting female to observe the male. Five species of bowerbirds build maypole bowers, and eight species build avenue bowers. Phylogenetic analyses of DNA base-pair sequences indicate that maypole bower builders are nearest relatives of one another. The same is true for the avenue bower builders (Kusmierski et al. 1997).

Modestly colored species tend to have more elaborate bowers than do brightly colored species. In addition, the size of a bowerbird's brain correlates with its bower-building behavior (Madden 2001). Bower builders have larger brains than those of species that don't build bowers. Also, species that build complex bowers have larger brains than those of species that build simpler bowers (Figure 13–13).



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DATA FROM MADDEN 2001

Figure 13–13 Bowerbirds that build bowers have larger brains than those of the related catbirds that don't build bowers and other species of passerine birds.

Bowerbirds decorate their bowers with a diversity of found and gathered objects, some brightly colored. The decorations are as extraordinary as the bower structures themselves, deemed candidates for true art (Diamond 1986). Some species paint the walls of their bowers with fruit pulp, charcoal, or shredded dry grass mixed with saliva. Other species decorate their bowers with mosses, living orchids, fresh leaves turned upside down, colorful fruits, fungus, or even caterpillar droppings. The birds replace wilted flowers or leaves with fresh ones as necessary. Modern-day bowerbirds improvise. The Spotted Bowerbird of Australia, for example, is notorious for pilfering household and camp items—scissors, knives, silverware, coins, jewelry, car keys, and even a glass eye snatched from a man’s bedside (Marshall 1954). Despite such variety, male Spotted Bowerbirds show strong and consistent preferences for certain objects, such as green nightshade berries, that increase their mating success (Madden 2003).

Different species—or even populations—have preferences for gathering and displaying different materials. Males of the Satin Bowerbird, which have brilliant blue eyes, decorate their large avenue bowers with anything blue that they can find. Originally confined to natural objects, including parrot feathers and flowers, this species now exploits blue human trash. One bower was decorated with glass fragments, patterned crockery, rags, bus tickets, candy wrappers, a child’s blue mug, a toothbrush, hair ribbons, and a blue-bordered handkerchief. However, males do not prefer rare or costly decorations, reducing their values as indicators of quality (Madden and Balmford 2004).

Constructing a bower and provisioning it with fresh decorations is a challenge, partly because males harass each other and tear one another's bowers apart if they can (Borgia and Gore 1986). Satin Bowerbirds steal prized decorations from rival males, such as blue parrot feathers. Dominant males are better able to protect their bowers and have more time to visit and degrade the bowers of nearby competing males, which must constantly rebuild and struggle to keep up an acceptable bower.

Borgia and Gore's video cameras recorded the bower visits and the preferences of female Satin Bowerbirds for well-made and well-decorated bowers (Borgia et al. 1985). A female Satin Bowerbird visits an average of 3.6 bowers in a local area before mating with a particular male. The females preferred well-made bowers with special decorations. Of 22 males, five accounted for 56 percent of the 212 copulations recorded in 1981. These five males had the most blue parrot feathers, snail shells, and leaves as decorations, as well as the best bower structures, judged in regard to symmetry, stick size, stick density, and quality of construction. Males whose leaf decorations were experimentally removed from their bowers obtained fewer matings than did control males.

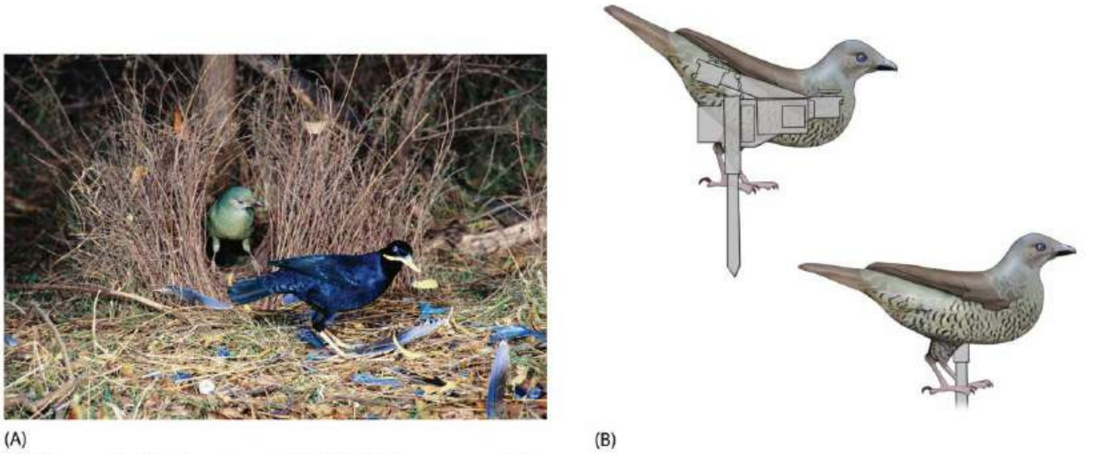
The studies above reinforced the classic male-oriented view of sexual selection, namely, that bowers are decorative badges of male quality, even substitutions for plumage ornamentation (Gilliard 1969; Kusmierski et al. 1997). The alternative **threat reduction hypothesis** of bower evolution focuses instead on how bowers evolve by female choice to facilitate safe female assessment of males and their decorations at close range (Borgia 1986; Borgia and Presgraves 1998). Male bowerbirds are extremely aggressive, even violent, among themselves and also towards females that visit a display court to assess a male and his decorations. The females are subject to attack, sexual coercion, and forced copulations (Box 13–2).

Box 13–2

Robot Bowerbirds

Gail Patricelli and colleagues explored the threat-reduction hypothesis using female robots (Patricelli et al. 2002, 2003, 2004). Real female Satin Bowerbirds communicate their level of comfort with male display by crouching in the bower. The remote-controlled, stuffed female bowerbird models, or "fembots," crouch in natural positions, look around, and fluff their wings realistically. Males responded as predicted to robot crouching postures, confirming that the female behavior functions as a signal to males. Males that were more responsive to female behavior during the experiments were less likely to startle wild females during natural visits by females to their bower and also were sexually more successful in natural encounters. Older successful males monitor the nervousness of the female and scale back on the aggressiveness of their displays until she is more relaxed. In follow-up studies, females also proved to be more tolerant of intense courtship display with attractive males (i.e., males that were ultimately chosen more frequently by other females). And they became more tolerant of intense display as they narrowed the choices down to fewer and fewer, more attractive males.

In conclusion, bowers evolved through the indirect benefit to females of reducing male sexual coercion through forced copulations. Male bowerbirds, it seems, have completely lost control over fertilization as a result of the evolution of female mating preferences and controls. Male reproductive variance follows female sexual choice, although males still contribute indirectly through competitive destruction and plundering of each other’s bowers and collections.



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(A) Nature Picture Library/Alamy. (b) Data from Patricelli et al. 2015

(A) Female Satin Bowerbirds assess a male’s quality from the protection of the avenue bower decorated with bright blue objects. (B) Remote-controlled female robots were designed to test male responses to the crouching position.

Bower architecture protects the female from coercive copulation, preserving her capacity to choose freely. The female can either fly out of the front of an avenue bower when the male tries to mount her from behind, or she can hop to the side to maintain the central maypole between her and the threatening male. In contrast, female Tooth-billed Bowerbirds visit their species’ simple, open court without a bower, only to mate. These females are immediately and aggressively mounted by the male with no time for coyness or careful assessment. The visits of female Satin Bowerbirds to the elaborate avenue bowers of males, on the other hand, often last for several minutes, allowing for assessment of male attributes. These females exhibit greater tolerance of risky, aggressive display behavior from more attractive males.

The protection of females from sexual coercion by bower architecture fostered an explosive diversification of bower ornamentation (Prum 2015). By selecting various types of architecture—avenue or maypole bowers—females have advanced their control over fertilization and limited male efforts to subvert female mating preferences. Consequently, females can inspect individual males and their gathered materials at intimate distances without loss of their sexual freedom. The result has been a proliferation of the breadth and diversity of bowerbird aesthetics.

13.3 Songs and Mates

The preceding sections of this chapter focused on physical ornaments and behaviors. Song repertoires also enhance a male's attractiveness to females and his ability to compete with neighboring or rival males. Songs and song repertoires evolve by both mate choice and mating competition. Winning vocal duels is one route to local dominance. Territorial songs signal to potential rivals that the resident male is prepared to protect his exclusive use of that space and any associated females (see section 8.10).

The elaborate songs of male Brown-headed Cowbirds vary in their impact, defined by how readily estradiol-treated females solicit copulation (West and King 1980; West et al. 1981). Male cowbirds, even those hand-raised in isolation, are capable of singing high-potency songs, but only the top-ranked dominant members of a group actually do so. If a subordinate dares to use potent vocalizations while displaying, it invites attack by the dominant male. As a result, subordinate males deliberately downgrade their vocalizations and wait for an opportunity to sing their best songs without risk. In addition, differences in these male songs distinguish regional dialects in the western United States. A female cowbird distinctly prefers the high-potency songs of a male singing in her home dialect (Freeberg et al. 2001).

Female birds use the songs of males to assess the quality of their potential mates, choosing older, more experienced mates and thus increasing their own social or reproductive potential. Long songs and vigorous singing are preferred by the females of many species

(Nowicki and Searcy 2005). They also may be indicators of male quality. In one study, female House Finches prefer long songs delivered at fast rates, which may indicate a male’s energy reserves (Nolan and Hill 2004). In another study, song rate and bout length of Common Starlings predicted their immune system response; more robust singers exhibited enhanced immunity (Duffy and Ball 2002). Female starlings, therefore might assess the immunocompetence of males without checking blood chemistry with laboratory equipment!

How could large song repertoires reveal superior male qualities? Direct support for this idea is surprisingly weak (Gil and Gahr 2002). However, it may work in ways that brings us back full circle to the process of song learning by young birds (see Chapter 8). Recall that the size of the song nuclei in the brain may be correlated with repertoire size. The size of the song nuclei is subject to the allocation of energy and neural tissue invested in them during the development of the nestling bird. When stressed, for example, by food deprivation during periods of food shortage, poor parental care, or laboratory manipulation, baby birds invest less into the growth of song nuclei. Smaller nuclei did reduce both the accuracy and the quantity of song learning in subsequent weeks but did not affect song repertoire size (Nowicki et al. 2002a). In elegant experiments, Steve Nowicki and his colleagues at Duke University demonstrated that female Song Sparrows chose the superior songs and repertoires of males not damaged by early developmental stresses (Nowicki et al. 2002b). Other studies now support the so-called **deprivation hypothesis** of female preferences for song quality as a valid indicator of male quality (Nowicki and Searcy 2005).

13.4 Monogamy

The elaboration of songs and displays due to sexual selection tends to be most extreme in species that are promiscuous or **polygynous** (one male to multiple females). Only a minority (less than 10 percent) of bird species, however, exhibit such mating systems, which we explore in further detail in Chapter 14. Most birds are monogamous, at least socially. An introduction here to monogamy provides the foundation for further understanding avian mating strategies.

Monogamy refers to a prolonged pair bond with a single member of the opposite sex for purposes of raising young. Birds are classically among the most monogamous of organisms. Most birds spend weeks or months tending their eggs and young. In contrast, most reptiles simply lay their eggs and leave them. Avian eggs and chicks require more parental care than do the offspring of most vertebrates, so the participation of both sexes is frequently essential.

The parental-care roles of monogamous male birds can be substantial. Defense of the territorial space, usually by the male, secures food supplies for the female and young. Most monogamous males also help their mates build nests and feed young, and some share incubation. Hence, a monogamous female bird should assess her prospective mate’s commitment and ability to sustain efforts in raising young.

Monogamous pair bonds may last for a breeding season or for life. Most pairs of parrots, eagles, and pigeons sustain lifelong associations. Long-lived birds—including swans and geese, albatrosses, and some shorebirds—also rarely divorce, which would penalize their reproductive output (Ens et al. 1996). Even long-distance migrant shorebirds maintain their partners. Paired male and female Black-tailed Godwits migrate and winter separately, but they return at the same time (within three days) to their nesting territories in Iceland and renew their pair bond (Gunnarsson et al. 2004). Failure to arrive together (more than eight days apart) leads to divorce. Some year-old Barnacle Geese sample prospective mates by forming trial liaisons before making a final, lifelong choice when two to three years old (van der Jeugd and Blaakmeer 2001). As a result, they achieve greater lifetime reproductive success than do birds that pair right away.

In other species, divorce initiated by the female increases her reproductive success. Female oystercatchers, for example, leave their mates to move to better nesting sites close to good feeding grounds (Heg et al. 2003). They produce more chicks as a result. Abandoned partners remate and continue to commute from the nest to the mudflats to feed, thereby exposing offspring to predation and new mates to opportunities for infidelity.

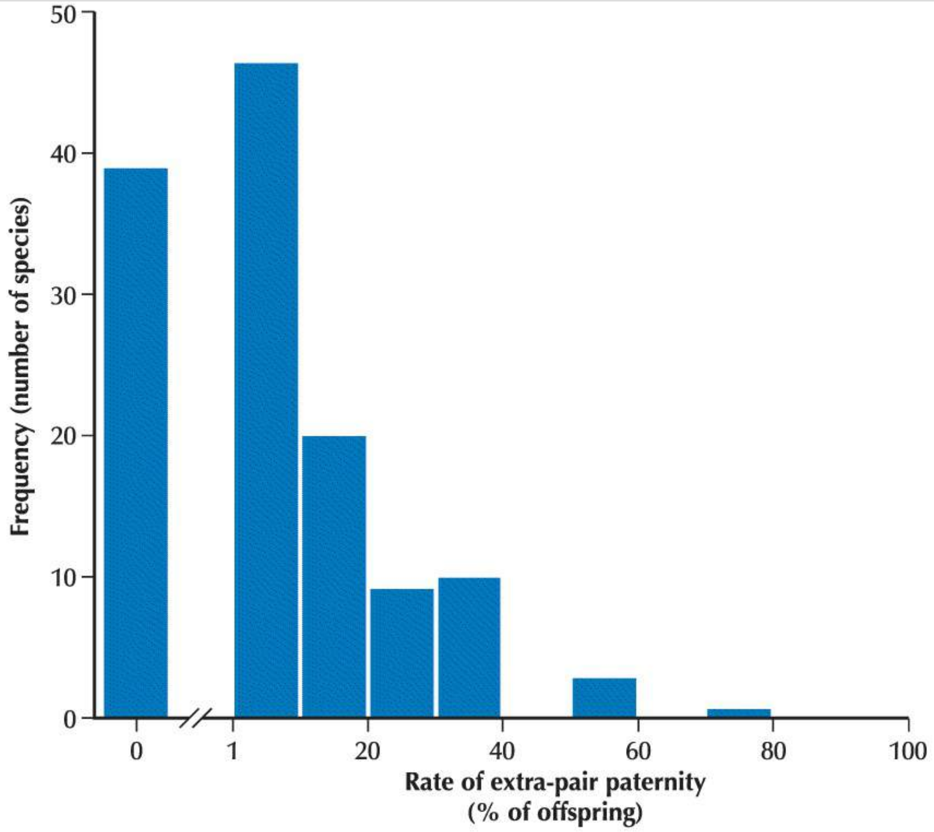
Similarly, female Blue Tits and Black-capped Chickadees typically divorce for better options. Blue Tits form pair bonds that endure many breeding seasons on the mainland of Europe. On the island of Corsica in the Mediterranean, however, females leave their mates 59 percent of the time (Blondel et al. 2000). Breeding sites vary greatly in quality on this island, so, when there are openings, female tits shift to habitats with more food, denser vegetation, and fewer parasites. Reproductive performance with their former mates is not an issue. A study found that, in North America, female Black-capped Chickadees typically left their partners between the first and second breeding seasons for males of higher social rank and did not leave on the basis of previous reproductive success (Ramsay et al. 2000). The females that left their partners, however, had a more significant tendency toward broods of mixed paternity before divorce than that of females that stayed with their first partners.

13.5 Extra-Pair Mating

> Well over nine-tenths (93%) of all passerine subfamilies are normally monogamous. . . . Polyandry [multiple male mates] is unknown. [Lack 1968, p. 35; see Griffith et al. 2002]

These statements by David Lack—the father of avian life-history theory—summarize the working assumptions of 50 years ago. Since then, research with the use of DNA technologies has brought about a dramatically different understanding of monogamy among most birds. Monogamy is a social relation between members of the opposite sex for reproduction. Our historical view of monogamy was built on the assumption that the offspring are truly their genetic offspring, but this assumption has often proved to be false. Strict monogamy, in which the social pair are the genetic parents of all offspring, has been established in the Common Loon, Long-eared Owl, Florida Scrub Jay, and other species. Instead, the broods of many bird species exhibit mixed paternity due to copulations by females with additional males—called **extra-pair copulations.** Consequently, ornithologists have come to refer to this breeding system as **social monogamy,** implying that the pair form a social bond for reproduction, even if it is not sexually exclusive. On average, more than 11 percent of offspring are sired by males other than the social father (Griffith et al. 2002; Figure 13–14). The proportion of chicks sired through extra-pair copulations may be more than 50 percent in some Tree Swallow populations (Lifjeld et al.

1993). Extra-pair copulations are a significant source of sexual selection for bright plumage in monogamous species (Møller and Birkhead 1994).



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DATA FROM GRIFFITH ET AL. 2002

Figure 13–14 Frequency of extra-pair paternity (percentage of offspring that are fathered outside the pair bond) in 130 species of birds.

Extra-Pair Fertilization in Purple Martin Colonies

The social life of the colonial Purple Martin has been unveiled (Wagner et al. 1996; Brown 1997). Native Americans used to attract Purple Martins by hanging hollow nesting gourds. Elaborate, multistory, white condominiums—sometimes with hundreds of nest chambers—now attract large local colonies of martins (Figure 13–15). Appreciation of his backyard martins piqued Smithsonian ornithologist Eugene Morton and his colleagues (1990) to learn more about social life inside his 24-room backyard martin mansion. Among his findings was rampant fertilization by older, extra-pair males.

© JOHN CALCALOSI/ARD/AGE FOTOSTOCK

Figure 13–15 Colony of Purple Martins, a species in which older males recruit young males to the colony and then exploit the weak mate-guarding abilities of these young males to increase their own reproductive fitness.

Older, experienced male martins arrive first and take charge of the top floors, where the nests are safest from predators. After establishing themselves with their mates in the best available nest cavities, the experienced male martins sing a special song high in the dark predawn sky to attract later-arriving yearling males to the colony. The older males then concentrate on copulating with the mates of their naive, young neighbors—with much success. Through their extra-pair copulations, adult males added an extra 3.6 fertilized eggs to the 4.5 eggs produced by their own mates. They fathered 43 percent of the offspring in the nests of yearling males. In some years, a single older male is responsible for most or all of the extra-pair fertilizations (Wagner et al. 1996). Conversely, yearling males fathered only eight percent of the offspring in the nests of a few of the older males.

Female Purple Martins are active participants in these social interactions. Those that pair with older males generally avoid extra-pair copulations, whereas those that pair with the younger males actively accept extra-pair copulations by older males. How successful these females are in mixing the paternities of their offspring depends on the guarding efforts of their mates. Young males that are larger than their mates and that actively guard them are better able to prevent extra-pair copulations by their mates and to achieve higher levels of paternity of their offspring. For young males, extra-pair paternity is simply one of the costs of coloniality. Regardless, some offspring are better than none at all. More importantly, with time, yearling males inherit the prime nest chambers and sing their predawn songs to attract junior neighbors to the suites below.

Quality Offspring?

Because extra-pair fertilizations do not provide any direct benefits to a female or her offspring, it has been hypothesized that socially monogamous female birds seek extra-pair copulations to enhance the genetic quality of their offspring (Petrie et al. 1998; Griffith et al. 2002). Whereas males can increase their reproductive success by siring additional offspring, females are limited by their clutch size. Some females can improve their lifetime reproductive success by enhancing the genetic quality of their offspring.

How then can extra-pair copulations improve the quality of one’s offspring? Insurance against the infertility of one’s mate is one possibility (Krokene et al. 1998). Increased genetic variability may be another source of improvement. Genes from multiple males can improve the quality of offspring through improved immunocompetence (Johnsen et al. 2000) and, more generally, through the fitness advantages of heterozygosity. Across a variety of bird species, the proportion of extra-pair offspring directly correlates with genetic variability among males and, hence, variability in the quality of potential male mates (Petrie et al. 1998).

Blue Tits of Europe provide one of the best examples of how females improve their breeding success through extra-pair copulations (Foerster et al. 2003). In a long-term study of two populations of Blue

Tits, one in Germany and the other in Norway, distant males less related to the female than her mate or her neighbors sired half of the offspring. Deliberate outbreeding with genetically different males increased the heterozygosity of those offspring, which, as a result, were more likely to survive their first winter and to breed locally. Heterozygous young sired by distant males were most likely to beat the low odds (1/11) of making it to the next spring. In addition, heterozygous young males in this study had brighter ultraviolet crown patches, which also confer advantages (see Box 13–1).

Female Blue Tits also consort with neighboring males that do not, on average, increase genetic diversity. But the females chose quality neighbors with “good genes,” specifically those that were larger and older than their social mates. Thus, females increased the diversity and quality of their broods by two initiatives—deliberate outbreeding and selection of superior neighbors. Studies of the related Black-capped Chickadee revealed that a female also listens carefully when her mate engages a neighbor in a dominance-controlling singing contest. If the mate loses, the female chickadee is more likely to consort and copulate with other males, thereby increasing the number of extra-pair young in the brood (Minnell et al. 2002).

The next chapter considers other features of birds’ reproductive strategies in a continued but expanded context of life-history theory. The complexities and conflicts between what is best for males versus females and groups versus individual birds foster diverse breeding systems that range from competitive to cooperative to parasitic.

REVIEW KEY CONCEPTS

13.1 Mate Choice and Sexual Selection

Female choice drives sexual selection for elaborate courtship displays and sexual dimorphism in plumage. Three hypotheses prevail. The good genes hypothesis proposes that distinctive male features are favored if they convey information about the quality or health of the male. The direct benefits hypothesis proposes that sexual ornaments are indicators of direct benefits to individual survival or fecundity, such as higher territory quality or avoidance of sexually transmitted diseases. The arbitrary choice and runaway selection hypothesis proposes that mating preferences for sexually attractive ornaments lead to the coevolution of popular traits and the preferences for them.

Key Terms: sexual selection, sexual dimorphism

13.2 Lek Dynamics and Displays

Competition for mates is extreme in lek species, in which a few males attract the most mates. The lek mating system of the Ruff includes a set of three alternative mating strategies, each implemented by a different type of male initiator. Male bowerbirds build and decorate elaborate mating arenas that reduce threat of sexual coercion to females as they choose a mate.

Key Terms: leks, “hot spot” model, “hotshot” model, female preference model, independents, satellites, faeders, bowers, threat reduction hypothesis

13.3 Songs and Mates

Songs evolve through both mate choice and mating competition. Female birds may prefer quality males that vigorously sing long, complicated or high-potency songs.

Key Term: deprivation hypothesis

13.4 Monogamy

Social monogamy is the most common avian mating system, but it masks an underground of sexual activity. Monogamous pair bonds may last for a breeding season or for life.

Key Terms: polygynous, monogamy

13.5 Extra-Pair Mating

Extra-pair fertilizations sire a substantial fraction of offspring in most species of songbirds. It has been hypothesized that females improve the quality of their offspring by increasing heterozygosity and good genes, but meta-analyses have failed to support this conclusion overall.

Key Terms: extra-pair copulations, social monogamy

APPLY YOUR KNOWLEDGE

1. Explain the conditions during which a male's fitness is increased that in turn helps another male's successful breeding?
2. Compare the good genes hypothesis with the arbitrary choice hypothesis. What constitutes a superior mate under each evolutionary mechanism?
3. Provide multiple examples of how a male's parasite load may be

evaluated by a female.

4. Describe the various factors that may increase female fitness through infidelity and extra-pair copulations.
5. Distinguish between hot spot and hotshot models of lek formation. Are these two models in conflict with the female preference model? Explain.
6. What is the advantage to subordinate males of joining a lek where there is high competition for females?
7. Describe the bowers of bowerbirds, and how the features of the bower and the behavior of males influence the success of a male mating with females that visit.
8. Describe the influence of vocalizations in defining territories and how song may indicate the quality of a male.
9. Explain the reasons for the high proportion of monogamy among birds and what factors lead to divorce.
10. Compare the lek system of the Sage Grouse and colonial nesting of Purple Martins. How are they the same? How are they different?

CHAPTER 14 *Breeding Systems*

FLPA/ALAMY

Foster-parent Dunnock (*right*) feeding a parasitic young Common Cuckoo.

> The Reverend F. O. Morris (1856) encouraged his parishioners to emulate the humble life of

> the dunnock, or hedge sparrow *Prunella modularis*. . . . Had his congregation followed suit, there would have been chaos in the parish. [DAVIES 1992, P. 1]

The pair bonds of birds vary from brief sexual unions to sustained mutual associations. For many species, the raising of young requires a major and consuming effort by two or more adult birds. Males and females may share the parental effort equally or unevenly. They may allocate their time to several broods. At stake are their individual selfish best interests, which often conflict with each other's and with the interests of their offspring.

From an evolutionary perspective, all that really counts in the end is a bird's genetic contribution to future generations. There are two primary ways to do so: (1) directly by producing young with one's own genes and (2) indirectly by helping relatives to raise young that possess some of one's own genes. Many birds do both.

Microsatellite DNA analyses, however, reveal that extra-pair mating increases the genetic diversity of many broods, as stated in Chapter 13. The prevalence and patterns of extra-pair fertilizations blur the classical distinctions of mating systems based on the overt social relations of individual birds. Similarly, birds can increase their lifetime reproductive success by helping kin. Studies of inclusive fitness expose new depths of the social behavior and extended family structures of birds.

This chapter shifts our attention from sexual selection and the social veil of monogamy, discussed in Chapter 13, to the diverse so-called mating systems of birds and their relation to the availability of food and to the care of offspring. Then, we look more closely at overtly **polygynous** bird species (one male to multiple females) and overtly **polyandrous** bird species (one female to multiple males).

Next, we consider **brood parasitism.** The females of many species lay extra eggs in other birds' nests. Obligate brood parasites such as cowbirds and cuckoos take this behavior to extremes. The final sections explore cooperative breeding and the roles of **helpers,** which are often young birds that stay at home rather than disperse to establish their own breeding territories. The elaborate family structures of bee-eaters of Africa and fairywrens of Australia illustrate the potential complexities of the relationships among kin in cooperative systems.

14.1 Diversity

The diversity of avian mating systems is rooted deeply in the evolutionary and phylogenetic histories of major taxa and has been refined in response to local ecological opportunities (Ligon 1999). The abilities of each sex to control appropriate reproductive resources and attract one or multiple mates define the principal breeding systems of birds (Table 14–1). Guiding the evolution of alternative systems are life-history trade-offs between current and future reproductive efforts as well as uncertainties about parentage.

Table 14–1 *An Ecological Classification of Avian Breeding Systems*

Monogamy	(Greek: *mono*, single; *gamos*, marriage) The predominant avian mating system in which two parents are involved in raising and caring for the offspring. Shared parental care maximizes reproductive success. Social monogamy refers to breeding systems in which the social pair is not sexually exclusive.
Polygamy	(Greek: *poly*, many; *gamos*, marriage) Any mating system including multiple mates of the opposite sex.
Polygyny	(Greek: *poly*, many; *gyna*, woman) A kind of polygamy in which males mate with multiple females. In polygynous birds, the reproductive success of males is more variable than that of females. About 2 percent of all birds are polygynous.

	Territorial Polygyny Males control breeding territories with sufficient resources to attract multiple females to nest within them. Males invest in territory defense and may invest in other additional aspects of parental care. *Lek* or *Arena Polygyny* A polygynous breeding system in which females do all of the parental care and choose their mates from among males that display on solitary arenas or leks. Traditional leks include multiple, neighboring male territories. Male display territories include no resources necessary for reproduction except opportunities to mate.
Polyandry	(Greek: *poly,* many; *andros,* man) A kind of polygamy in which females defend or provide sufficient resources to attract multiple males and each male provides extensive paternal care. In polyandrous birds, female reproductive success is more variable than that of males. In serial polyandry, females lay a clutch of eggs for a series of different males over the breeding season. In territorial polyandry, the female defends a territory that contains sufficient resources to attract multiple males, each of which cares for his own clutch. Fewer than 1 percent of all birds are polyandrous.
Polygynandry	(Greek: *poly,* many; *gyna,* woman; *andros,* man) A highly variable type of polygamy in which both males and females mate multi-fold. In some species, several females and several males may form a communal breeding unit in a

	shared territory. Individuals share territorial defense and parental care. In most paleognaths, by contrast, males provide all of the parental care and raise mixed clutches of eggs laid by multiple females. Females lay their eggs in a male's clutch and leave.
Cooperative Breeding	Any breeding system in which more than three individuals participate in raising offspring that cannot all be their own. Includes communal breeding (see above) and helpers at the nest in which young of the previous year remain with their parents and help to raise a brood of their siblings.
Brood Parasitism	A breeding system in which females lay eggs in the nests of other individuals, forgoing all parental care. Facultative brood parasites raise their own broods but also lay some eggs in the nests of other individuals of the same or different species. Obligate brood parasites lay all of their eggs in the nests of other species. They build no nest and provide no parental care.

The options for mating and parenting are likened to an evolutionary game in which each parent has to choose between taking care of the young or abandoning them and seeking additional mates (Maynard Smith 1977). At one extreme, reduced confidence of paternity can promote desertion or infanticide. Tree Swallows, for example, practice deliberate infanticide. Intense competition among males for nest sites results in a floating population of unmated males. In one study, five of seven such males replaced males that were experimentally removed. The replacement males then killed the nestlings of their predecessors (Robertson and Stutchbury 1988). One of the killers mated with the widowed female, but two others brought in new mates.

At another extreme, the facade of a cooperative social order often hides a swirl of competition, strife, and harassment. Helpers may deliberately interfere with parental reproduction to increase turnover and thereby increase their own chances of breeding. Conversely, adults may sabotage the initial breeding efforts of young to increase the incentives for the young to stay at the nest as helpers. Young helper males sometimes mate with their stepmothers, and helper females sometimes slip an egg of their own into the parental clutch.

In a different direction, cooperative social interactions appear to be altruistic but are actually selfish. Individual selfishness does arise beneath the veneer of communal breeding by Groove-billed Anis, large black cuckoos of the New World Tropics that form social units of one to four monogamous pairs. All members of the unit lay their eggs in a single nest, and all the birds in the unit help incubate and feed the communal brood. The main advantage of communal nesting in this species is in sharing the high risks of nocturnal predation during incubation and brooding, thereby improving individual survivorship (Bowen 2002).

Female anis, however, compete among themselves to ensure the success of their respective contributions to the clutch. Because one nest cannot hold all the eggs that females can lay, the females throw one another’s eggs out to make room for their own. Young subordinate females start laying first. The older females toss out some of these eggs to make room for their own eggs, which make up most of the clutch.

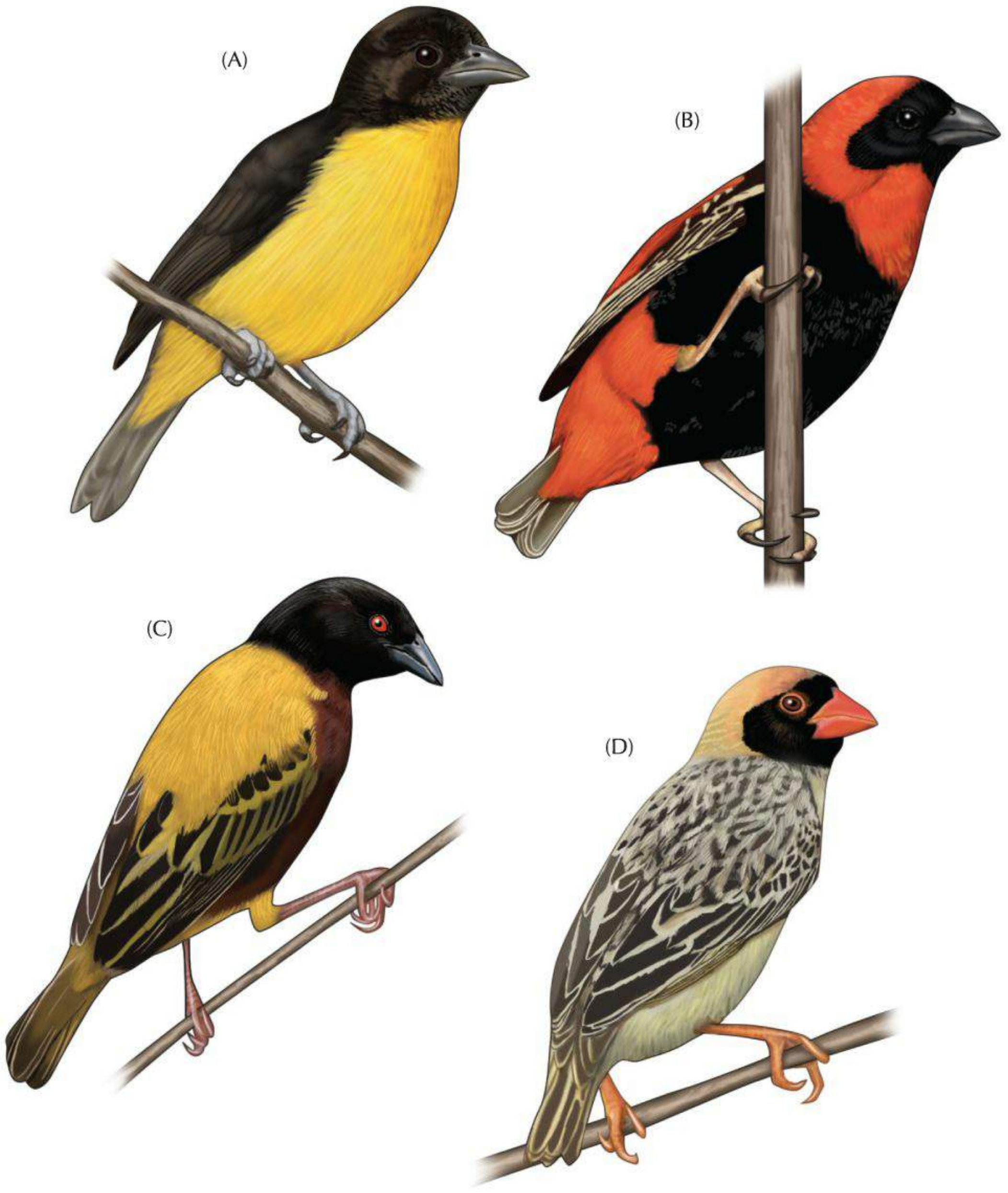
Subordinate females counter these actions by increasing the total number of eggs that they add to large clutches by prolonging the interval between eggs laid and by producing a “late egg” as the clutch size nears completion. However, there are natural limits to a subordinate female’s attempts because the last-born nestling is the smallest and most vulnerable member of the brood.

Generally, monogamy prevails when male help is essential for raising young or when males cannot commandeer the resources that they need to support extra mates. When one sex alone can take care of young, multiple mates become a viable option. Arctic sandpipers, for example, produce a fixed brood of four precocial young that require little posthatching care beyond defense from predators. Their fixed clutch size and reduced parental-care requirements amid abundant resources favor increasing the number of clutches achieved through alternative mating systems (Ligon 1993). As a result, arctic sandpipers exhibit a diversity of mating systems: monogamy, polygyny, and polyandry. Fifteen species are monogamous, with shared incubation at a single nest. Two or three species are socially polygynous or polyandrous, and different birds incubate successive clutches. Two or three other species feature polygynous males that provide no parental care. Three species are lek species, such as the Ruff described in Chapter 13.

A comprehensive view of avian mating systems embraces the full diversity of social systems that describe individual efforts to maximize their lifetime reproductive success. Different roles affect individual reproductive output. Female birds can increase their reproductive success by recruiting more parental care and by producing additional clutches. Conversely, males can allocate energy to extra-pair fertilizations or to varied levels of sustained parental care.

14.2 Polygyny

Careful study of color-marked birds often reveals a few bigamous males in an otherwise monogamous species. Only about 2 percent of all birds, however, are overtly polygynous. In the United States and Canada, these birds include 14 of the 278 breeding songbird species, 11 of which nest in marshes or grasslands. Throughout the Tropics, birds that nest colonially in “safe” trees or in places with abundant or easy-to-find food tend to be polygynous (Figure 14–1). Because marshes are so rich in insect food resources, females of many marsh-nesting blackbirds, wrens, and European warblers care for their young with little or no help from males by exploiting aquatic insects emerging on prime territories.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company

Figure 14–1 African weavers have different mating systems. (A) The Dark-backed Weaver and other species of stable forest habitats with uniform food distributions tend to be territorial, solitary, and monogamous. (B) The Southern Red Bishop, a territorial polygynous species, and (C) the Golden-backed Weaver, a colonial polygynous species, both live in highly seasonal or unpredictable savanna habitats. They practice resource-defense polygyny. Males of these species can control the limited safe nest sites near good food supplies. (D) The most abundant of the savanna weavers, the Red-billed Quelea is monogamous even though it nests near abundant food. Queleas nest in colonies so large that their members deplete nearby food stores during nesting and must commute farther and farther to gather food for their young. Male assistance becomes essential to ensure that older nestlings are fed.

Control of quality resources leads to the evolution of territorial polygyny. Clumped resources are easier to monopolize than are uniformly distributed resources. Extending Brown’s concept of economical defensibility (see Chapter 11), the environmental potential for polygyny increases with clumped resource distributions. Extreme variation in the quality of controllable territories can lead to polygyny. Multiple females that join a male on a single territory do so because they can do better than when alone on a territory of poorer quality. Polygynous male Marsh Wrens and Indigo Buntings, among others, control better-quality territories than do unmated or monogamous males in the same area. The number of female Marsh Wrens on a territory increases directly with the availability of good nest sites (Kroodsma and Verner 1997).

Females may share male help, but at a cost. Among Great Reed Warblers, for example, more nestlings of polygynous males die from starvation than those of monogamous males (Dyrcz 1977). Starvation is most frequent during cold, wet spells when food is scarce and the young depend on food delivered by the male as well as by the female parent. But reduced nest predation on polygynous territories with safer nesting sites offsets losses to starvation.

Fruit and nectar diets favor the evolution of polygynous mating systems in birds, especially lekking. Males of many tropical, fruit-eating birds do not help care for their young. Unlike insects, fruit and floral nectar are conspicuous food sources that have evolved to be eaten and require little searching. Insects, by contrast, make themselves cryptic, prickly, toxic, hard to find, and hard to handle. As long as the energy requirements of nestlings can be mostly satisfied with fruit, the female parent can raise them successfully. Males of these species devote themselves to display to attract additional mates. Polygynous frugivores include most species of birds-of-paradise, bowerbirds, manakins, and cotingas. Likewise, all species of hummingbirds for which breeding systems are known are also polygynous.

14.3 Polyandry

In only a few bird species do female birds attract and pair overtly with several males. These males incubate the eggs and take care of the young. In territorial, or classical, polyandry, females defend territories, compete for males, and initiate courtship. Males build nests and care for separate clutches within the territory. In most cases, sexual selection on females leads to sex-role reversal—the evolution of larger and more brightly colored females. In serial polyandry, a female will lay a series of clutches for different males. For example, female phalaropes, a kind of sandpiper, are the brightly colored sex. They compete for males in congregations at productive feeding sites and initiate courtship with males. Males incubate the resulting clutch of eggs by themselves and do not tolerate the female near the nest after the clutch is complete. Females then lay additional clutches for other males.

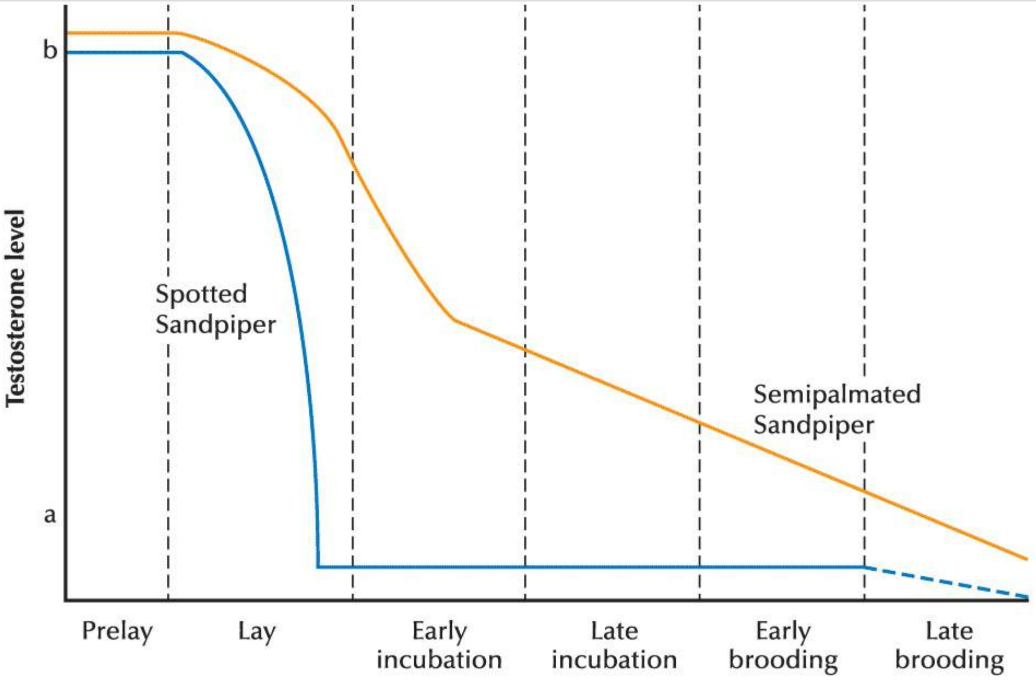
Classic polyandry has evolved primarily in the Order Charadriiformes, including the buttonquails, jacanas, painted snipes, the Plains Wanderer of Australia, the ploverlike Eurasian Dotterel, and a few sandpipers. The mesites and some rails are also polyandrous. Like all avian breeding systems, polyandry exhibits substantial phylogenetic consistency. The jacanas, painted snipe, and Plains Wanderer form a polyandrous clade that is over 30 million years old (Prum et al. 2015).

The Spotted Sandpiper of North America provides a classic case study of avian serial polyandry (Oring et al. 1997). Female Spotted Sandpipers are 25 percent larger than males. They defend large nesting territories and fight one another for the available males (Figure 14–2). Initially, females pair monogamously, and many (but not all) share parental duties. As additional males arrive on breeding grounds, females compete for them. A female's reproductive success increases directly with her ability to obtain extra mates. At some locations, Spotted Sandpipers breed monogamously, and females help care for young. At other locations, including Minnesota, some females become polyandrous and attract as many as four males. In this case, a female lays separate clutches of four eggs each sequentially for her primary male and for one to three secondary males. Each male assumes most of the parental care. It incubates its clutch of eggs, defends a surrounding territory against other males, and cares for the brood. When a male loses its clutch of eggs to a predator, the female quickly replaces the clutch with a new set of eggs. One female produced five clutches for three males in 43 days.

LARRY SELMAN/MOSTLYBIRDS.COM/GETTY IMAGES

Figure 14–2 Polyandrous female Spotted Sandpipers defend their territory against neighboring females.

Changes in the levels of hormones that mediate aggression and parental behavior match the reversal of sex roles in this sandpiper (Oring and Fivizzani 1991; Figure 14–3). Levels of the sex hormone testosterone are lower in males than in their aggressive females. Testosterone also inhibits incubation behavior. Low levels of this hormone in male Spotted Sandpipers facilitate their increased incubation effort. Conversely, high levels of the hormone prolactin promote incubation and other parental behavior.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
Data from Oring and Fivizzani 1991

Figure 14–3 Seasonal changes in the circulating testosterone levels of male Spotted Sandpipers and Semipalmated Sandpipers. In male Spotted Sandpipers, which perform all or most of the parental care, testosterone levels drop sharply from (b) the elevated levels that support sexual activity before eggs are laid to (a) basal levels at the onset of incubation. In male Semipalmated Sandpipers, which share incubation with their mates, testosterone levels decline gradually throughout the parental-care period.

Male incubation seems unlikely to evolve unless the male is confident of his paternity of the clutch that he parents (Oring et al. 1997). Extra-pair paternity accounts for about 10 percent of Spotted

Sandpiper young. Mixed paternities are the result of fertilization by sperm that females store from their other mates. Females store sperm for as long as a month and use it to fertilize some eggs in later clutches.

Paternity assurance accrues for both primary and secondary males in several ways. First, within-pair copulation rates peak when females are most likely to be fertilized—on the day before the first egg is laid. Second, mates copulate frequently within one minute when they are reunited after a separation. Third, females usually reject attempts at extra-pair courtship (Oring et al. 1993). But, in the end, younger, secondary males incubate and then parent some young that are not their own. Doing so is better than not reproducing at all. And, as if to compensate, they get more assistance from the female than does the primary male. All’s fair it seems.

Sex-role reversal is even more striking in the jacanas (Family Jacanidae), long-toed marsh birds of the Tropics. They provide the most extreme examples of reverse sexual size dimorphism among birds (Emlen and Wrege 2004). Females are from 50 to 83 percent larger than males in seven of the eight species in the family. Female–female competition over territorial control has contributed to the evolution of unusual weapons—either wing spurs on the carpometacarpus (*Jacana*) or a sharp bladelike radius (Old World genera). Female Wattled Jacanas also have more elaborate ornamentation (facial shield and wattles) and larger wing spurs than do males, which they dominate physically. Males and females of another species, the Lesser Jacana, are the same size and share equally in all aspects of parental care. In the remaining species of jacanas, however, males build the nest, incubate, and raise their young (Jenni and Mace 1999).

Female Northern Jacanas and the closely related Wattled Jacanas bond with as many as four males simultaneously in rich habitats with high densities of males. Each male defends its own nesting territory, aided by the female, within the female's larger territory. When Stephen Emlen and his colleagues (1989) removed resident females—thereby creating opportunities for new females to take over the undefended territories and associated males—the takeover females killed or evicted three of four existing broods of chicks. They solicited copulations from four of the five "widowed" males to start all over again with their own young.

As with Spotted Sandpipers, the multiple males paired with a single female Wattled Jacana may lose substantial paternity to each other, as much as 74 percent of the chicks in their broods (Emlen et al. 1998). The female copulates frequently with all the males of her harem during the production and laying of eggs. The risk of mixed paternity therefore increases with the number of males in the group. Single mates of monogamous females experience full paternity. The result is that male jacanas compete with one another not only for the receipt of a clutch but also for copulations to fertilize both the eggs in their primary clutch and the eggs tended by other males in the harem.

Diverse species practice **cooperative polyandry,** in which several males cooperate to assist one or several females. Such species include Galápagos and Harris's Hawks, Dusky Moorhen and Tasmanian Nativehen, Acorn Woodpecker, Eclectus Parrot, and sometimes

Dunnock.

The games of allocation of resources to parental care motivated by the probability of paternity reach their zenith in the complex mating systems of the Dunnock, a drab, sparrowlike songbird that lives in the dense hedgerows of Europe. The complex and variable sexual relations of Dunnocks include monogamy, polygyny, polyandry, and polygynandry (Davies 1992; Gibson 1993).

Dunnocks eat the tiniest soil arthropods in dense cover, where exclusive nesting territories are difficult to maintain. Only the female incubates. The sexes establish independent but overlapping territories in relation to food density. The patterns of overlap prescribe the varied pair bonds. Where food is dense, one male may overlap the small territories of one female (monogamy) or two (bigamy). At lower food densities, however, males cannot monopolize the food resources required by females and their chicks. Females then have large territories that overlap with two (unrelated) males. Because they fledge the most chicks when they have two males helping them, such females solicit copulations from both males, increasing the commitment of each male to the parental care of her chicks. The experimental addition of food causes reductions in territory size and can promote polygyny rather than polyandry. More complex groups of two or more females may share two or more males, depending on the spatial arrangements of their feeding territories.

Contrary to the female’s best course, Dunnock males fare best as bigamists. The resulting conflicts lead to intense copulation rates (as in

Smith’s Longspur; see Box 12–3) and sperm competition. Preceding copulation is an elaborate display in which the male Dunnock pecks the female’s cloaca, thereby stimulating her to eject sperm from previous matings and simultaneously increasing the probability of egg fertilization by the latest—namely, his—ejaculate. Underneath that complexity, each sex adjusts its personal and parental relationships in ways that optimize reproductive success. To tell whether they are the fathers of certain young and, therefore, how much they should feed them, the males monitor the appearance of eggs in the nests of the females with which they have mated.

14.4 Brood Parasitism

The demands and conflicts of parental care invite both cheating and cooperation. Brood parasitism—the laying of eggs in another female or pair's nest—is a relatively common form of cheating. It allows females to increase the number of eggs that they lay without increasing their parental care costs. It also provides a female with the opportunity to dilute the risk of losing all her offspring to predation, which weighs heavily on nests and nestlings.

Brood parasitism among birds takes place both within species and between species. Many species practice facultative (or occasional) **intraspecific brood parasitism;** that is, they sometimes lay extra eggs in the nests of other females of the same species as a supplement to those tended in their own nest. A few species are facultative interspecific brood parasites. In addition to tending her own nest and clutch, female Redheads, for example, lay eggs in the nests of other Redheads and other duck species. This kind of behavior inspired the fairy tale of *The Ugly Duckling,* though swans do not engage in it.

Obligate brood parasites, reviewed next, never build their own nests or raise their own young. Instead, they depend entirely on other species for parental care. Needless to say, the costs for the "host" of the egg of a brood parasite are very great, setting up the conditions for an evolutionary "arms race" that has led to some of the most remarkable adaptations and counteradaptations documented in vertebrate systems.

Intraspecific Brood Parasitism

Intraspecific brood parasitism is widespread among birds, being reported in at least 234 species in 16 orders (Yom-Tov 2001). The habit is most prevalent among waterfowl, but the practitioners also include grebes, fowl, gulls, ostriches, pigeons and doves, and songbirds. American Cliff Swallows nesting in large, dense colonies in southwestern Nebraska regularly lay their eggs in one another's nests (Brown and Brown 1995). Careful daily monitoring of the number of eggs in nests revealed that at least 24 percent of the nests in colonies of more than 10 pairs of swallows received eggs from neighbors. Parasitic females quickly deposited eggs in host nests when the hosts were away; in one instance, it took only 15 seconds to do so. Such parasitism reduced the reproductive success of host females, which acted as though the parasitic eggs were their own and laid fewer eggs themselves.

Common Starlings commonly lay eggs in other nests of their own species. Like those of the cliff swallows, one of every four early nests in both New Jersey and Britain acquires foreign eggs (Evans 1988; Cabe 1993). Breeding females guard against parasitism by removing foreign eggs deposited before they themselves start to lay. After a female has started her own clutch, however, it cannot distinguish the parasitic eggs. Often, a roaming, parasitic female removes one of a host's eggs and replaces it with her own. In addition to making detection more difficult, egg removal by the parasite keeps the clutch size closer to the optimal number (six) for nest success, to its own benefit as well as that of the host. At least one species, the American Coot, optimizes its clutch size by keeping count of its own eggs versus distinguishable parasitic eggs (Box 14–1). Wood Ducks nesting in artificial nest boxes have been documented to have “dump” nests in which several females may lay as many as 30 to 40 eggs (Semel and Sherman 1986).

Box 14–1

Coots Count

American Coots are almost comical, ducklike rails whose name also refers to a simpleton or stupid person. Quite the opposite. They are champions of the game of optimizing their allocation of eggs to their own nests versus the nests of neighbors. They even keep count of how many eggs are in their own nests (Lyon 2003).

Intraspecific nest parasitism is high in British Columbia, where 41 percent of coot nests include eggs placed there deliberately by other females. Thirteen percent of all eggs laid were in the nests of other females. Female coots recognize about half of the parasitic eggs by the timing of their appearance and, in some cases, by distinctive color patterns. They either kill such an egg by burying it in the nest material or move it to an inferior incubation position in the clutch, which delays hatching and increases the likelihood that the chick will not survive.

Faced with the likely addition of parasitic eggs to the clutch, the female coot keeps an ongoing count of how many eggs in the nest she recognizes as her own. She continues to add eggs to the optimal clutch size. Her count excludes eggs that have been added by others but that she later rejects. She doesn’t spot all the parasitic eggs, however, and counts some of them as her own. She lays one egg fewer of her own for each accepted parasitic egg to reach her correct clutch size.

Deciding when it pays to put some eggs in the nests of neighbors rather than in the female’s own nest adds more complexity to the game.

Generally, coot chicks from the earliest-laid eggs in a clutch survive best. A female coot parasitizes another nest when an early addition to the neighbor's clutch has a better chance of succeeding than does a late addition to her own clutch.

NFKENYON/SHUTTERSTOCK

An American Coot.

Intraspecific parasitism could be the first step in the evolution of obligatory brood parasitism. Facultative parasitism of the nests of closely related species would be the next step. The Black-billed Cuckoos and Yellow-billed Cuckoos of North America, for example, parasitize each other, particularly when abundant food encourages the production of extra eggs (Hughes 2001). The acceptance of a parasite's eggs and successful raising of its young then lead logically to increasing parasitism and possibly to obligatory interspecific brood parasitism.

Obligate Brood Parasitism

Cowbirds of North America and cuckoos of Eurasia are the most familiar species that entirely relinquish care of their young to foster parents of other species (Davies 2000). Such obligate brood parasites always lay their eggs in the nests of other birds. This breeding strategy is unusual; about 1 percent of the world's bird species are obligate brood parasites. A few fish and social insects (but no mammals) also are obligate brood parasites. Because bird eggs develop outside the body of the female, birds are among the most vulnerable of all taxa to brood parasitism. Among birds, the practice has evolved independently several times, including in cowbirds (Icteridae; five of six species), honeyguides (Indicatoridae; 18 species), cuckoos (Cuculidae; 53 of 135 species), African brood-parasitic finches (Viduidae; 19 species), and the Black-headed Duck (Anatidae) (Payne 1998).

Given the advantages of brood parasitism and the potential vulnerability of birds to this practice, it is remarkable that there are not more obligate brood parasites. By reducing their costs, risks, and commitments, birds that are obligate brood parasites can lay more eggs each season. Additionally, by not putting all their eggs into one nest, brood parasites improve the chances that some of their offspring will escape predation. Female Brown-headed Cowbirds lay from 30 to 40 eggs per season in weekly sets of two to five eggs (Lowther 1993) but they are physiologically capable of laying up to 77 eggs per year (Holford and Roby 1993). The tropical Shiny Cowbird of South America may lay as many as 150 eggs per breeding season (Kattan 1997)! Most host nests have only one cowbird egg, but some may have as many as 12 as a result of visits by multiple female cowbirds. African cuckoos of several species lay from 16 to 25 eggs per season in batches of three to six eggs, but they lay only one egg per nest (Davies 2000).

Obligate brood parasites have a remarkable series of adaptations that increase their success at parasitizing the parental care of their hosts. The thick shells of parasitic cuckoo eggs prevent cracking or punctures by hosts that try to reject them. Female cuckoos drop their eggs into deep nests, sometimes damaging the hosts' eggs rather than their own. Some parasites also remove a host egg before laying one of their own, perhaps because some hosts count their own eggs and reject extra eggs that appear out of sequence. Males of many species of cuckoos resemble bird-eating *Accipiter* hawks and may scare hosts away from their nests, enabling parasitism by the less conspicuous females (Davies and Welburgen 2008). Flocks of Giant Cowbirds have a different strategy: they raid host colonies of American blackbirds such as caciques and oropendolas. The males perch openly and invite attack to distract the hosts while the females sneak into nests from hidden perches.

Obligate brood parasites also have other life-history adaptations that make brood parasitism more effective. Brood parasites are often much larger than their hosts but have relatively small inconspicuous eggs for their body size. Their nestlings, which tend to be larger than those of their hosts, gain preferential feeding by the parents. As a rule, the eggs of brood parasites require less incubation time (from two to four days less) than do those of the host. This timing ensures earlier hatching and dominance by the young parasite. The Pied Bronze Cuckoo and Common Cuckoo get a head start by incubating eggs in their oviducts for as long as 18 hours before laying. Hatchling parasites also grow faster than nonparasites, enabling them to garner most of the parental attention. Common Cuckoo chicks are even more direct (Kilner et al. 1999). They stimulate the host parent Great Reed Warblers to bring more food faster by imitating the begging calls of warbler nestlings. Parents increase food deliveries in proportion to the volume of begging calls. Therefore, a cuckoo chick imitates not just one of its foster nestlings but a chorus of *si* . . . *si* . . . *si* . . . *si* calls from the entire brood. Initially, the cuckoo chick’s loud begging calls are equal to the calls of four foster warbler nestlings. As the cuckoo chick grows, the volume of its robust begging call grows, too, ultimately matching that expected from eight warbler nestlings.

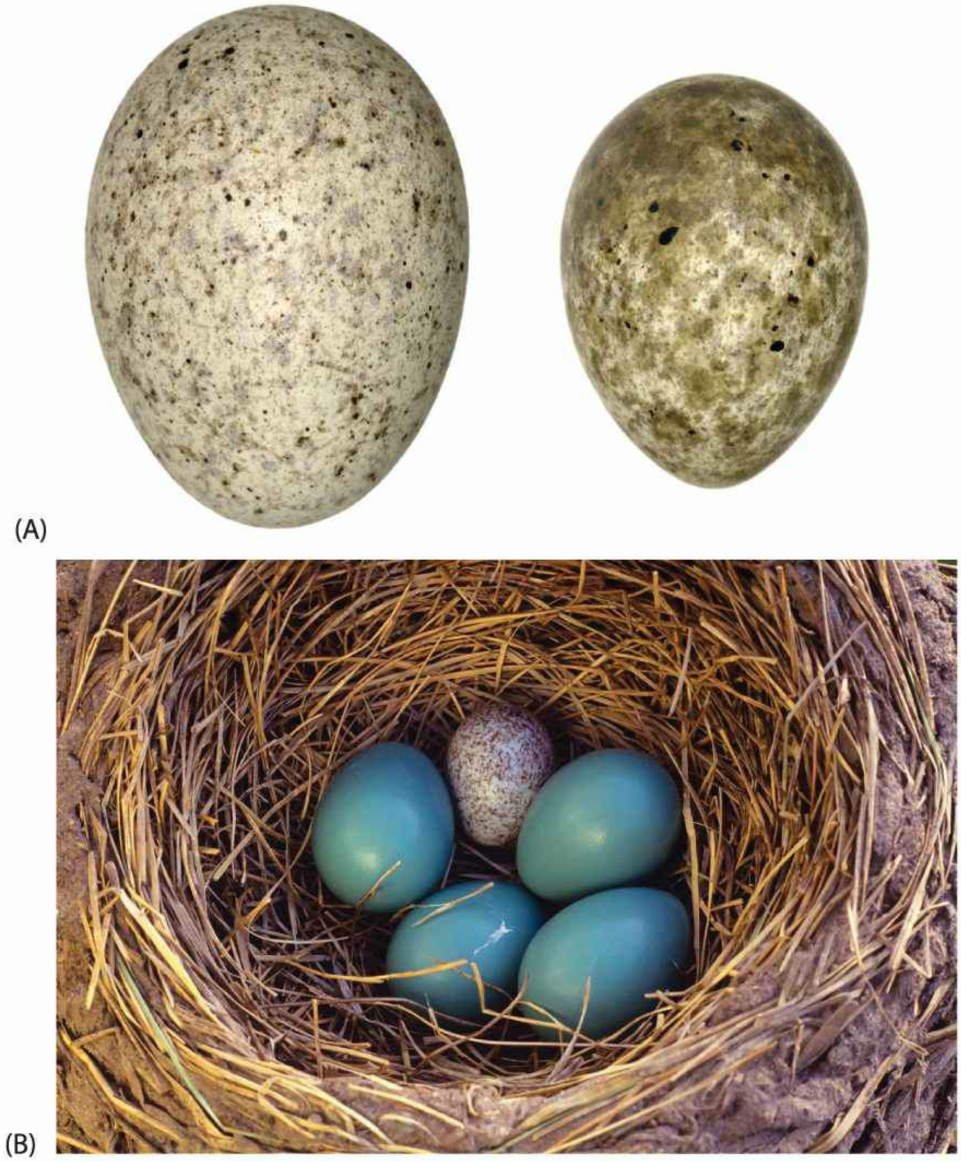
Nestlings of some brood parasites actually kill their host nest mates to reduce competition for food with the parents. Hatchling cuckoos shove the unhatched host eggs up and out of the nest using their concave backs (Figure 14–4). This behavior is a reflex and begins before the baby cuckoo’s eyes are even open. Baby honeyguides have fanglike hooks at the ends of their bills for murdering their foster nest mates.

(A) ULLSTEIN BILD/GETTY IMAGES. (B) CLAIRE SPOTTISWOODE

Figure 14–4 Blind, featherless, precocial baby brood parasites dispose of their nest competitors. (A) A hatchling Common Cuckoo pushes the eggs of the host from the nest. (B) A hatchling Greater Honeyguide kills host nestlings with the hooklike tip of its bill.

Some obligate brood parasites are highly specialized birds that target specific hosts. To minimize detection and destruction of their eggs by the host, many cuckoo eggs have evolved to resemble or mimic those of their primary hosts. In Africa, the eggs of the Dideric Cuckoo are so similar to those of its host, the Vitelline Masked Weaver, that one ornithologist resorted to chromosome analysis to distinguish them (Jensen 1980). The eggs of the Red-chested Cuckoo (and perhaps other species) closely match their hosts' eggs in the ultraviolet spectrum and other aspects not visible to the human eye (Cherry and Bennett 2001). Such ultraviolet mimicry may prove to be more widespread than we had realized (Aidala et al. 2012).

Throughout Eurasia, Common Cuckoos parasitize a variety of host species that have eggs with different colors and color patterns. In these cases, the Common Cuckoos' eggs have evolved to mimic those of their multiple hosts (Figure 14–5A). Females raised by one host species tend to return to parasitize nests of the same species. Because the genes for egg color and pattern are inherited on the female-specific W sex chromosome, the result is the evolution of dozens of distinct host-specific egg color morphs, or gentes, which coexist across parts of Europe and Asia. Thus, Common Cuckoos lay matching blue eggs in the nests of Common Redstart and Whinchat and greenish eggs with dark markings to match the Great Reed Warbler. Although the gentes coexist, they are not different species. Females mate freely with males raised by any host species. Because the egg color genes on the W chromosome cannot recombine, their fidelity to their own natal hosts allows different matrilines to specialize in brood parasitism of many different hosts.



(A) NATURE PHOTOGRAPHERS LTD/ALAMY. (B) DON JOHNSTON/ALL CANADA PHOTOS/AGE FOTOSTOCK

Figure 14–5 Some brood parasites produce eggs that mimic their specific hosts' eggs, whereas others take a more generalist approach and do not produce eggs that resemble their targeted nests. (A) Matched pair of the Common Cuckoo (*left*) and host Reed Warbler (*right*). (B) An American Robin nest with a cowbird's egg.

Cowbirds, on the other hand, are generalist brood parasites that do not closely mimic the eggs of most of their hosts (Figure 14–5B). The Brown-headed Cowbird, for example, has more than 200 documented host species. Cowbirds sometimes (but not always) remove a host egg before laying one of their own, and nestling cowbirds do not evict their foster nest mates, as do many cuckoos and honeyguides. Rather, cowbirds rely on their larger size (they are more than twice the size of most of their hosts) and louder begging to monopolize the food delivered to the nest.

Brood parasites may even “farm” hosts by wrecking unparasitized nests and forcing the hosts to build a new nest open to future parasitism. Or they may respond to egg rejection by destroying nests from which their eggs have been removed (Hoover and Robinson 2007). This form of punishing species for egg rejection has been experimentally demonstrated in Great Spotted Cuckoos and Brown-headed Cowbirds. If this behavior proves to be widespread, it may provide a partial answer as to why many host species accept cowbird eggs.

Many brood parasites have specialized adult diets that might not be good or available seasonally for developing nestlings. Cuckoos, for example, largely eat toxic, hairy caterpillars that are difficult to digest, especially for nestlings. Honeyguides largely eat wax, which would also be difficult for nestlings to digest. Cowbirds often feed with livestock as much as 15 kilometers away from forested areas where they prefer to search for nests. Historically, they followed nomadic herds of bison, a behavior that conflicted with a local residency.

Counteradaptations of Hosts

Brood parasitism is extremely costly to the hosts and strongly selects for counteradaptations to prevent it. These counteradaptations then select for counter-counteradaptations on the part of the parasite and so on. This evolutionary “arms race” has been the subject of some of the classic experimental studies demonstrating the host–parasite coevolutionary process, which has been widely studied in plant-insect herbivory and in host–pathogen systems such as human diseases but has received less attention in vertebrate–vertebrate interactions.

Perhaps the simplest form of defense by hosts is to simply defend the nest against brood parasites by mobbing them or chasing them away. Even if they are too small to physically evict the parasites, they can distract the parasites and make it more difficult to find the nests and lay their eggs without distraction. Some hosts can prevent parasitism by sitting on the nest during the morning hours when cowbirds lay their eggs to prevent access. These behaviors may have selected for the hawk mimicry of male cuckoos mentioned above.

The next simplest form of defense is to simply remove the parasitic egg from a nest. Some host birds accept the eggs of a brood parasite, but others do not. Stephen Rothstein (1975) placed artificial cowbird eggs in 640 nests of 30 species of North American birds. Twenty-three of these species usually accepted the eggs (meaning that they threw them out less than 30 to 40 percent of the time), whereas seven species usually rejected the different eggs. “Rejectors” typically threw out the parasite eggs as a natural extension of nest sanitation behavior, albeit at some risk to damaging their own eggs. Some cuckoo hosts are more likely to eject a cuckoo egg from their nests if they have seen a cuckoo nearby (Lotem et al. 1995).

Another costly form of defense by hosts is to abandon parasitized nests rather than raise broods that will be dominated by cowbird nestlings. Some birds, such as the American Yellow Warbler, respond to the discovery of a cowbird egg by deserting the nest or by burying the entire clutch in additional nest materials and laying a fresh clutch of eggs on top; sometimes the renests are also parasitized, which may lead to multistory nests built on top of each other. Others desert the nest and start over again elsewhere.

The rejection defenses of American Robins against cowbird parasitism vary with location (Briskie et al. 1992). In Churchill, Manitoba, north of the range of cowbirds, American Robins are more likely to accept a parasitic egg than in southern Manitoba, where cowbirds have parasitized local birds for centuries. One-third of the southern robins rejected an experimental egg placed in their nests by “parasitic” ornithologists, whereas all Churchill robins accepted them.

The observation that egg rejection exists only where host populations are at risk of parasitism suggests that it may be a costly behavior. Egg rejection is tricky business when a female experiences both intraspecific brood parasitism and the attentions of an obligate brood parasite. Rejecting eggs from multiple sources increases the host’s risk of damaging some of her own eggs. Conversely, the one duck that is an obligate brood parasite, the Black-headed Duck, suffers substantial costs to its own eggs due to, incidentally, the host coots’ responses to their own high levels of intraspecific brood parasitism (Lyon and Eadie 2004). The Black-headed Duck parasitizes mainly two species of coots in South America. Unlike those of all other brood-parasitic birds, the Black-headed Duck young leave the nest on hatching and require no parental care from the host. Yet the eggs are rejected at high rates (38–65 percent), and few of those that remain will hatch. Like the related American Coot, South American coots experience frequent brood parasitism by their neighbors, so they are vigilant for foreign eggs. They reject the duck eggs at high rates as a result of their vigilant rejection of any other coot's eggs.

Not all brood parasites exert strong selection for host defenses. Carrion Crow nests parasitized by Great Spotted Cuckoos, for example, suffer less nest predation than those that are not parasitized. An experimental study showed that the cuckoo nestlings exude a foul-smelling substance from their cloacal gland when approached by a predator, to the benefit of host nestlings too (Röder et al. 2014). Great Spotted Cuckoo nestlings are also roughly the same sizes as those of their hosts, do not evict their nest mates, and do not monopolize most of the food as they would in a much smaller host. Conversely the crow hosts tolerate the parasitic eggs, an apparent example of a mutualism.

Coevolution in African Finches

All 18 species of *Vidua* finches in Africa are parasitic specialists on single grass finch host species (Estrildidae) (Box 14–2). Through a coevolutionary arms race, the host nestlings have evolved bold mouth color patterns that distinguish them from parasites, but parasites have evolved to closely match the mouth patterns of the hosts. The mimicry of mouth color and markings of their host's nestlings allows young *Vidua* brood parasites to deceive their foster parents (Payne 2005b; Figure 14–6). The adults also mimic host songs, which fosters the fidelity of successive generations of parasite to their specific host. How? Briefly, both males and females imprint as nestlings on the song of their host. Males of each *Vidua* species later sing the host song to attract females, which were raised by the same host. The females then lay their eggs in the nests of the same hosts, which the females identify by the familiar song.

Box 14–2

Aggressive Mimicry in Viduine Finches

The brood-parasitic finches of Africa and their hosts are sources of insight into the coevolutionary dynamics of brood parasitism in birds. The practice of brood parasitism in this group evolved only once, about 20 million years ago. The family Viduidae includes 19 species of indigobirds and whydahs and the distinct Cuckoo-finch. Together, they are the sister group of the firefinches and pytilias that are their hosts. The two related sets of species, one parasitic on the other, have evolved and speciated in a long and enduring association. The females of these parasitic finches closely mimic the plumage of their sociable hosts and thereby gain access to their nests without being driven away. This sort of female mimicry is known for fish such as bluegills and in Ruffs and Reeves (see Chapter 13). The Cuckoo-finch, which shifted to certain African warblers as its hosts, practices a deeper deception. Female Cuckoo-finches mimic the plumage pattern of female bishops and widowbirds (genus *Euplectes*), unrelated and nonparasitic weavers that the warblers tend to tolerate (Feeney et al. 2015).

Claire Spottiswoode

Female Cuckoo-finches (*left*) closely resemble the female Southern Red Bishop (*right*).

Robert B. Payne, Nestling mouth markings and colors of Old World finches Estrildidae: mimicry and coevolution of nesting finches and their Vidua brood parasites. Miscellaneous Publications, Museum of Zoology, University of Michigan, no. 194, Ann Arbor

Figure 14–6 The mouth pattern of a nestling of the Black-bellied Firefinch includes a ring of five large black spots against a bold white palate and large red gape swellings with white corners. The lower mouth is black, and the tongue is pink with a broad black band.

How, then, did the different host-specific species of *Vidua* finches come to be? Did they co-speciate—split, speciate, and coevolve in concert with their grass finch hosts? Or did some females switch hosts opportunistically and start new host-specific lineages? Analysis of the patterns and timings of speciation in both grass finches and *Vidua* finches suggests that co-speciation did not take place. Rather, the colonization of new hosts (like the colonization of a new island) was the principal way that the *Vidua* finches evolved into new host-specific species.

Bob Payne and his colleagues (2002) documented a switch to a novel host species by one *Vidua* species, the Village Indigobird. This species normally mimics and parasitizes the Red-billed Firefinch. But one population on the Zambezi River in southern Africa parasitizes the nests and mimics the song of the Brown Firefinch. It is the only population of Village Indigobirds known to do so. Nestlings of this pioneering population still have mouth markings that match those of their traditional hosts. The two host-specific races, old and new, coexist as distinct breeding populations.

Effects of Brood Parasites on Host Populations

Because brood parasites reduce host fitness, they have the potential to cause problems for heavily parasitized host populations. Parasitism levels of most cuckoo hosts are relatively low; typically, less than 5 percent of cuckoo host nests are parasitized, although there are exceptions. Cuckoo-host parasitism systems are evolutionarily very old, and it appears that they have evolved toward host–parasite specialization and reduced virulence, a situation analogous to many diseases that begin as a severe outbreak but, with time, evolve toward reduced negative impacts on hosts. If parasites drive their hosts to near extinction, their own populations will also suffer, which should select for less costly parasitism. There is growing evidence that some cuckoos are no more fecund than their hosts over the course of their breeding season and that most host nests within their territories are not parasitized. Given these low levels of parasitism, it is unlikely that cuckoos are a significant threat to host populations.

The Brown-headed Cowbirds and Shiny Cowbirds, however, pose much more severe threats to some of their hosts. Generalist brood parasites like these can potentially drive one host species to extinction—especially rare species that suffer high costs from parasitism—without suffering much from reduced fitness because they have other hosts to parasitize. These cowbird species are more abundant than most of their hosts, many of which have not yet evolved effective defenses. Brown-headed Cowbirds parasitize three-fourths of the nests of Neotropical migrants in small forest fragments in Illinois, often with two or more cowbird eggs (Robinson et al. 1995). Combined with high rates of nest predation, few nests succeed. Because of their tremendous impact on host populations, the control of cowbirds is an important tool for the management of highly endangered species such as the Black-capped Vireo in Texas, Bell’s Vireo in California, and Kirtland’s Warbler in Michigan. Populations of these species have been so reduced by habitat loss that their only remaining populations live in areas where cowbirds are abundant.

Cowbirds were believed to be partly responsible for the precipitous decline of the endangered Kirtland’s Warbler in Michigan (Mayfield 1992). In 1957, parasitism was high (about 55 percent), and 75 percent of the nests examined between 1957 and 1971 were parasitized. In just one decade, the number of singing male Kirtland’s Warblers dropped from 502 (1961) to 201 (1971), and parasitized nests produced nearly 40 percent fewer young than unparasitized nests. Emergency removal of cowbirds, which started in 1972, caused nest parasitism to drop to just 3 percent. The warbler population stabilized at about 200 pairs but did not increase until 1990, when it grew in response to new habitat created by a wildfire. Cowbird control may be a short-term, expensive management tool for endangered species, but it cannot substitute for the acquisition and management of quality habitat (Rothstein and Robinson 1994).

The long-term effect of brood parasitism by cowbirds may not be severe in species that have several broods of young a year (Payne 1998; Payne and Payne 1998). For example, rearing a cowbird nestling has little effect on the lifetime reproductive success of an adult Indigo Bunting. It does not affect the bunting’s ability to nest again in the same season, nor does it affect adult survival and reproductive success in future years.

14.5 Cooperative Breeding

Brood parasitism and cooperative breeding are opposite extremes of the breeding-systems of birds. Obligatory brood parasites are selfish cheaters whose evolution is consistent with Charles Darwin's theory of natural selection. Individual advantages are not as obvious in **cooperative breeding,** in which "helpers" care for young that are not their own. Hundreds of bird species breed cooperatively.

The apparent altruism of cooperative breeding challenges the basic tenets of evolution by natural selection: Darwin himself offered the discovery of altruistic behavior as a way to disprove his theory. A century later, V. C. Wynne-Edwards (1962) proposed that individual organisms place the good of their populations or species above their individual well-being. Helpers at the nest seemed to offer compelling cases of altruism.

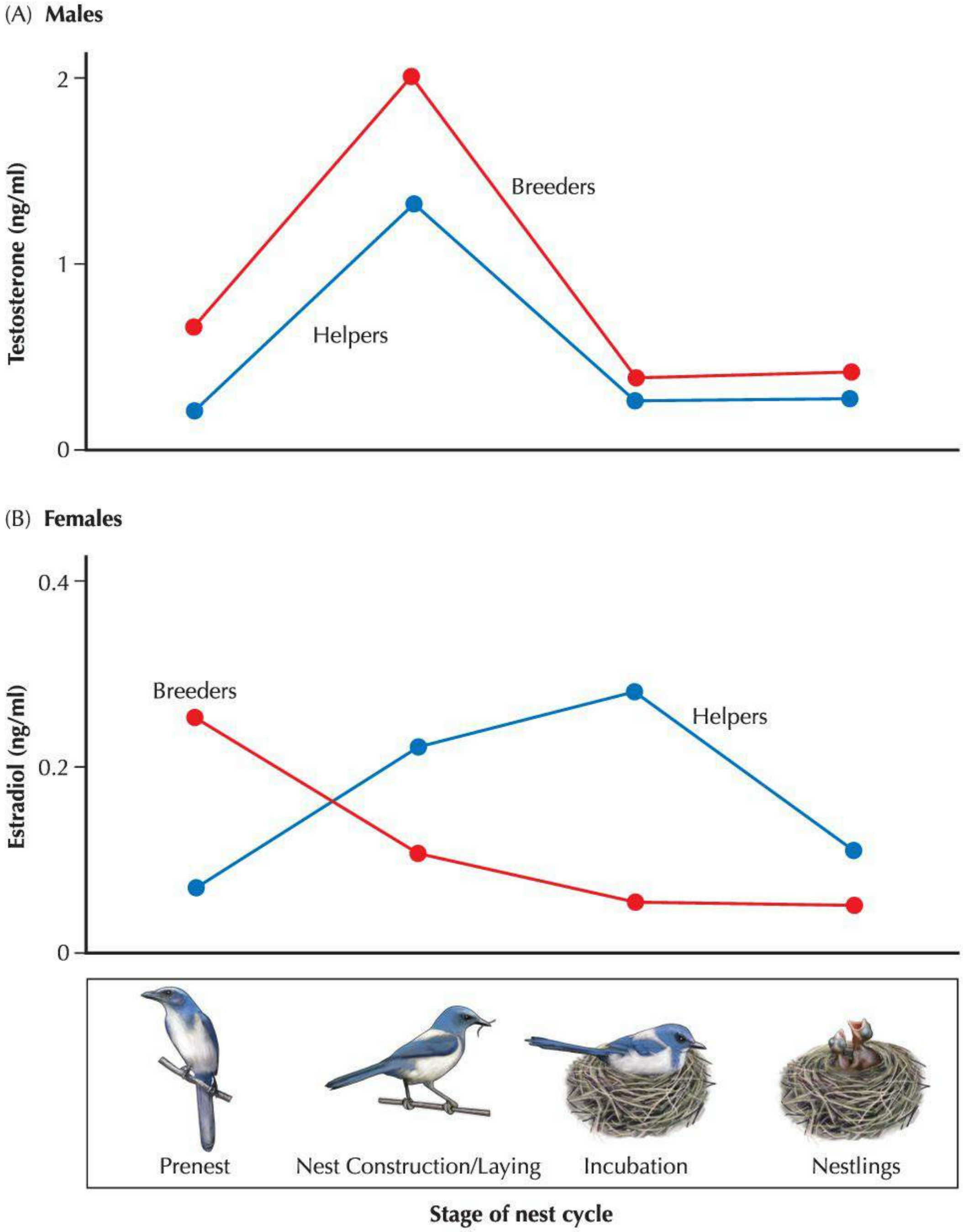
Do helpers really sacrifice their own reproductive potential to help others? Or do they benefit individually in some way? Two possibilities stand out. First, helpers might directly enhance their later reproduction by gaining experience from delaying their own dispersal and helping at their parents' nest. Second, helpers might obtain indirect benefits, either by enhancing their inclusive fitness through the production of genetic relatives, called **kin selection,** or by obtaining help in return, called **reciprocal altruism.** Kin selection is one way of understanding complex social behavior in ants, bees, and wasps, in which sterile castes help their mother produce sisters. Reciprocal altruism could be in an individual organism's best interest as long as there is no cheating.

Field studies of cooperative breeders reveal that helpers achieve both direct benefits and, in some cases, indirect benefits. Helpers contribute to parental care by contributing to defense of the territory and protection and feeding of the nestlings in a diverse array of cooperative-breeding systems. In Florida Scrub Jays, helpers are an integral part of the social system (Woolfenden and Fitzpatrick 1996; Figure 14–7). The basic social unit is a breeding pair with as many as six helpers that stay for one to seven years. About half of the breeding pairs of this jay have helpers, which defend a territory throughout the year.

STEVE BYLAND/SHUTTERSTOCK

Figure 14–7 The Florida Scrub Jay is one of the most thoroughly studied species of cooperative-breeding birds.

Neither male nor female helpers are psychologically or hormonally neutered. Surveys of varied bird species consistently indicate substantial testosterone activity in helpers, albeit at lower levels than in breeding adults (Schoech et al. 2004; Figure 14–8). Helpers of both sexes of Florida Scrub Jays, for example, are reproductively capable (Schoech 1998). Testosterone levels of helpers increase and then decrease in parallel with those of parents. Levels of prolactin, which mediates incubation and other parental behavior, average lower in helpers than in parents, but they increase in all participants to maximal levels during incubation and nestling stages of the nesting cycle.

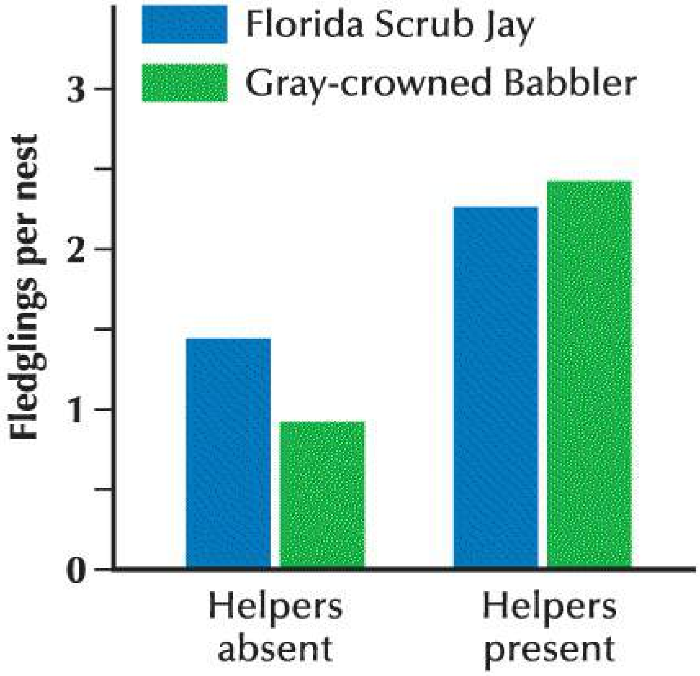


Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
DATA FROM SCHOECH 1998

Figure 14–8 Changes in sex-hormone levels during the breeding season in male and female Florida Scrub Jays. The graphs show sex-hormone levels in helpers compared with nonhelpers, or breeders. (A) Levels of testosterone in the blood are higher in breeding males than in helper males. Testosterone levels increase in both groups during the early stages of the nest cycle but then drop to low levels during incubation and care of the nestlings. (B) Levels of the estrogen estradiol drop steadily in breeding females but increase in helper females during the later stages of the nest cycle, when helper females tend to disperse in search of their own territory.

Help or Nuisance?

Do helpers really help? Or do they just hang out and interfere or compete for resources because they lack a place of their own? Most studies show that helpers truly help rather than hinder the parents in their social unit (Figure 14–9). Parental tolerance of grown offspring on their natal territories is a key step in the evolution of cooperative-breeding systems. Reasons to tolerate the continued presence of young from preceding broods center on their helpful contributions to reproduction as well as to the survival of the breeding pair itself.



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DATA FROM WOOLFENDEN 1981, BROWN ET AL. 1982

Figure 14–9 Groups with helpers fledge more young. Groups of Florida Scrub

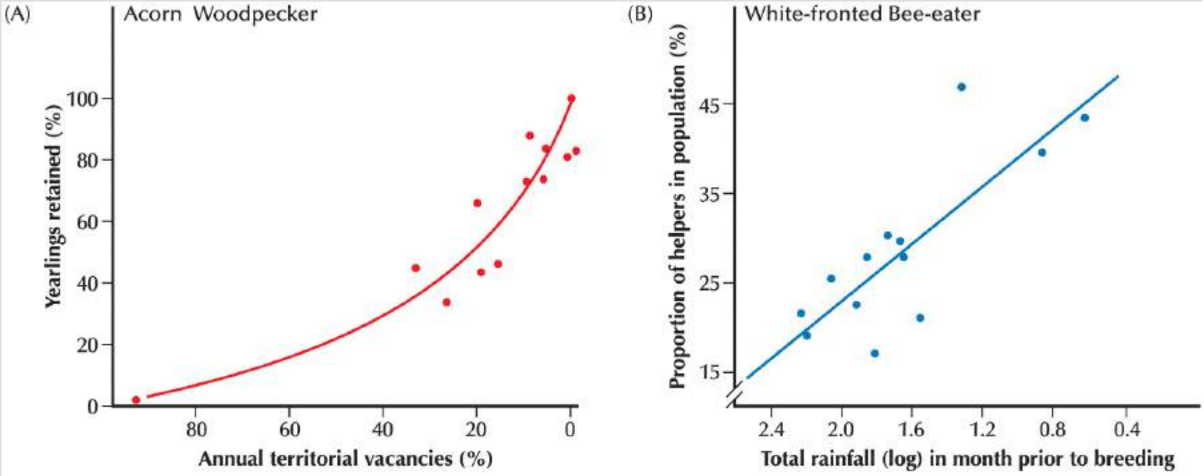
Jays with helpers produce more fledglings per nest than do pairs without helpers. The experimental removal of helpers from breeding groups of Gray-crowned Babblers reduces the average number of young fledged per nest.

Many field studies document that the number of young fledged increases with the number of helpers. Breeding pairs of Florida Scrub Jays with helpers fledged more young per season than did groups without helpers, principally as a result of better group defense against snakes, the primary predator on young jays. Temporary removal of helpers from some territories at the beginning of the breeding season showed that breeding pairs with helpers produced more young that fledged from the nest (2.2 versus 1.6) and lived longer after they left the nest than did breeding pairs without helpers (Mumme 1992). In addition to increasing the production of surviving fledglings, helpers improved the survival of the breeding parents. Breeding Florida Scrub Jays with helpers survived longer with higher lifetime reproductive success than did those without helpers.

Ecological Constraints and Delayed Dispersal

It may be in the parents’ best interests to have helpers, but why do the helpers themselves not disperse from their natal territory and breed elsewhere on their own? Young Florida Scrub Jays achieve three times the individual reproductive success when they breed on their own compared with helping their parents produce half siblings. Yet these young birds delay dispersal and reproduction on their own for several years, even though they may be physiologically capable of breeding.

Stephen Emlen (1984) proposed the general hypothesis that ecological constraints limit successful dispersal and reproduction of young birds entering the breeding population (Figure 14–10). Unpredictable or difficult breeding conditions and long-term territoriality favor cooperative breeding in some birds. For example, many species that live in the dry forests of Africa and Australia breed cooperatively. Some are nomadic. Others, such as the White-fronted Bee-eater of East Africa, are resident and colonial. Their nestlings often starve when adequate rains and good supplies of insects fail to materialize. Helpers help by increasing the rate of food delivery. They could start their own nests, but they can raise young successfully by themselves only in environmentally good years. Consequently, the size of cooperative groups increases with environmental harshness, as measured by low rainfall and poor food availability in the month preceding the onset of breeding.



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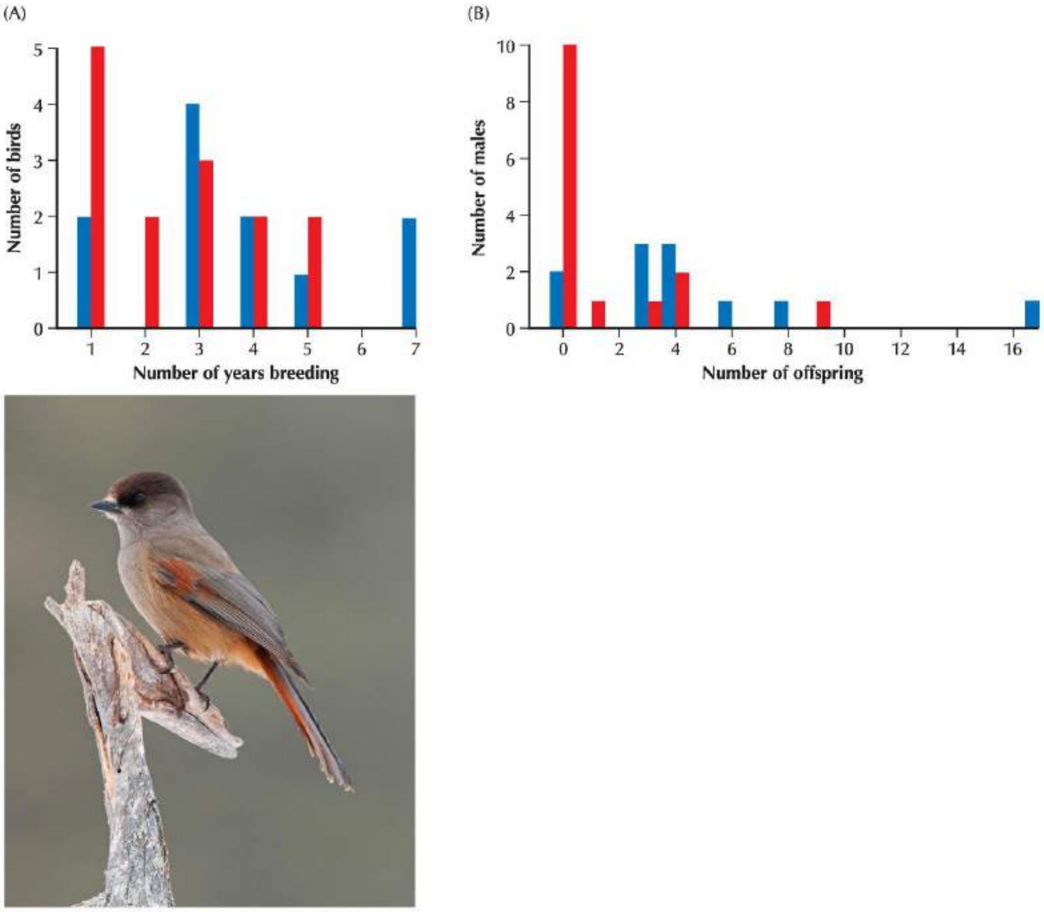
Data from Emlen 1984

Figure 14–10 The retention of young may result from ecological constraints, such as (A) territory shortage in regard to the Acorn Woodpecker and (B) environmental harshness (lack of rain) in regard to the White-fronted Bee-eater.

Recent analyses of all birds demonstrate that cooperative breeding is much more frequent in geographic regions and habitats that have low annual rainfall, high mean temperature, and high climatic variance among years, especially central Australia, sub-Saharan Africa, the Middle East, and India (Jetz and Rubenstein 2011). These data strongly imply that cooperative breeding is an adaptation to reproduction in harsh environments with unpredictable variations.

Delayed dispersal and group living, it turns out, reflect both extrinsic ecological constraints, such as habitat saturation, and intrinsic social benefits, such as improved survivorship and learning essential skills. The shortage of high-quality territories, however, is a primary constraint that discourages and delays dispersal, leading to helping one's parents initially and waiting before going it alone. Female scrub jay helpers wait for openings. They monitor nearby groups and move quickly to replace breeding females that disappear. Males, however, wait to inherit breeding positions on their natal territories. The dominant (usually oldest) son replaces its deceased father, stepfather, or brother. In other species, daughters stay to help, whereas sons tend to disperse.

Delayed dispersal increases the lifetime reproductive success of male Siberian Jays. These birds have limited access to quality habitat in the boreal forests of northern Sweden (Ekman et al. 1999). Young males that delay dispersal until a quality territory becomes available achieve higher lifetime reproductive success (Figure 14–11). Parental nepotism is a key factor in delaying dispersal by young male Siberian Jays (Ekman and Griesser 2003). Parents tolerate their own offspring over immigrant birds that try to join a family group. By blocking unrelated males from joining a group, fathers favor their sons and provide them with a safe haven of high quality with minimal competition for resources. Experimental removal of fathers led to their replacement by despotic immigrant males and the departure of the retained sons.



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DATA FROM EKMAN ET AL. 1999. PHOTO: BLICKWINKEL/MCPHOTO /ALAMY STOCKPHOTO

Figure 14–11 Lifetime reproductive success of male Siberian Jays that delayed dispersal from their natal territory (blue bars) compared with males that immigrated to a territory after dispersal in their first year of life (red bars). (A) Males that stayed bred more times in significantly more years. (B) Males that stayed produced significantly more offspring in their lifetimes.

Many side benefits can favor delayed dispersal. Among them is the acquisition of critical behavioral skills and social status required to control territorial space, acquire mates, and feed young. Young White-winged Choughs, an Australian crowlike bird, depend on food provided by helpers for almost seven months as they acquire the foraging skills needed for independence (Heinsohn 1991). In addition to waiting for a territorial opening in saturated habitats, a young bird might stay in a home territory that contains key resources not readily available elsewhere. For example, acorn storage granaries are the key resource for Acorn Woodpeckers (see Figure 11–3), and tree holes for nesting and roosting are a key resource for the endangered Red-cockaded Woodpecker. Both of these species of woodpeckers are cooperative breeders that employ young helpers from preceding broods.

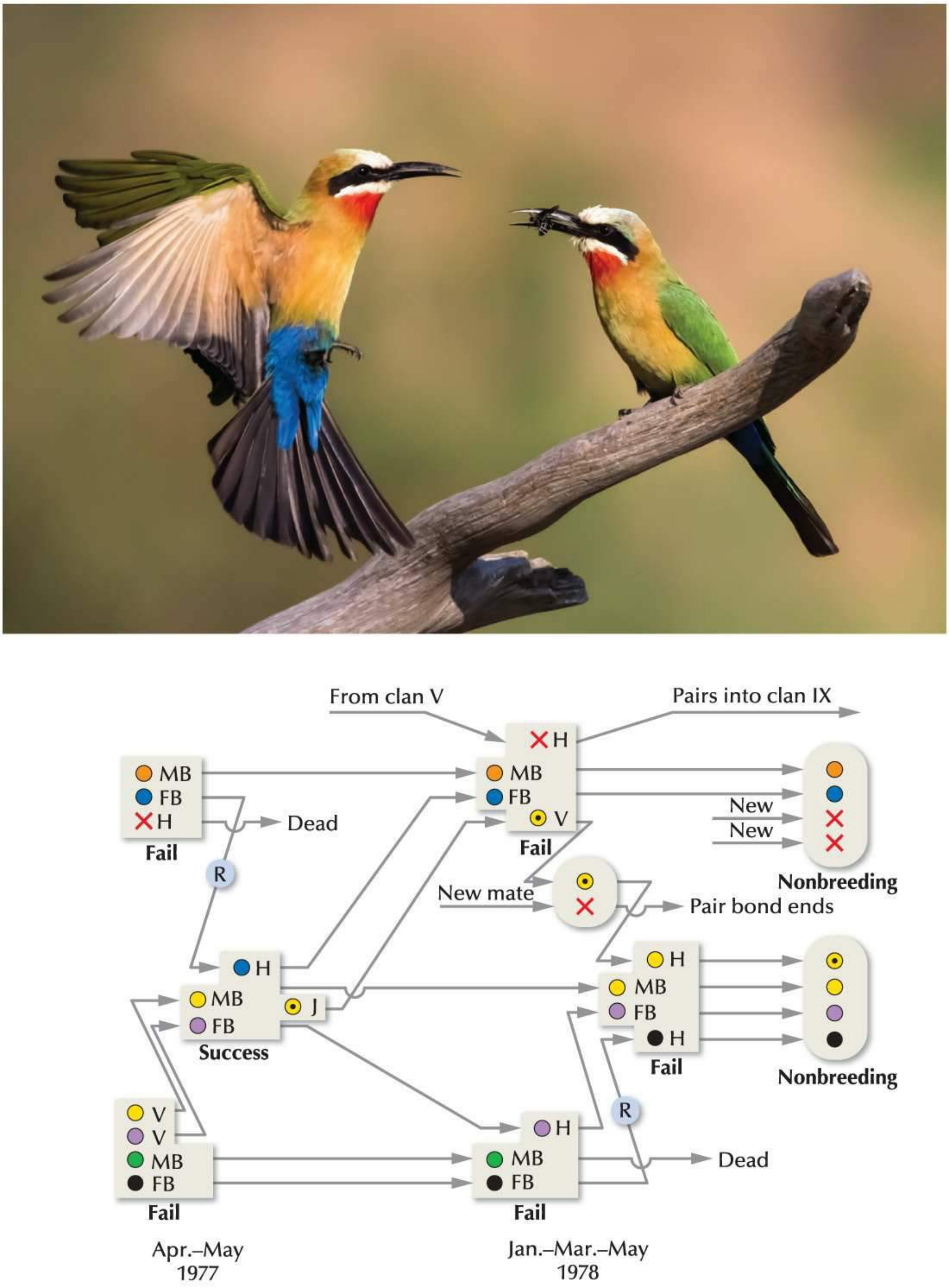
Alliances with younger siblings is a side benefit of some cooperative breeders. Green Wood Hoopoes, medium-sized hole-nesting birds of the African savannas, live in extended family groups of helpers (Figure 14–12). Large roost holes in dead trees are a key resource for these cold-sensitive birds. They stay warm at night by sleeping together inside a deep hole. Where suitable roost holes abound in some habitats in southern Africa, young wood hoopoes disperse readily to new territories, leaving pairs of adults to breed on their own (DuPlessis 1990). In the lakeside forests of the Rift Valley of East Africa, however, roost holes are scarce, and competition for territories containing them is keen. There, pairs of young wood hoopoes, usually an older and a younger sibling or half sibling, cooperate to secure new breeding space. In the avian version of the television series *Survivor,* young male wood hoopoes recruit help from their former charges to take control of a quality territory. In this way, the initial cooperation leads to long-term working alliances between siblings. The alliance is in the younger sibling’s interest because it will eventually replace its partner as the breeding male of the new unit.

DATA FROM LIGON AND LIGON 1983. PHOTO: MARTIN MECNAROWSKI/ SHUTTERSTOCK.COM

Figure 14–12 Extended families of the Green Wood Hoopoe breed cooperatively, but older helpers recruit younger offspring to help them take over a nearby breeding territory.

14.6 Complex Family Structures

The potential for complex social relations is greatest where contacts with large numbers of birds are frequent and predictable, as for colonial breeding birds. The White-fronted Bee-eater is a case in point (Emlen et al. 1995; Figure 14–13). These bee-eaters are strictly monogamous. They breed in large colonies of burrows dug into a dirt bank along the Rift Valley of East Africa, but they function on a daily basis in clans or extended families of three to 17 members from several generations. A colony usually includes from 15 to 25 families. Members of each family feed, roost, and breed cooperatively. They defend a group territory within 20 miles of the colony. Family units exhibit both stability and instability. Membership in a family provides great benefits and exacts significant costs.



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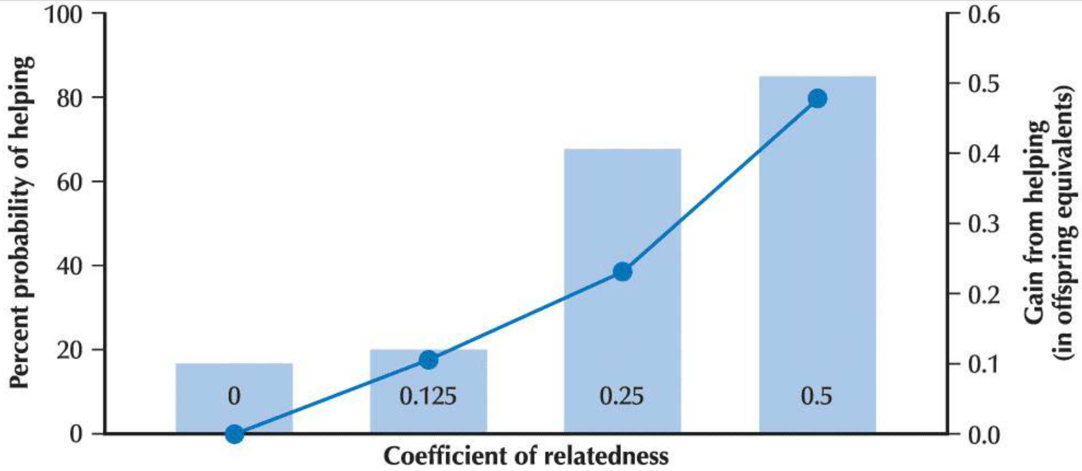
Data from Hegner et al. 1982. Photo: © Willie van Schalkwyk/Moment Open/Getty Images

Figure 14–13 The social relations of members of a clan of White-fronted Bee-eaters illustrate the complexity of a cooperative-breeding system as well as ornithologists’ ability to follow the behaviors of known, color-marked individual birds. Core members of the clan are identified individually by colored symbols. Connecting lines trace their social movements over time. Each box represents a breeding or roosting chamber in the colony: MB, male breeder; FB, female breeder; H, helper; R, redirected helping by breeders whose own efforts failed; V, visitor (i.e., a bee-eater that roosted in the chamber but did not help in the nesting effort); J, juvenile; X, temporary associate.

In 1977, this clan consisted of three chambers with monogamous pairs (MB/FB) and their associates. Two of the pairs failed in their breeding attempts. One chamber (green, black) hosted two visitors (yellow, purple), which then moved as a breeding pair to a new chamber. Blue female joined them as a helper. Their offspring (dot yellow circle) relocated as a visitor to the another chamber (orange, blue) in 1978. Blue female returned to this chamber in 1978, but failed again.

The fabric of the complex bee-eater society is a “mixture of openness and fluidity of group memberships on the one hand, with stability and fidelity of certain social bonds on the other” (Emlen 1981, p. 224). Individual birds appear to remember past associations. They leave groups to join other groups but return months or years later to roost or nest with old associates. Those that breed usually require help in feeding young. The open cooperative-breeding system of the White-fronted Bee-eater is adapted to the unpredictable environment of the Rift Valley. In some years, pairs can breed successfully by themselves, but, in other years, they cannot do so without help.

Despite their flexibility and fluidity, personal relations based on individual recognition and long-term memory are the social foundations of social complexity. Bee-eater society includes subtle forms of reciprocal altruism, social manipulation, and kinship responses (see Figure 14–13). Each family includes an assortment of the possible relatives: grandparents, uncles, aunts, nephews, and nieces as well as parents, brothers, and sisters. The nonbreeding male members of the family help the most closely related breeding pair and even opt not to help if no close kin are available (Figure 14–14). This choice requires some ability to recognize kin versus nonkin (Box 14–3).



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
DATA FROM EMLEN ET AL. 1995

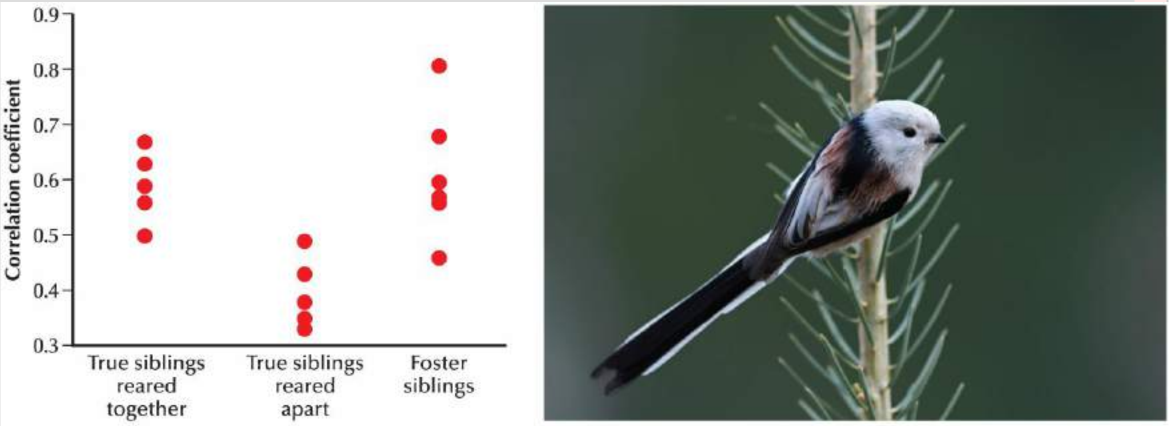
Figure 14–14 Helper White-fronted Bee-eaters chose to help the most closely related breeding pairs, thereby increasing their inclusive reproductive fitness. Their gain in indirect reproductive benefits (line) increases with their degree of genetic relatedness to the juvenile bee-eater that they help.

Box 14–3

Knowing Kin by Their Calls

Like the White-fronted Bee-eaters of Africa, the Long-tailed Bushtits of Europe help their kin. Helping in this system has a different basis: the redirection of efforts by those birds that lose their nests to predators late in the breeding season. Unable to nest themselves, failed breeders gain substantial fitness benefits indirectly by increasing the brood productivity of their close relatives. By tracking exactly which birds a failed breeder helped, Stuart Sharp and his colleagues (2005) showed that helpers chose nests of a sibling that had been fed in preceding seasons by the same parents or by related helpers. They found these kin by their distinct contact calls. Cross-fostering experiments demonstrated that the Long-tailed Bushtits learned their parents’ call signatures while in the nest. Unrelated foster siblings reared together ended up with call characteristics more alike than true siblings reared apart.

In another set of experiments, Sharp and his colleagues unveiled this system of kin recognition by measuring the responses of the bushtits to playbacks of recordings of the *churr* contact call. The ornithologists broadcasted *churr* calls from known relatives and from nonrelatives. They also manipulated the calls by erasing the highest and lowest frequencies of the call. The bushtits responded more strongly to the unmanipulated calls of their relatives than to those of nonrelatives (see graph). They also responded to manipulated calls of kin as if they were nonkin. This result suggests that the bushtits use the high and low frequencies of the calls to identify their kin.



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Data from Sharp et al. 2005. Photo: Michal Pesata/ Shutterstock.com

Cross-fostering experiments demonstrate that the calls of Long-tailed Bushtits raised together in the same nest acquire similar *churr* calls, whether or not they are genetically related siblings. Adult Long-tailed Bushtits respond more strongly to playback broadcasts of the *churr* calls of known relatives than to those of nonrelatives.

Unlike closed cooperative-breeding systems in saturated stable environments, adult bee-eaters resort to coercion and temptation to exert control over the breeding options of mobile, potential helpers. Hence, male bee-eaters actively harass their sons, blocking the nest chamber or doing whatever it takes to disrupt their early nesting attempts. They then recruit their young sons as helpers for a couple of years before the sons achieve the dominance required to breed successfully on their own. To recruit helpers, potential breeders sometimes allow helpers to share the paternity or maternity of group clutches to attract their assistance. Young female bee-eaters help only as a last resort. The first goal of a young female is to pair with a male that has the status and ability to attract or coerce others in the family to help. If she fails at that, she switches to the tactic of brood parasitism by inserting her own eggs into the clutch of her mother or a close relative. Breeding females actively discard parasitic eggs, challenging a parasite both to overcome her active defenses and to add the parasite egg within a two- or three-day period when the host female is laying her own eggs and can’t afford to make a rejection mistake.

Flexible helping and complex social relations are not restricted to colonial bee-eaters. More than 300 bird species exhibit **family structures,** defined as social groups in which offspring continue to interact beneficially with their parents into adulthood (Emlen et al. 1995). Parents of the well-studied Seychelles Warbler go beyond the relatively simple paradigms of accepting help. They manipulate the gender and parentage of their offspring in relation to habitat quality (Box 14–4). They must also deal with **inbreeding depression,** the reduced survival and fertility of offspring of related individuals, which is a potential cost of cooperative breeding with relatives. One way for females to improve offspring heterozygosity is to mate with more males, called extra-pair paternity. Close inbreeding, for example, occurred in about 5 percent of matings in the Seychelles Warbler, but 40 percent of the young were the result of extra-group paternity, despite guarding of the female by the primary male (Richardson et al. 2001).

Box 14–4

Helpful Daughters

The Seychelles Warbler is an endangered species, confined until recently to the tiny island of Cousin in the Seychelles islands of the western Indian Ocean. The territories of this drab island species consumed all the available habitat, and young warblers had no choice but to wait as helpers until a breeding adult died.

As an initial step in 1988 to prevent the extinction of the Seychelles Warbler by establishing a second population, Jan Komdeur and his colleagues transplanted breeding adults from 16 territories on Cousin to the nearby islands of Aride and Cousine. The endangered population grew from 320 to over 2,000 in just 14 years. Every individual on Cousin was color-banded and followed closely to measure lifetime reproductive success. Over 25 years of elegant experiments and research on this warbler have revealed subtle dynamics of cooperative breeding, including the roles of habitat quality and female manipulation of the sexes of her offspring (Komdeur 2003; Richardson et al. 2003).

At the outset, all the new vacancies created on Cousin were quickly filled, sometimes within hours, by birds that had been helpers. The transplanted pioneers started to breed on Aride without help. Their 61 young dispersed and bred independently on territories of their own the next year. Given opportunities to breed on their own, they did not serve as helpers. In addition to being a conservation success story, this experiment demonstrated that lifting the ecological constraint of habitat allows the birds to shift to the first-choice practice of breeding rather than helping. With time, the territories of transplanted warblers and their progeny saturated the habitat available on Aride, restoring the conditions that favored helping, especially on high-quality territories with more insect food.

Helping by young from previous broods nearly doubles the reproductive success of a breeding pair of Seychelles Warblers from 0.85 to 1.62 yearlings per year. Young females, particularly, tend to stay home to help their parents raise half brothers and half sisters. Older grandparents that are deposed from top breeding status switch to helper roles that continue production of kin. Young males, on the other hand, tend to disperse first to high turnover openings on low-quality territories, where limited insect food renders potential helper individuals a liability that reduce reproductive success. So, breeding pairs on low-quality territories do better by raising mobile sons rather than helpful daughters. Conversely, breeding pairs with many female helpers on high-quality territories gain an advantage by producing male offspring that disperse to new territories. It follows that female breeders should favor the sex of their single-egg clutches according to territory quality—male eggs on low-quality territories and female eggs to have more helpers on high-quality territories—and they do—apparently by sex-biased release of gametes before ovulation (Komdeur et al. 1997, 2002). Females on high-quality territories produced 88 percent female eggs, whereas unassisted females on low-quality territories produced 77 percent male eggs. Breeding pairs that were transferred from low- to high-quality territories switched from the production of male to female eggs. Helper removal experiments confirmed that sex-ratio bias was for the purpose of producing helpers. When females on high-quality territories had their female helpers experimentally removed, they switched from producing all sons to producing 83 percent daughters.

The cooperatively breeding fairywrens of Australia enhance genetic diversity of offspring through promiscuity (Figure 14–15). Breeding groups of fairywrens are essentially extended families. They consist of a socially monogamous pair plus up to five male helpers that help to provision the group's siblings or half siblings. All the male relatives in a family are sexually active and help rear the young, but females deliberately mate with external males just before dawn when all males chorus continuously, much like the lek behaviors of other promiscuous bird species. Within-pair copulations follow, mixing sperm of different males. Almost all nests of the Superb Fairywren contain young sired by males on territories of other breeding groups (Double and Cockburn 2003). Just a few males achieve most of the extra-pair copulations, but their sperm must compete with the sperm of the social mate. Sperm competition has favored the evolution of unusually short sperm in fairywrens as well as elevated sperm production. Female fairywrens store and strategically use sperm from their dawn-pair liaisons, especially short sperm with a relatively large head (Rowe and Pruett-Jones 2011). Females of at least one species, the Splendid Fairywren, reduce inbreeding depression of their offspring by increasing heterozygosity through extra-pair paternity. They do this by favoring fertilization by other males if paired with a close relative (Tarvin et al. 2005).

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Figure 14–15 Male Superb Fairywren. Rampant promiscuity reduces potential inbreeding depression in this species which features a kin-based cooperative-breeding family structure.

REVIEW KEY CONCEPTS

14.1 Diversity

Uncertainties about genetic parentage govern each partner’s commitment to care of the young. Trade-offs between current and future efforts, conflicts between parents and their offspring, uncertainties about parentage, and opportunities to cheat or to cooperate guide the evolution of alternative breeding behaviors. Brood parasitism and cooperative breeding lie at opposite ends of the spectrum of parental-care strategies among birds.

Key Terms: polygynous, polyandrous, brood parasitism, helpers

14.2 Polygyny

Polygyny is a viable system when females can take care of young without the assistance of males. Species that tend to be polygynous include those with precocial young (which are relatively developed when they hatch, compared with other hatchlings, and are soon mobile) and those that feed on easily accessible resources, such as fruit.

14.3 Polyandry

Polyandry, found primarily in the Orders Gruiformes and Charadriiformes, is a system of sex-role reversal and female dominance. Territorial females, which are generally larger than their male counterparts, pair with multiple males that incubate the eggs and care for their young, sometimes cooperatively. The complexity of these systems increases with the uncertainties of paternity.

Key Term: cooperative polyandry

14.4 Brood Parasitism

Intraspecific brood parasitism—leaving eggs in nests of other females of the same species—is quite common among birds. Facultative parasitism of other species is a step toward the evolution of obligatory brood parasitism. Adaptations for brood parasitism include egg mimicry, nestling mimicry, host mimicry, egg size and hardness, and the destruction of host eggs and young. Countermeasures coevolved by hosts include egg recognition and nest abandonment.

Key Terms: intraspecific brood parasitism, obligate brood parasites

14.5 Cooperative Breeding

Cooperative breeding evolves under conditions of ecological constraint—for example, when lack of breeding territories delays dispersal and prevents young birds from breeding on their own. By helping to raise other broods, these birds enhance their own chances for breeding through the inheritance of a territory or through other forms of territory acquisition. Breeding pairs with helpers fledge more young than do those without helpers, primarily because they suffer less stress and hence survive longer and are more likely to renest.

Key Terms: cooperative breeding, kin selection, reciprocal altruism

14.6 Complex Family Structures

Personal relationships based on individual recognition and long-term memory are the social foundations of social complexity. Manipulation of the gender and parentage of offspring reduces inbreeding depression and mitigates the effects of habitat quality.

Key Terms: family structures, inbreeding depression

APPLY YOUR KNOWLEDGE

1. What factors favor polygamous mating systems over monogamy?
2. How does the distribution of nesting sites and food resources influence the type of mating system?
3. How does the type of food (seeds, nuts, nectar, fruit, insects, small vertebrates, etc.) influence the type of mating system?
4. For what reason(s) is polyandry rare in birds? Consider physiology, behavior, and mate selection factors.
5. How does polyandry influence migration to breeding grounds and behavior upon arrival to breeding grounds?
6. Obligate brood parasitism is rare among birds, yet there is great savings of energy by neither constructing nests nor raising young. Why is obligate brood parasitism rare among birds? And why does brood parasitism occur in so few animal groups?
7. How do some birds determine that the eggs in their nests are their eggs and not those of a brood parasite?
8. It is often stated that there is an “evolutionary arms race” between brood parasites and their hosts. What adaptations confer success of the parasites, and what host countermeasures are effective at reducing parasite success?

9. Cooperative breeding, in which “helpers” increase the fitness of other birds, appears to be counter to Darwin’s theory of evolution by natural selection. How has altruistic behavior of helpers been explained as having a selective advantage to the helpers themselves?

CHAPTER 15 *Nests and Incubation*


IRINA MOS/SHUTTERSTOCK.COM

Birds, like the American Robin, construct nests to provide a secure location and a stable environment for incubation of their clutch of eggs and, often, for raising of dependent young.

> The great diversity of nests built by birds of the order Passeriformes helps explain their success . . . and their occupation of most

> terrestrial habitats over the world. [COLLIAS 1997, P. 267]

No bird gives birth to live young. Instead, birds prepare nests to cradle their eggs and their developing young. Caring first for the eggs and then for the young requires a major commitment of time and energy, often by both sexes. The associated risks also are great. The vulnerable eggs, nestlings, and attending parents tempt a host of predators. Additionally, activity at the nest—comings and goings to and from rest breaks or feeding a mate on the nest—draws attention to the nest and increases the risk of predation. Diverse nest architectures, nest materials, and social arrangements evolve in response to these challenges.

Successful reproduction also requires attention to the narrow thermal tolerances of the embryos and, later, to those of nestlings. Unlike other reptiles, the embryos inside bird eggs need heat from their parents' bodies to grow to hatchlings. They must also be protected from excessive heat, lethal cold or deadly desiccation. The incubation behaviors of parents respond to the requirements of their offspring, but incubating birds also must balance the costs of caring for eggs in the nest against the benefits of fending for themselves away from the nest.

This chapter starts with a review of the nests and nesting behaviors of birds. Then follow the challenges of the incubation of eggs that contain developing embryos. The first of these two major topics surveys the adaptive architectures and construction materials of bird nests, followed by more detailed discussions of how nests thwart predators, how birds build their nests (including the role of experience), and the importance of nest microclimates. The second section—on incubation behavior—presents evidence that birds adjust their behavior sensitively to the risks of predation as well as to the basics of keeping eggs warm, cool, and viable. Variable incubation periods support different patterns of embryo development as well as the ways that mates share the costs and risks of this stage of parental care. The chapter concludes with the ways in which chicks hatch from the eggs, with a feature on the nests and hatchlings of the highly precocial megapodes of the Australasian region.

15.1 Nests

Successful nesting is the driving force of bird breeding behavior. The challenges, however, are many. The causes of nest failure include predation, starvation, desertion, hatching failure, and adverse weather. In general, nesting success increases in northern latitudes, in hole-nesting species, and in large species with hardy young.

Predation causes by far the greatest number of annual nest losses, in all habitats and on all continents. Predation on nests and their contents severely reduces breeding success: more chicks may leave the nest through the stomach of a predator than on their own. This megasource of natural selection affects not only nest architecture and nest placement but also the evolution of life-history traits, such as clutch size. Nest predation also forces species to compete locally for limited safe nest sites and thereby affects which species can coexist (Martin 1988a, 1988b).

Songbirds hide their smaller nests in diverse sites, including green plants overhanging water and the outer twigs of bushes and trees, or suspend them from vines. Domed nests that hide the contents from predators overhead came to characterize many of the smallest songbird species throughout the world. The woven nests of caciques and weavers dangle from crowded tall trees, often over water.

The diverse nesting behaviors of birds correspond to their diverse solutions to the local challenges of reproduction. Most birds build isolated, hidden nests. The nests of approximately 20 percent of all bird species remain unknown or poorly known to science. At the other extreme are conspicuous, open-breeding colonies, some with millions of pairs. In Africa, from 2 million to 3 million pairs of the finchlike Red-billed Quelea nest in less than 100 hectares of thornbush savanna. On the Peruvian coast, black-and-white Guanay Cormorants pack together at densities of as many as 12,000 nests per acre and attained colony sizes of 4 million to 5 million birds. The burrows of nocturnal auklets, petrels, and shearwaters riddle the hillsides of some oceanic islets.

Birds build nests to protect themselves, their eggs, and their young not only from predators but also from adverse weather. Structure and function are inseparable in nest architecture (Hansell 2000). Conspicuous nest features provide protection. Subtle features aid in the regulation of temperature and humidity.

Nest Materials and Architecture

Bird nests have genuine architecture. Bird nests are constructed from a variety of natural materials by specific methods into highly functional designs that mediate the needs of the birds, their broods, and the conditions in their environment.

Other animals, including other reptiles, build nests, but birds do so in an extraordinary variety of forms, materials, and sites. Bird nests range from precarious constructions on bare branches to enormous communal apartments and from simple scrapes on the ground to elaborate stick castles (Figure 15–1). In size, they range from the few sticks assembled by some doves to the gargantuan aeries of eagles. One Bald Eagle aerie weighed more than two tons when it finally fell in a storm after 30 years of annual use, repairs, and additions (Herrick 1932).


(A)


(B)


(C)


(D)


(E)

(A) © Brian E. Small/VIREO. (B) © F. Truslow/VIREO. (C) Danita Delimont/Getty Images. (D) Rick and Nora Bowers/Alamy. (E) Bonita R. Cheshier/Shutterstock.com. (F) G. Ronald Austing/Getty Images. (G) Daniel A. Leifheit/Getty Images. (H) © J. Fuhrman/VIREO. (I) © B. Miller/VIREO

Figure 15–1 The nests of birds vary from simple to elaborate and from large to small. (A) Sandy scrape nest of Wilson’s Plover. (B) Floating platform nest of Western Grebe. (C) Stick nests of Great Blue Herons. (D) Hole nest (in cactus) of Gila Woodpecker. (E) Mud nests of American Cliff Swallows. (F) Suspended cup nest of Warbling Vireo. (G) Cup nest of Broad-tailed Hummingbird. (H) Suspended nests of Crested Oropendolas. (I) Stick nest of Rufous-fronted Thornbird.

Many birds nest in colonies, but only a few actually build compound, communal nests divided into individual compartments. Instead of nesting in excavated cavities or burrows, as do most parrots, Monk Parakeets of Argentina occupy huge, communal, stick nests that can also house nesting pairs of Speckled Teal and Spot-winged Falconets (Martella and Bucher 1984). These nests are now a familiar sight in the eastern United States, where introduced Monk Parakeets are increasing in numbers (Figure 21–3B).

The nests of the Sociable Weaver of southwestern Africa are the largest and most spectacular of all communal avian nests. Each one resembles a huge haystack in a thorny tree. The weaver pairs that will occupy the structure share in building the common roof that covers 100 or more separate nest chambers. These chambers are cool by day and warm by night. The geographical distribution of this species is limited to the extremely arid sections of southwestern Africa, perhaps because rain would saturate the nest and create an insupportable weight.

Nests may be casually constructed from ready-for-use pebbles and sticks or laboriously woven from natural fibers. Animal products, plant matter, and inorganic materials, including mud pellets, rocks, tinfoil, and ribbons, are used in nest construction. Selected aromatic plant materials provide fumigants to repel parasites (Box 15–1). The choice of nest materials can be extremely specific. For example, among the Neotropical ovenbirds (Furnariidae), the tuftedcheeks (*Pseudocolaptes*) line their pendant vegetation nests with the scales of tree ferns. The Chotoy Spinetail lines its stick nest with fuzzy caterpillar chrysalises. And the Great Rufous Woodcreeper lines its nest cavity with bark flakes and land snail opercula (Zyskowski and Prum 1999; K. Zyskowski, pers. comm.).

Box 15–1

Fragrance Helps

Nests made of plant matter may contain twigs, grass, lichens, and leaves. Some birds add green vegetation that helps to combat disease and ectoparasite infestations (Baggott and Graeme-Cook 2002). In general, hole nesters incorporate fresh, green vegetation more regularly into their nests than do open nesters. Common Starlings select by odor certain plants, such as red dead nettle and yarrow, which contain volatile chemical compounds that inhibit the growth of bacteria and the hatching of the eggs of arthropod nest parasites (Clark 1991). The experimental removal of these green plant materials leads to a dramatic increase in the populations of blood-sucking mites, tiny parasites that can drain the blood volume of a starling chick.

Once the chick has hatched, Broad-winged Hawks bring fresh green branches of white cedar, ferns, and hardwood trees every day to line their platform nest (Heinrich 2013).

Blue Tits on the island of Corsica also add fragrant plants to their nests (Petit et al. 2002). They select by odor fragments of as many as five herb species that Corsicans themselves use to make aromatic house cleaners and herbal medicines. The birds also refresh the bouquet of odors, selectively replacing, by using olfactory cues, herbs that wane or are removed.

Birds go to extremes to get prime materials, which may be in short supply. Thievery is common, especially in large seabird, heron, and penguin colonies. It is often much easier to steal than to collect fresh materials. Competition for small stones can be intense at Adelie Penguin colonies. Female Adelie Penguins have been observed soliciting copulations from extra-pair males in exchange for the opportunity to take as many as 10 pebbles from that male's nest (Hunter and Davis 1998).

Most swifts (subfamily Apodinae) use their own, hardened saliva to glue their stick nests together. Palm swifts mix their saliva with fine plant fibers to create a feltlike material. Entirely self-sufficient are the cave nesting Edible-nest Swiftlets of Southeast Asia. They make their nests entirely of their own (hardened) saliva. This sticky form of glycoprotein cements the nest together and attaches it to a cave wall. Because this unusual glycoprotein maintains its gluey consistency even when cooked, swiftlet nests are a critical ingredient of bird's-nest soup. This gastronomic delicacy supports a substantial trade in harvested nests for sale to the Asian food industry (Box 15–2).

Box 15–2

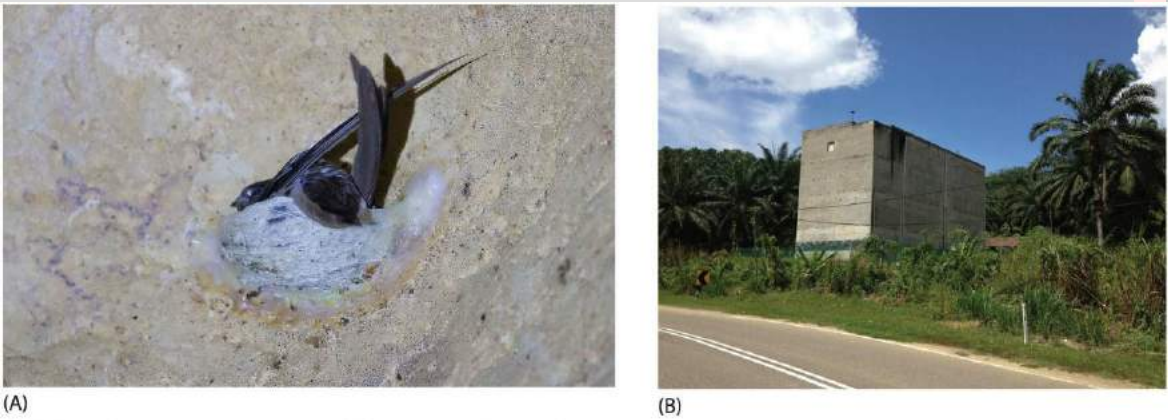
Edible-Nest Swiftlet Cultivation and Conservation

The nest of the Edible-nest Swiftlet is entirely composed of the bird's hardened saliva. The unique glycoproteins in the nests have been used for centuries in various east Asian countries to thicken bird's-nest soup, where it is viewed as a delicacy and a health tonic (Medway 1963). High-quality swiftlet nests are very valuable and can fetch prices of $2,000 to $3,000 per kilo—about $85 per ounce or $20 per nest (Thorburn 2015). Over the 20th century, unregulated harvest of the nests from swift colonies in caves contributed to endangerment and even extinction of many local populations.

Swiftlet farming was first developed in East Java in 1880s, where entrepreneurs constructed cavelike “swift houses” to attract the swifts from nearby caves. The practice of swiftlet farming boomed after a severe economic crisis in 1997–1998 left thousands of newly constructed houses, shops, and buildings empty (Thorburn 2015). Tens of thousands of swiftlet houses are now found across Indonesia, Malaysia, Thailand, Vietnam, Cambodia, and Myanmar, with most of the trade in harvested nests going to China.

Swiftlet farmers attract the birds to new colonies by playing loud recordings of swiftlet calls. Farmers have also discovered that the closely related Mossy-nest Swiftlets are great foster parents to the highly valued Edible-nest Swiftlet, and they accelerate the development of a new colony by transferring eggs among nests. Swiftlets are highly philopatric—they return to breed in the same places they were born—so established colonies can be self-sustaining.

Although the domestically produced nests have taken collecting pressure off of wild colonies, there is some genetic evidence that the domesticated swiftlets are a genetically distinct form descended from domesticated Javan populations (Cranbrook et al. 2013). The clade of cave swiftlets is known for explosive speciation. Domesticating swiftlets for nest production may have further evolutionary impacts on the diversification of this group.



(A) © Geoff Jones/barraimaging.com.au. (B) Courtesy of Richard O. Prum

(A) The pure white nest of the Edible-nest Swiftlet is composed entirely of saliva. (B) A swiftlet house in rural Teras, Pahang, Malaysia.

Many birds nest in burrows, holes, or tree cavities. Birds can either adopt a natural cavity or construct one. Hornbills have the most unusual cavity nesting behavior. A pair of hornbills adopts a natural cavity in a tree. The female seals herself into the cavity with a wall of mud with the help of the male. During incubation, the male feeds the female and later the chicks through a slit in the mud wall. In some species, the female molts her tail and wing feathers while inside the nest cavity.

Beyond basic construction materials, birds use spiderwebs for mooring or adhesion and feathers and hairs for the final lining. Feathers are often a major component of the nest and, especially, the nest lining. The nests of Long-tailed Bushtits and Goldcrests in Europe may contain 2,000 or more feathers. Waterfowl pluck down from their own breasts, and the Superb Lyrebird plucks down from its flanks to line the nest. Many birds pluck hair, also a premium nest-lining material, from livestock. Galápagos Mockingbirds snatch hair from the heads of surprised tourists.

In one remarkable example of unusual nest materials, Black-eared Sparrow-Larks of southern Africa add to the edges of their nests the scarlet-colored lids that cover the burrows of a particular species of trap-door spider (Hockey et al. 2005). The geographical distribution of this sparrow-lark coincides closely with that of the spider. Great Crested Flycatchers and their relatives sometimes add snakeskins to their nests, prompting speculation that they help protect the nest from predators. Black Kites in Spain decorate their platform nests with white materials, often plastic bags and other trash (Sergio et al. 2011).

Passerine songbirds construct the most diverse and the most elaborate nests of all. Their nests fall into three basic categories: (1) cavity or hole nests (in a burrow in the ground or in a tree), (2) open-cup nests (outside of holes), and (3) domed nests (with a constructed roof; Collias 1997). Eggs in a covered nest are less visible to potential predators when parents are absent than are eggs in an open nest. Snakes cannot easily reach pensile nests or easily crawl inside protruding entrance tubes. But cup nests can be smaller and less obtrusive than pensile nests.

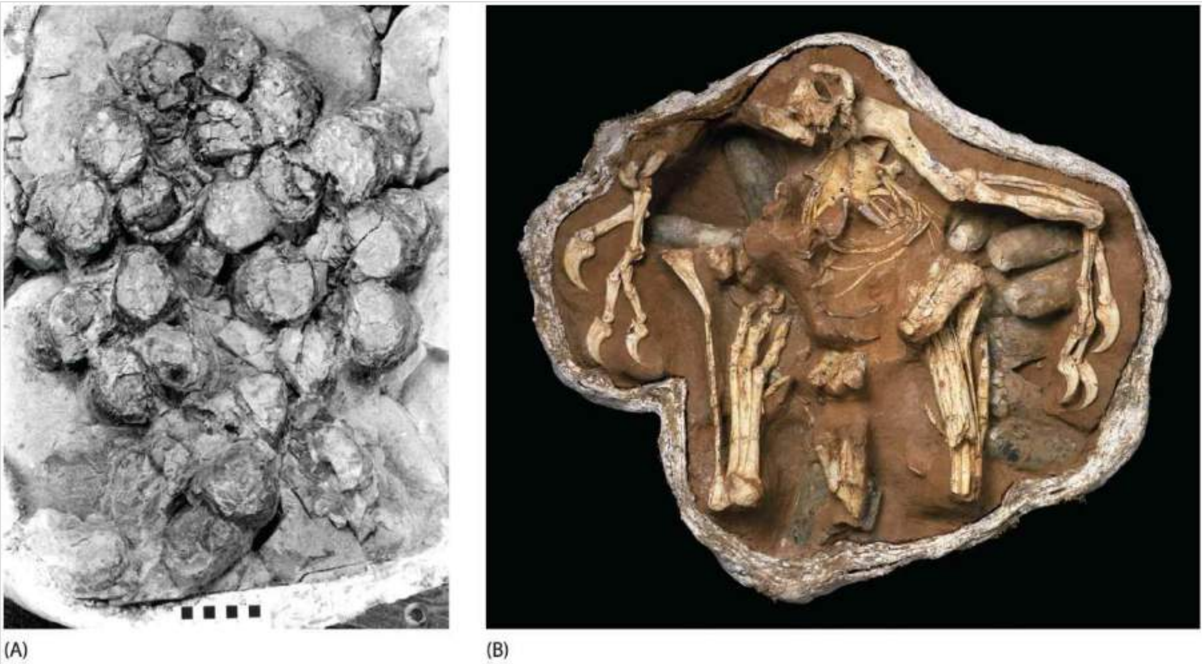
Pensile nests are among the most elaborate of specialized nests. Some hang delicately by silky cobwebs or by wiry, black fungal fibers. Some are suspended far below a main branch. Others, such as those of the Baltimore Oriole, hang from the thin, outermost branches of large trees. The integrity of pensile nests derives from their tightly woven construction, tough knots, and strong binding materials. The intricately woven, meter-long nest of Cassin’s Malimbe, a West African weaver, may well be the pinnacle of avian nest construction (Collias and

Collias 1984).

Nest Evolution

The nest is an artifact, or production, of a pair of birds or an individual bird. Like a beaver dam or a buffalo wallow, the nest is a component of the **extended phenotype** of the bird: the total of the individual's effect on its environment. Nests are a complex product of the bird's genes, morphology, behavior, and previous social experience interacting with its environment, including potential nest sites, the variety of available nest materials, and the individual's social environment, such as social density, competition, and its social relations with its mate. Natural selection acting on genes for morphology and behavior mediated by all these other factors results in the evolution of the nest among species and lineages of birds.

Many reptiles create a nest in which to lay their eggs, often a simple burrow. Alligators and crocodiles lay their eggs in mounds of vegetation, where they are incubated by environmental heat. The theropods *Oviraptor* and *Troodon* laid eggs in well-organized clutches on the ground, with the eggs partially buried in sediment (Figure 15–2). The discovery of *Oviraptor* fossils at nests in Mongolia was originally interpreted as evidence that they were plundering the eggs of other species—*Oviraptor* means "egg thief" (Osborn 1924). But dramatic discoveries have subsequently shown that these individuals were brooding, and perhaps even incubating, clutches of eggs (Norell et al. 1995; Figure 15–2). Although the ancestor of living birds clearly nested on the ground, the evolution of modern avian reproduction, including incubation of a sediment-free clutch of eggs, likely occurred within the Mesozoic birds (Varricchio and Jackson 2016). Nest placement, architecture, and materials have diversified significantly among Neoavian birds (see Figure 15–1).

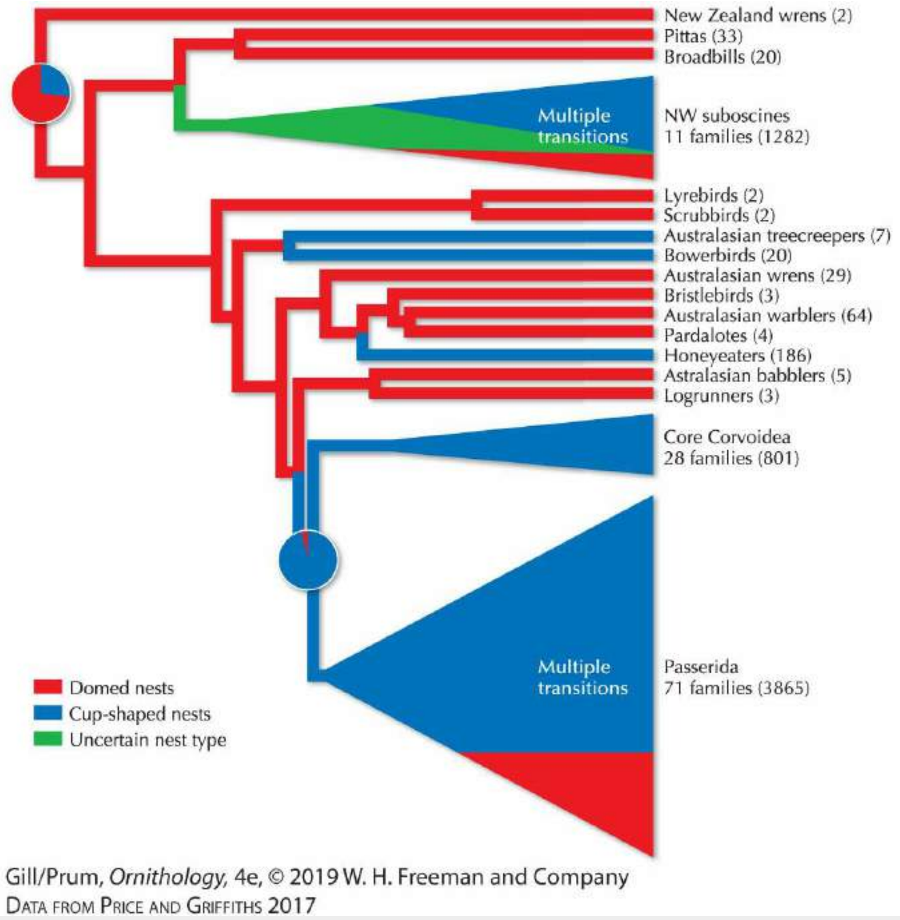


(A) Courtesy of Dr. David Varricchio, Department of Earth Sciences, University of Montana. (B) Mick Ellison

Figure 15–2 Ground nests of nonavian theropod dinosaurs. (A) A clutch of *Troodon* eggs were laid in pairs by one or more different females and cared for by the male. (B) A male *Oviraptor* fossilized while brooding (or perhaps incubating) its clutch of eggs.

Nicholas Collias (1997) suggested that the building of elaborate nests was a key feature of the adaptive radiation and evolutionary success of the songbirds (Order Passeriformes). The generally small body sizes of songbirds, combined with their strong powers of flight and flexible nesting behaviors, allowed them to compete with the hole nesters, which prevailed first in terrestrial habitats. This hypothesis is corroborated by time-calibrated molecular phylogenies of the radiation of land birds, which place the radiation of the cavity-nesting coraciimorph birds about 8 million years before the origin of the passerine birds (Prum et al. 2015).

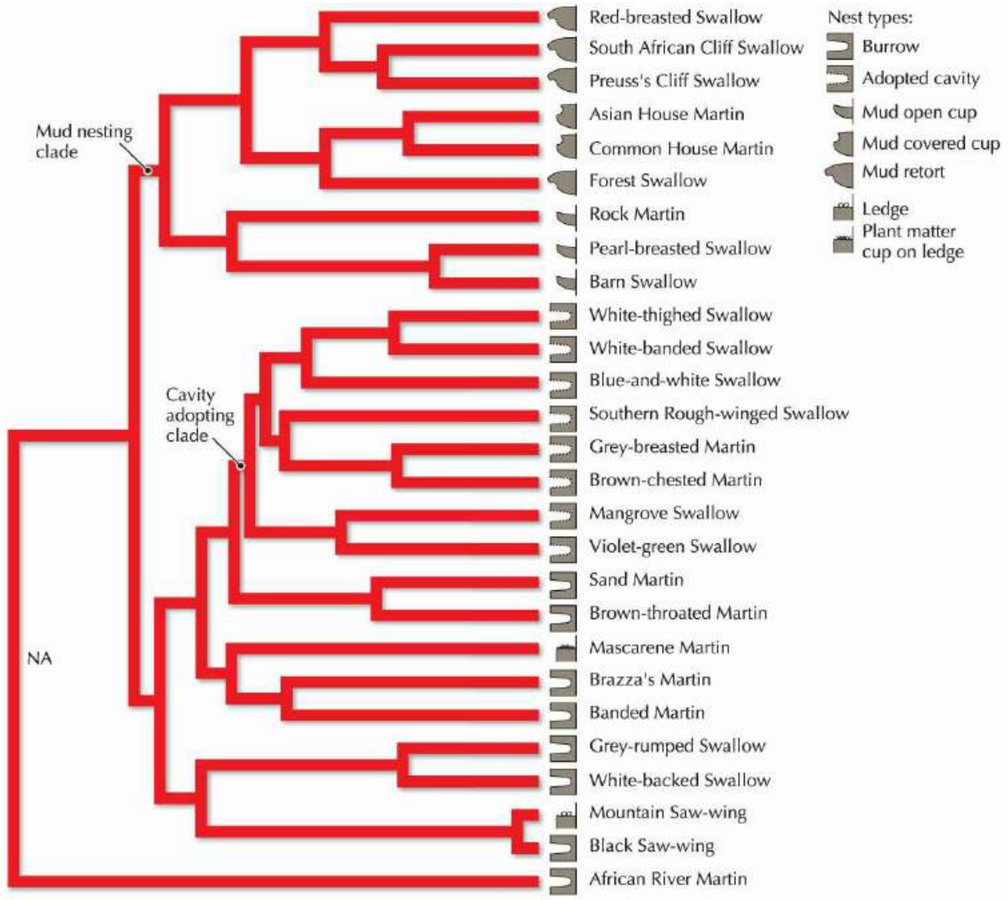
Phylogenetic analyses indicate that the enclosed vegetation nest was the ancestral nest type of all passerine birds (Price and Griffith 2017; Figure 15–3). The open cup nest evolved at least three independent times among oscine songbirds and multiple additional times among New World suboscine perching birds.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
Data from Price and Griffiths 2017

Figure 15–3 Phylogenetic analysis of the evolution of nest type in passerine birds demonstrates that the most recent common ancestor of passerine birds likely had an enclosed, domed vegetation nest. The open cup nest evolved multiple times independently within suboscine and oscine birds.

Nest architecture is extremely diverse among species of swallows, and the phylogeny of swallows provides insights into their nest evolution (Winkler and Sheldon 1993; Sheldon et al. 2005). Some swallows burrow into hillsides, others adopt tree cavities, and still others build mud nests on cliffs or human constructions. The use of pure mud to construct hanging nests is unique among all birds. The phylogeny of swallows reveals that burrow nesting is primitive to the family (Figure 15–4). Adoption of tree cavities evolved once within the clade of core martins and tree swallows. Mud nesting evolved only once and originated with an open cup attached to a vertical wall. Subsequently, the covered mud cup and the “retort” nest with a tunnel entrance evolved once each in sequence. The construction of these mud nests actually parallels their evolutionary history (see below).



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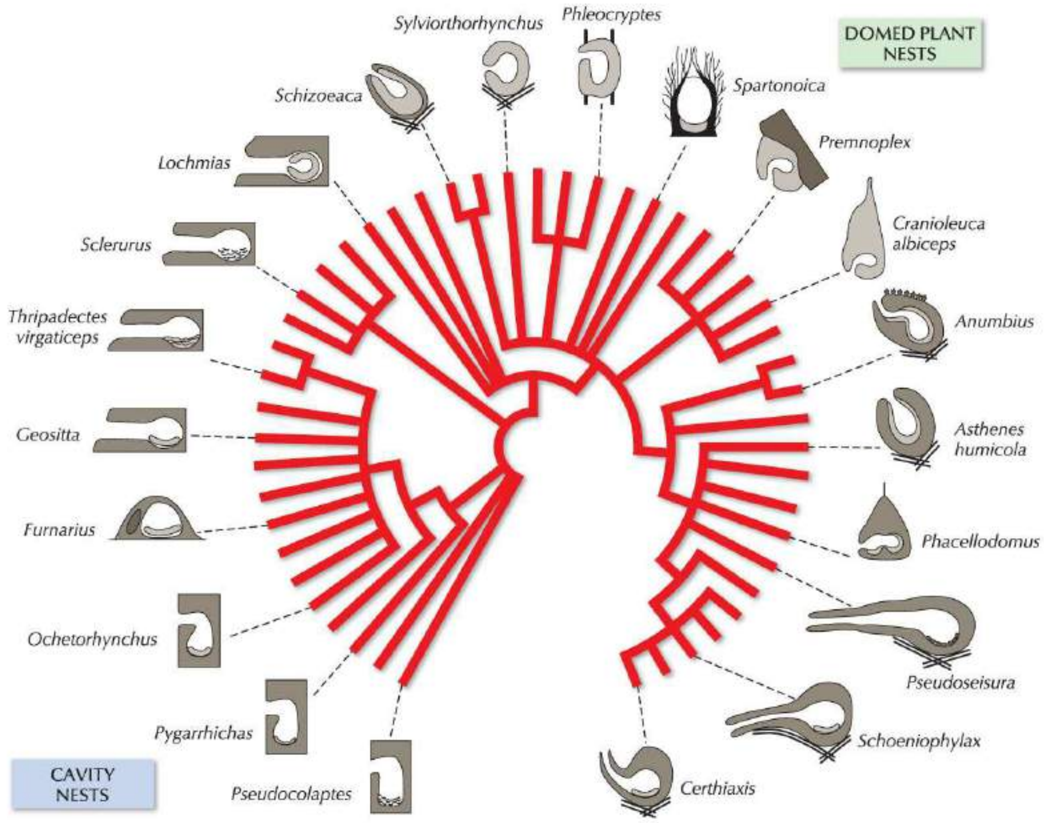
DATA FROM WINKLER AND SHELDON 1993, SHELDON ET AL. 2005

Figure 15–4 The phylogeny of swallows (Hirundinidae) reveals that tree cavity adoption and mud nesting evolved independently from burrow nesting. The roofed and retort nests evolved after the origin of a mud cup in the Barn Swallows.

Even more dramatic is the architectural variety of the nests of the ovenbirds and woodcreepers (Family Furnariidae) of South and Central America. This group of birds is one of the most diverse families of suboscine songbirds in morphology, behavior, and nests (Zyskowski and Prum 1999; Derryberry et al. 2011). Some species resemble larks; others resemble jays, tits, creepers, nuthatches, wrens, thrushes, thrashers, dippers, warblers, or woodpeckers. Their nests are similarly diverse in their structure and in siting (Figure 15–5).



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DATA FROM ZYSKOWSKI AND PRUM 1999

Figure 15–5 Adaptive radiation of nest architectures of the genera of ovenbirds (Furnariidae) of South America. Diverse domed nests made of plant matter followed the original mode of cavity nesting. Black exterior materials indicate cavities in trees or the ground. The Sharp-tailed Streamcreeper (*Lochmias*) and its relatives build domed plant nests inside cavities. The clay ovenlike nests of horneros (*Furnarius*) are unique replacements of a cavity nest.

The ancestral ovenbirds nested in cavities. Derived from and replacing cavity nests are diverse domed nests made of vegetation, ranging from modest grass nests to huge stick piles. The horneros (*Furnarius*) sculpt novel, domed, ovenlike structures made of mud. Despite their tremendous diversity, all ovenbird nests feature an enclosed, dark brood chamber.

Nest Construction

Birds inherit behavioral preferences to seek out particular sites and materials in their environments and manipulate them in specific ways to create their nests. The methods of nest construction are as diverse as the nests themselves, including scraping, digging, drilling, piling, jamming, interlacing, felting, sewing, weaving, tying, and accumulating mouthfuls of mud.

Either member of a pair of birds may build their nest, or they may do so jointly during courtship and pair formation. Most monogamous male North American passerines contribute to the nest-building effort. A male's presence at the nest site in the earliest stages of nesting, however, may be primarily to protect his mate from insemination by other males (to guard his paternity).

Nest-site selection can be an integral part of pair formation, often accompanied by special displays. Male wrens and weavers construct nests, and the females select their mates based, in part, on the evaluation of the nests they construct. If prospective mates reject a nest, male Village Weavers tear it down and build a new one. A male Marsh Wren may build more than 20 nests for comparison by a prospective mate (Kroodsma and Verner 1997). The unused nests also serve as dummy nests that help to distract nest predators. In wrens and weavers, both the male and his nest are under sexual selection, which may contribute further to the elaboration of nest architecture.

Nest building itself varies from the simple accumulation of materials to elaborate construction. The nonincubating parent may simply toss materials in the direction of the nest site, creating a mound of debris or a conspicuous rim near the eggs and leaving the incubating parent to delineate the nest site by drawing the materials toward itself. The deliberate transport of suitable materials to the nest site was a major step in the evolution of nest-building behavior among birds (Collias and Collias 1984). It led to the modification and design of the nest site and to more complex nest architecture, which can be a strenuous undertaking.

Birds usually carry nest materials in their bills or feet. Some lovebirds, which are small African parrots, transport their nest materials in an unusual way that is genetically determined (Dilger 1962). The Yellow-collared Lovebird carries one strip of nesting material at a time in its bill, but the related Rosy-faced Lovebird tucks the ends of several strips beneath its rump feathers and flies to the nest with the strips in tow. Hybrids between these two species try to tuck strips into their rump feathers but cannot do so correctly. Sometimes, the hybrids fail to complete the tuck. More often, they hold the strip by the middle instead of the end, fail to let go of the strip after tucking it, or tuck it into the wrong place, so many strips do not reach the nest box. The hybrid’s genetic program for carrying nesting material apparently contains conflicting instructions.

Bills and feet are versatile nest-building tools. Bills serve as wood chisels and drills, as picks for digging into the ground, as shuttles for weaving, as needles for sewing, as trowels for plastering, and as forceps for plucking and inserting (Skutch 1976). Birds also build nests by stamping, scraping, kneading, and scratching as their reptilian ancestors did. Burrow nesters dig by kicking loose soil backward. They then mold the internal nest dimensions by using their bills, breasts, and feet.

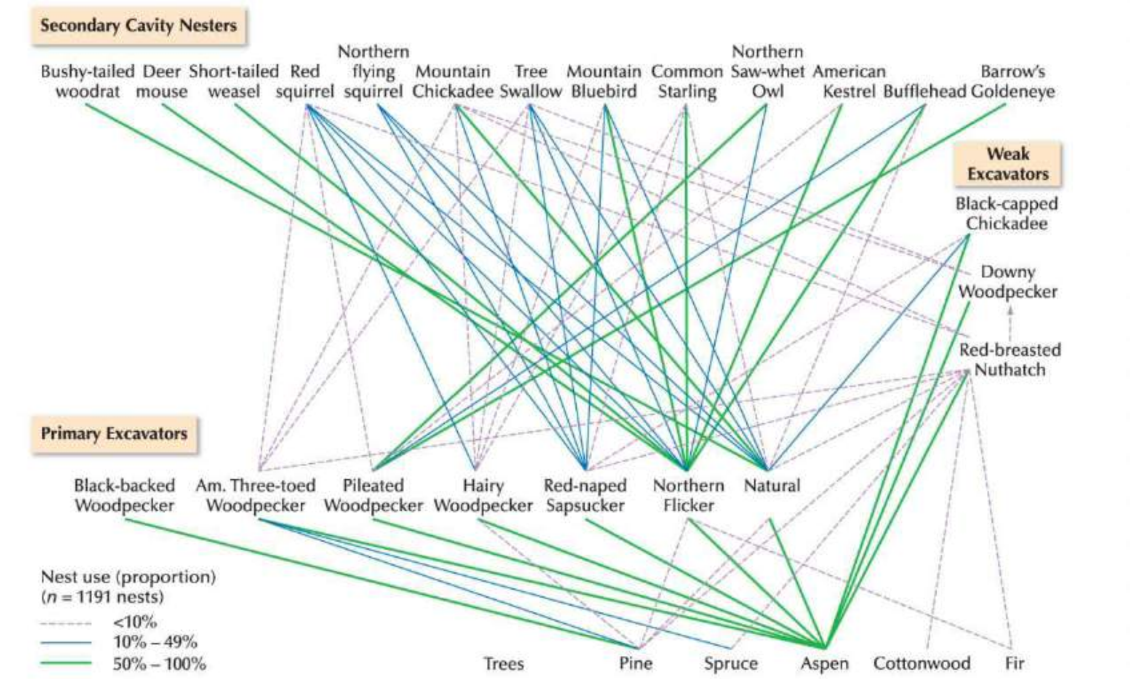
Some woodpeckers drill nest holes in hard, living trees. Most species select wood softened by fungal infections, which they spread to other trees by carrying fungal spores on their bills (Jackson and Jackson 2004). Other tree cavity nesting birds that are unable to make their own holes—thus called **secondary cavity nesters**—compete intensely for abandoned woodpecker holes (Box 15–3).

Box 15–3

Competition for Nest Cavities

The excavation of valuable nest holes by woodpeckers and their use by other species creates a complex web of community interactions. In central British Columbia, the Northern Flicker emerges as the keystone species (Martin et al. 2004). The nest holes that it creates, especially in aspens, provide housing for more than 13 mammal and bird species, ranging from rodents and weasels to owls and ducks.

Diverse species compete for the prime nest cavities produced by the flickers and other woodpecker species. This web diagram illustrates secondary cavity nesters’ use of nest cavities (and trees) excavated by six primary excavators, all woodpeckers, and three species of weak excavators in interior British Columbia. For example, as the different types of lines show, Bufflehead ducks primarily used flicker cavities, secondarily used Pileated Woodpecker cavities, and occasionally used natural cavities.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company

Courtesy of American Ornithological Society, from Kathy Martin, Kathryn E.H. Aitken, Karen L. Wiehe, (2004). "Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: Nest characteristics and niche partitioning." *Condor*, 106 (1): 5–19 , Figure 5.

Web diagram depicting the tree species used, the primary and weak cavity excavators, and the secondary cavity nesters that use the cavities the excavators create.

The cup nests of small arboreal land birds are usually built from the bottom up. Others, such as the open-cup nests (suspended by the rim) of vireos, are built by wrapping nest materials around the supporting twigs first and then by looping strands of material from side to side to form the framework of the cup. The long, hanging nests of tropical flycatchers begin as an accumulation of materials compressed into a tangled mass like felt. The flycatcher forces its way into the center and gradually expands the nest cavity from the inside out, and then it reinforces and lines the hollowed-out cavity (Skutch 1976). South American thornbirds construct complex, hanging stick nests in a unique way (Figure 15–6). They pile up sticks at the end of a thin branch to create a base. But the mass of the sticks eventually bends the branch downward and becomes the top of the hanging nest.

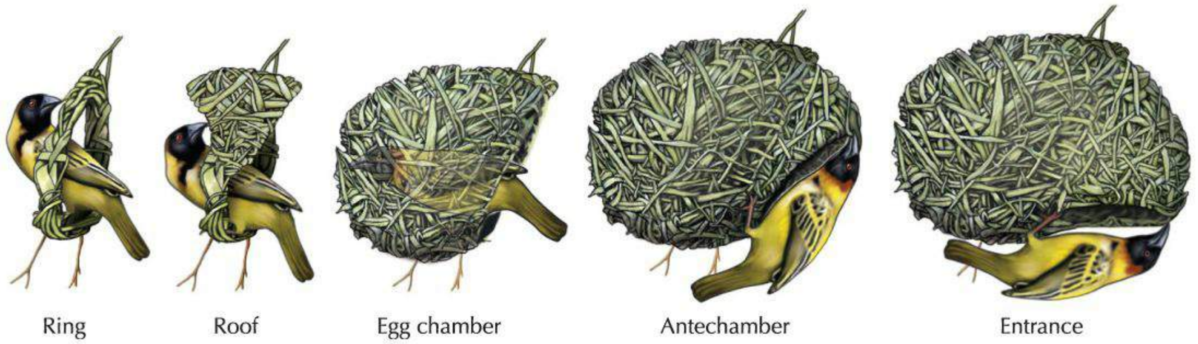

(A)

(B)

COURTESY OF KRISTOF ZYSKOWSKI

Figure 15–6 Thornbirds (*Phacellodomus*, Furnariidae) start nest construction with (A) a base of sticks on a thin branch. As the pile becomes heavier, the branch bends downward, and the “base” becomes the top of (B) the enclosed, pendant stick nest.

Weavers and New World orioles weave elaborate hanging nests. The male Village Weaver, for example, begins with a vertical ring to which it adds in succession a roof, the walls of the main nest chamber, an antechamber, and finally the finished entrance (Figure 15–7). The structural features of these nests are woven into their final positions with the use of special knots. The types of knots used are species specific. Some weavers tie simple knots, whereas others tie half hitches and slipknots (Figure 15–8).



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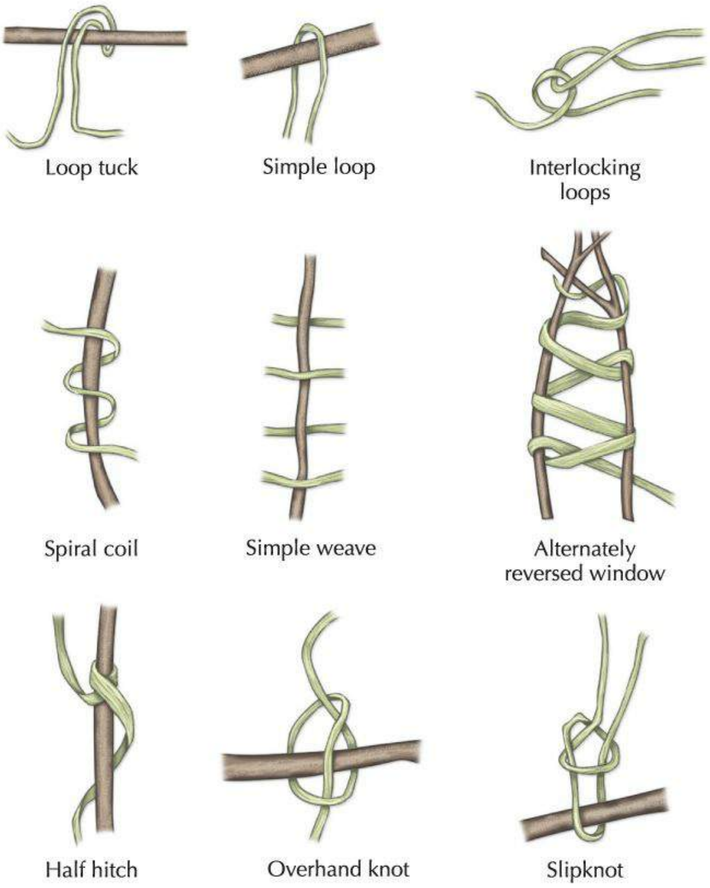
Data from Collias and Collias 1964

Figure 15–7 Stages of nest construction by the male Village Weaver.



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Data from Collias and Collias 1964

Figure 15–8 Some knots and stitches used by weavers in constructing their nests.

Most passerine birds build nests with architectural features so distinctive that we can identify the genus or species of the builder. How, then, does a young bird know how to build a complex nest similar to the one built by its parents? A male Village Weaver, hand-raised in isolation without ever seeing a nest, can build a nest that is typical of its species. This ability demonstrates a strong genetic control of this behavior.

Early experiences also play a role. Improvement in nest construction is particularly evident in the Village Weaver and other species that build elaborate nests (Collias and Collias 1964). Although immature males build crude structures at first, they become more skilled in the arts of tying knots and weaving. Older males build refined products.

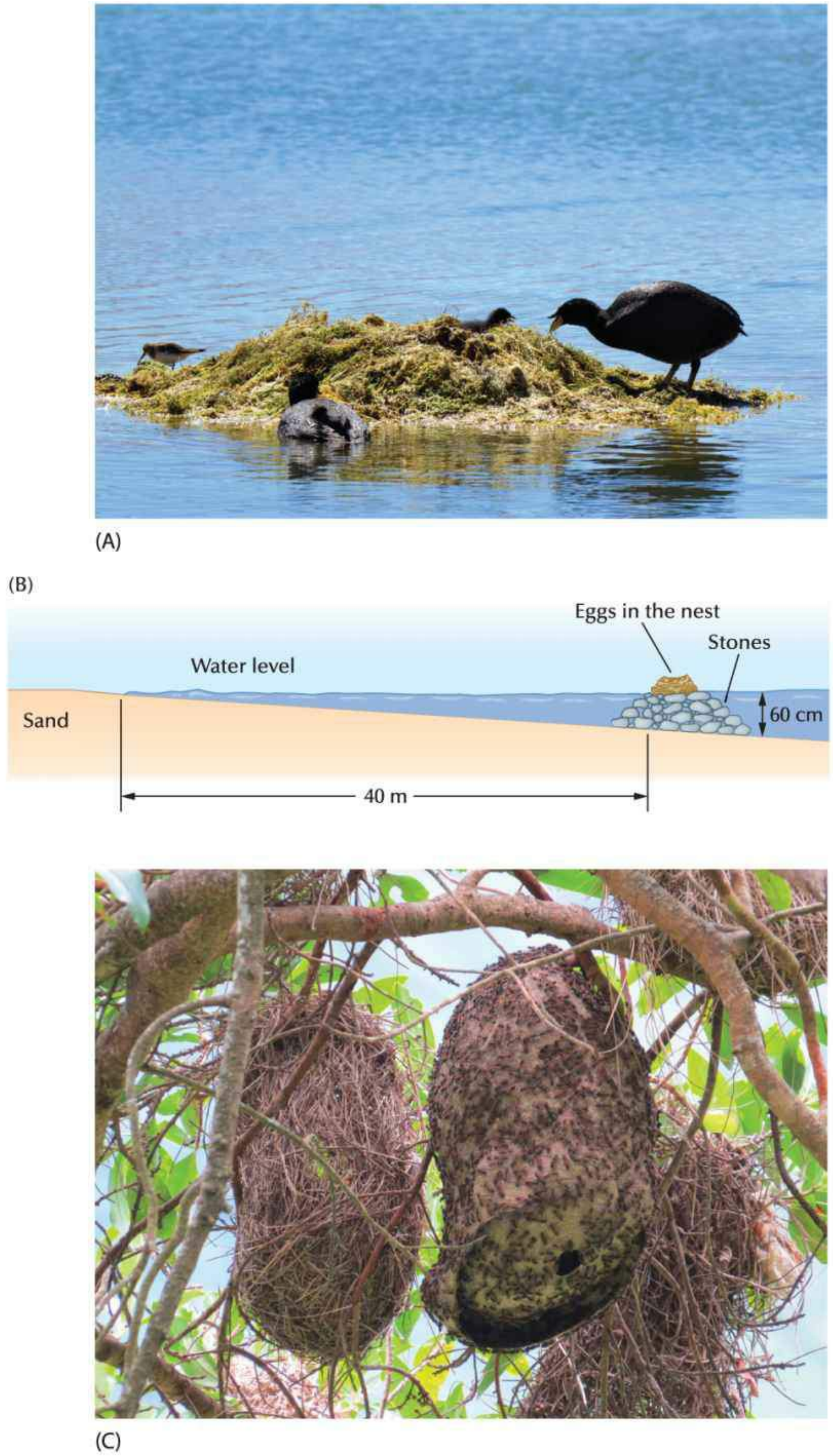
When nesting for the first time, the Western Jackdaw, a small European crow, rapidly improves its skills. It starts by making clumsy movements with inappropriate nest materials and progresses to efficient construction with a range of suitable nest materials. At first, the inexperienced young jackdaw tries to shove almost anything into the nest platform. Sticks of the right size and texture insert easily and firmly into the matrix, but objects such as lightbulbs do not. By the time the nest is complete, the range of materials gathered narrows to the types of twigs that are most suitable for nest construction (Lorenz 1969).

Raptors imprint on their natal nest sites. Consequently, they choose a similar situation several years later when they reach maturity (Temple 1977). Understanding this process is critical to the conservation of endangered species. The Mauritius Kestrel, for example, nested in tree cavities that were vulnerable to predation by introduced monkeys. As a result, the kestrel population declined to only a few endangered pairs in the 1960s. One of the last pairs of kestrels switched to a cliff ledge, out of reach of the monkeys, and raised young successfully. This change started a new tradition that helped the population recover, providing hope for the survival of the species.

Nest Safety

Invisibility, inaccessibility, and impregnability all contribute to nest safety. The camouflaged color patterns of incubating nightjars and of shorebird eggs render them nearly invisible. The lichen decorations on the sides of a hummingbird’s nest do the same.

Some nest sites are clearly safer than others. Cryptic sites in dense clumps of grass, vine tangles, or hidden crevices minimize the chance of discovery. Seabirds that nest on sheer cliffs and swifts that nest in deep caves or behind waterfalls achieve safety through inaccessibility. Horned Coots pile up stones in the middle of high Andean lakes to build their own nesting islands out of reach of terrestrial predators (Figure 15–9). Likewise, many grebes build nests of floating vegetation. Nests on the ground are more vulnerable to mammalian predators than are nests in trees or bushes. Tooth-billed Pigeons once nested on the ground on Samoa, but they shifted to nesting in trees after whalers introduced cats to this South Pacific island (Austin and Singer 1985).



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
(A) CHRIS HOWARTH/CHILE/ALAMY STOCKPHOTO. (B) DATA FROM RIPLEY 1957.
(C) SERGIO CHAPARRO HERRERA

Figure 15–9 Some birds go to extremes to build nests that are less vulnerable to predation. Horned Coots build their nests on stones, which they assemble in piles in high-altitude Andean lakes. (A) Horned Coot on its nest. (B) Diagram of its nest structure. (C) A colony of Yellow-rumped Caciques is located in a tree on an island with a large colony of wasps, providing the nests with multiple predator protection mechanisms.

The Yellow-rumped Cacique is one of the many species that builds a hanging nest. It nests in colonies in Amazonian Peru. These tropical blackbirds defend their closed, pouchlike nests against predators in three ways (Robinson 1985; Figure 15–9C). First, by nesting on river islands and near wasp nests, caciques are safe from arboreal mammals, such as primates, which destroy more accessible colonies of other birds. Caimans and otters also protect the island colonies by eating snakes that try to cross the open water surrounding a colony. Second, caciques mob avian predators, like caracaras and large toucans, in groups. The effectiveness of mobbing increases with group size, which increases with colony size. Third, caciques hide their nests from predators by mixing active nests with abandoned nests. Overall, nests in clusters on islands and near wasp nests suffer the least predation. Females switch colonies after losing a nest to a predator, usually moving to sites that offer better protection against that predator. In such ways, the best colony sites accumulate the largest numbers of nests.

Even within a species, some nest sites are more vulnerable than others. Thomas Martin and colleagues (2000) compared predation rates in successive years at specific sites used by several species of ground-nesting Arizona birds. Nest sites that failed during incubation in the first year suffered the highest rates of predation in the next year. Nest sites that were successful in the first year suffered the lowest rates of predation in the following year.

Cavity nesting is safer than open nesting. Half of the avian orders, among them all parrots, trogons, and kingfishers and their relatives, nest in cavities or holes. Owls, parrots, and Australian frogmouths nest in natural cavities, and trogons, titmice, and piculets excavate cavities in the soft or rotten wood of old trees. Woodpeckers are the preeminent excavators of cavities, which become a limited resource for the entire community of tree cavity–nesting birds. The unusual nesting behavior of the hornbill, in which the female is walled into the cavity for the entire nesting period, is thought to be an adaptation to reduce nest predation. South American thornbirds (*Phacellodomus*) build hanging stick nests with side entrance tunnels. Like the false chamber in a pharaoh’s tomb, however, a constriction in the entrance tunnel creates a false outer egg chamber; a small passage then leads back into the real egg chamber (Zyskowski and Prum 1999). Both chambers are lined. The false, outer chamber apparently functions to dupe predators like snakes into concluding that the nest is empty. The Plain Softtail builds an enclosed stick nest with two tunnel entrances to the egg chamber, which may provide the parents or nestlings with an alternative route to escape nest predators.

Some birds nest in an area protected by large animals or stinging insects. In the Chiricahua Mountains in Arizona, Black-chinned Hummingbirds nest in higher concentrations and have higher breeding success at nest sites within 170 meters of a Cooper’s Hawk or Goshawk nest (Greeney et al. 2015). Near hawk nests, flocks of Mexican Jays, the hummingbird’s main nest predator, forage higher above the ground, where they are safer from attack, but detect hummingbird nests at lower frequencies (Figure 15–10). Only 20 percent of Black-chinned Hummingbird nests are built outside of the zone of hawk protection. In Africa, the ploverlike Eurasian Stone-curlew nests on sandy shores beside nesting crocodiles. Bananaquits in the West Indies reduce rates of nest predation by nesting in association with wasps (Wunderle and Pollock 1985).

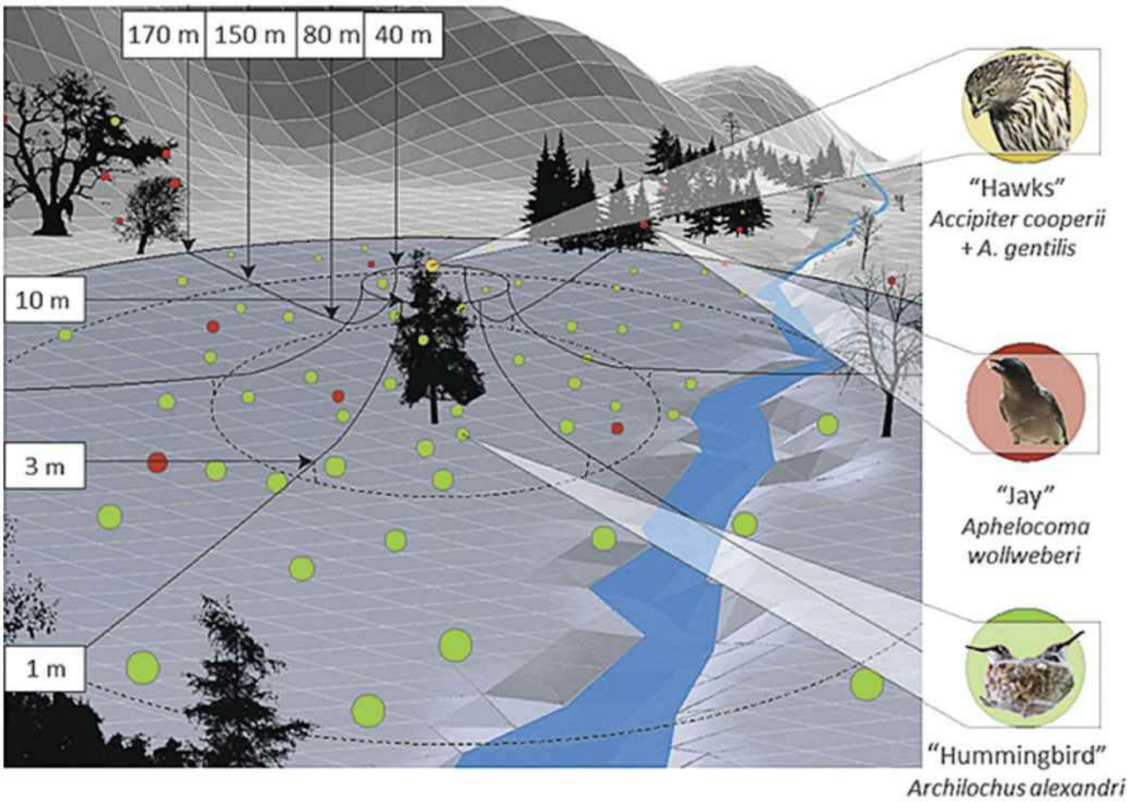


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Figure 2 from Harold F. Greeney, M. Rocio Meneses, et al., “Traitmediated trophic cascade creates enemy-free space for nesting hummingbirds,” *Science Advances*, 2015, September 4; 1 (8): e1500310, (DOI: 10.1126/sciadv.1500310) © The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. This work is distributed under CC BY-NC (http://creativecommons.org/licenses/by-nc/4.0/)

Figure 15–10 Black-chinned Hummingbirds nesting near an *Accipiter* hawk nest (yellow dot) have higher fledging success (green dots) than do nests farther away (red dots). The hawks force the Mexican Jays to forage higher in the forest (contour lines), where they are less likely to detect the hummingbird nests.

Many birds directly attack trespassers. Eastern Kingbirds chase anything that violates nearby airspace, hence the name kingbird. Northern Mockingbirds, Blue Jays, and Arctic Terns can draw blood and bits of fur from cats that come too close to their nests or young. They may attack people as well. Large owls and eagles with powerful feet and sharp talons can seriously wound climbers. In Australia, the common Australian Magpies (family Cracticidae) become extremely aggressive toward people during the breeding season (Jones 2002; Figure 15–11). Each year, the magpies cause significant eye injuries, making them one of the biggest urban wildlife issues in Australia.

THE AGE/GETTY IMAGES

Figure 15–11 Australian Magpies (*Cracticidae*) defend their nests aggressively, leading to frequent attacks of people in urban areas and multiple eye injuries.

Hoopoes defend their nest in a tree cavity with a combination of foul methods (Krištín 2001). The uropygial gland of the nesting female and the nestlings produce an evil-smelling stench like rotten meat. After six days following hatching, the nestlings can also accurately squirt a jet of feces and foul liquid 25 to 50 centimeters at an approaching predator.

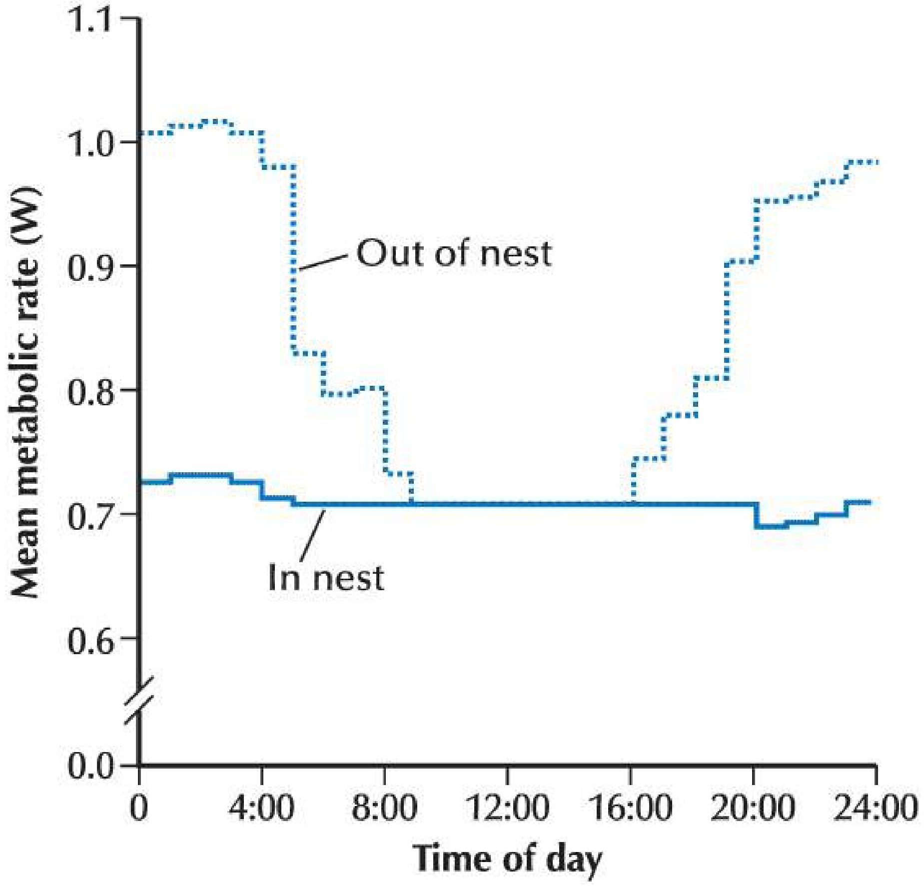
A parent flushed from the nest may attempt to draw a predator’s attention away from the nest site with distraction displays. The two most common nest-distraction displays in plovers are the injury flight and the rodent run (Figure 15–12). By using the injury-flight display—feigning a broken wing and calling in great alarm—an adult plover can easily draw a fox away from its nest. To keep the fox’s attention, the plover may then switch to the rodent-run display—running in a low crouch—an action that appeals to the mouse-catching instincts of the fox. Distraction displays are risky, but more often than not, the parent escapes, and the predator loses track of the original nest location.

NeonLight/Shutterstock.com

Figure 15–12 Distraction display of a Killdeer feigning injury.

Nest Microclimates

The microclimate of a nest is crucial to the successful incubation of the eggs and to the later health of baby birds. Nest microclimate also influences the daily energy requirements of the adults and, in turn, the amount of time that they spend on the nest incubating eggs and brooding young. The warmth of the nest is usually determined by the thickness of insulation and the heat produced by the incubating parent. The outstanding insulating properties of breast down used by eiders and other waterfowl, for example, greatly reduce the cooling rate of eggs that are not covered by the parent. Nest insulation also reduces the time that an incubating parent must be on the nest by reducing its own costs of thermoregulation and, in turn, the amount of time spent feeding itself (Figure 15–13).



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DATA FROM WALSBERG AND KING 1978

Figure 15–13 The effect of insulated nest microclimates on the energy expenditures (in watts) of a Red-winged Blackbird. The mean metabolic rates of birds perched outside the nest at night are higher than those while incubating inside the insulated nest.

The great thermal inertia of the enormous communal nests of the Sociable Weaver in southern Africa keeps them cool in the daytime and warm at night. Temperatures inside the nest at night remain from 18°C to 23°C above external temperatures. The warm nighttime temperatures are due partly to heat absorbed during the day and partly to heat generated by the bodies of large numbers of roosting birds.

Placing a nest in or out of the sun, shade, or wind has a major effect on its microclimate and, therefore, on a pair's breeding success. Early in the season in Arizona, Cactus Wrens build nests where they are protected from cool winds and are bathed in the warm morning sun. Later in the season, when it is hot, they build well-shaded nests that are exposed to cooling breezes (Proudfoot et al. 2000).

Placing nests in cavities and burrows also conserves energy. Cavity nests and burrow nests buffer eggs, parents, and young against fluctuations in external temperatures. For example, the temperatures inside the burrows of European Bee-eaters remain close to 25°C despite an outside temperature range of almost 40°C (Ar and Piontkewitz 1994).

Deep, cool burrow and cavity nests, however, have their drawbacks. Poor ventilation can limit the amount of time that parents can spend inside with growing young (Ar et al. 2004). On windless days, ammonia and carbon dioxide tend to build up as a result of decaying excreta amid unsanitary nest conditions, and oxygen levels occasionally decline until the occupants have difficulty breathing. Offsetting this problem, the diffusion of gases through the soil and the nest tunnel helps ventilate the air in the nest chamber. The movements of adults in and out of the nest pump air in and out, as a moving piston would (Ar and Piontkewitz 1994).

Nest microclimates, particularly the relative humidity of the air, also affect the rate of water loss from the eggs and hence their hatchability. Water loss from an egg and its embryo is inevitable because of differences between the water-saturated interior of the egg and its unsaturated external environment. During incubation, eggs lose from 10 to 23 percent of their weight, primarily as a result of the loss of water vapor, especially in deserts and at high altitudes. Excessive water loss may fatally dehydrate the embryo. On the positive side, the space vacated inside the egg becomes the air cell at the blunt end of the egg, which is the source of air for a chick as it starts to break out of the egg. An adequate volume of air must be available for the chick's first critical breaths.

Nest Sanitation

Fouling of a nest is common. The nests of many pigeons, raptors, and carduelline finches, such as the House Finch, are well known for their unseemly conditions. Many other birds are fastidious, regularly removing feces and other debris to prevent the nest from becoming a breeding ground for disease and insects and other parasites. Some young birds instinctively eject liquid feces away from the nest, and others eliminate feces accurately through nest hole openings. Adult female hornbills defecate through the narrow slit remaining in the mud-sealed opening. The larvae of a particular moth species help to clean the nests of the Golden-shouldered Parrot of Australia.

The young of most passerine birds and woodpeckers excrete fecal sacs, which facilitate nest sanitation. Fecal sacs are packages of excrement surrounded by a gelatinous membrane. The parent can easily pick up the sac and drop it away from the nest (Figure 15–14). Incomplete digestion by nestlings leaves some residual food in their fecal sacs, which are often eaten by parents for nutrition as well as sanitation purposes. In one study, fecal sacs provided 10 percent of the daily energy requirements of adult White-crowned Sparrows (Morton 1979).

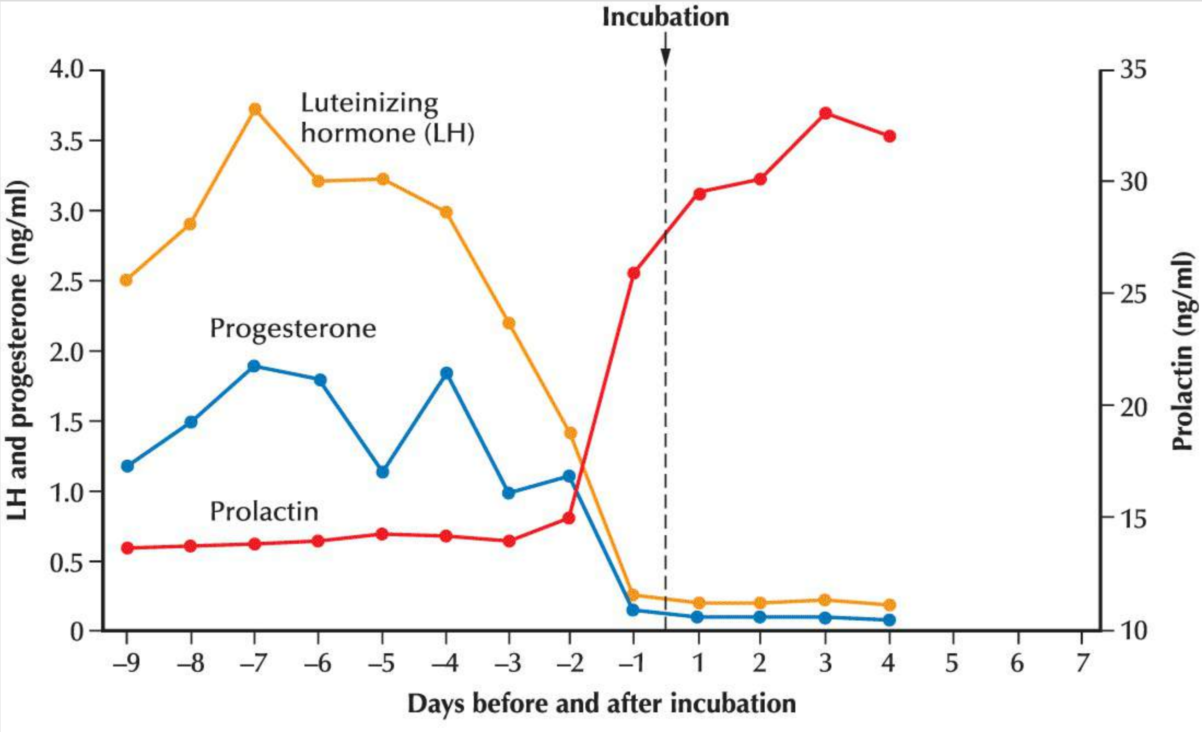
PAUL E TESSIER/AURORA PHOTOS/GETTY IMAGES

Figure 15–14 Gray Catbird removing a fecal sac from its nest.

15.2 Incubation

Birds incubate their eggs externally with a minor exception: some cuckoos jump-start incubation internally before laying their eggs in the nest of another species. The parents' task is to maximize the hatching success of their eggs by controlling the environment of the eggs steadily for several weeks (Deeming 2002a). The narrow temperature and hydration tolerances of embryos inside the eggs demand rigorous attendance by their parents. Increased energy expenditures required to thermoregulate at cool temperatures (and to heat larger clutches of eggs) challenge incubating parents (Tinbergen and Williams 2002). Yet the need to stay at the nest can compromise the parents' ability to feed themselves.

The hormone prolactin mediates the incubation behavior of birds (Vleck 2002). The levels of this hormone circulating in the blood rise sharply the day before incubation starts (Figure 15–15). Circulating blood levels of prolactin correspond to the incubation roles of males and females. Where one sex contributes most of the parental care, it has relatively high levels of prolactin. Conversely, the sex hormone testosterone, which mediates aggressive and sexual behavior, inhibits the expression of parental behavior in birds. Blood levels of testosterone in male birds that incubate drop sharply after egg laying has begun.



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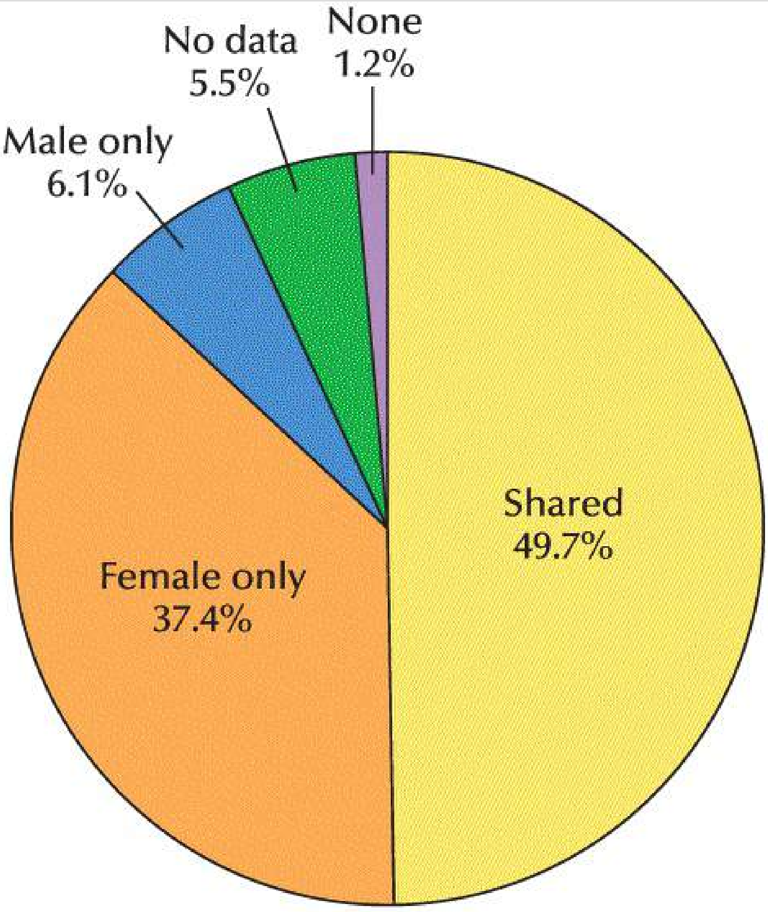
Data from Lea and Klandorf 2002

Figure 15–15 Daily changes in plasma hormone concentrations at onset of incubation. The rise of prolactin is associated with incubation behavior.

Incubation Shifts

The term *attentiveness* refers to the percentage of time spent by a parent on the nest incubating eggs compared with the time spent off the nest feeding or, in some cases, reducing heat stress. Both sexes incubate in a majority of avian families. The female incubates alone in about 37 percent of the families, and the male incubates alone in only 6 percent (Figure 15–16). The parents take regularly alternating shifts and achieve nearly continuous coverage of the eggs in many groups, including some penguins, woodpeckers, doves, trogons, hornbills, hoopoes, and antbirds. Incubation shifts may last for one or two hours, for 12 hours when one sex incubates by day and the other by night, for 24 hours when each sex takes a day at a time, for several days for many pelagic seabirds, or for more than a month for some penguins.



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DATA FROM DEEMING 2002B

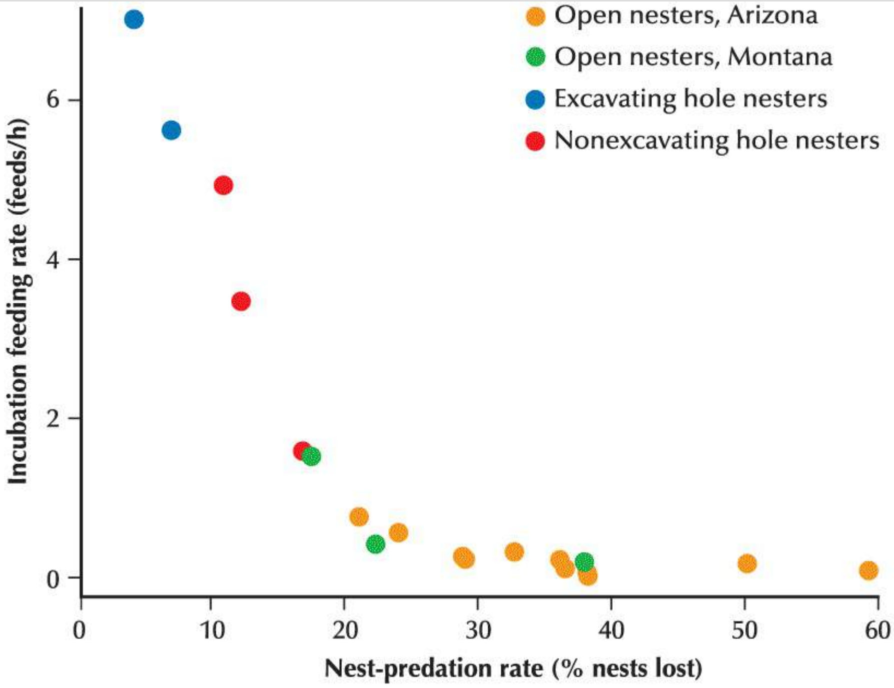
Figure 15–16 Distribution of different patterns of incubation in 163 families of birds. Both parents incubate in about half of the families.

Females that incubate alone often need their mates to bring food to them. Hornbills provide an extreme example. The male provides all the food for its mate while she remains inside the nest cavity. A female Red Crossbill also receives all its food from its mate, an arrangement that enables this species to incubate continuously in the middle of winter.

In some cases, the male may guard the nest against predators while the female leaves to feed. Each egg is important to the endangered Seychelles Warbler, which has one clutch with one egg each year and no time to replace an egg lost to predators (Komdeur and Kats 1999). Yet nest predation by another bird—the finchlike Seychelles Fody—is severe on two of the little islands on which the warbler persists. Egg loss at unguarded nests is seven times that at guarded nests. Therefore, males sacrifice their own feeding time and body condition to guard. When some of these males were transplanted to Aride, a nearby island without fodies, the males stopped guarding, foraged more for themselves, and improved the condition of their own bodies.

The risks of predation decrease with reduced parental activity at the nest (Martin et al. 2000). Birds should be sensitive to this risk and should adjust their daily behavior appropriately. In the longer term, natural selection should favor lower clutch sizes and risk-averse behavior most strongly in those species that are subject to high predation rates. As a rule, open-nesting birds are subject to more nest predation than are hole-nesting species. Birds that nest in the tropics are also subject to more nest predation than are birds that nest in the temperate zones.

Observations and experiments support these predictions. For example, North American bird species that endure high nest predation employ long on–off shifts rather than frequent short shifts (Conway and Martin 2000). This pattern reduces their activity at the nest. To explore this further, Thomas Martin and his colleagues placed models of predators near nests. They then measured the sensitivity of nesting birds to the simulated predation risk by measuring changes in their attentiveness and incubation feeding behavior. Males of both open-nesting and hole-nesting species reduced their deliveries of food to the incubating female when risk of predation increased (Martin and Ghalambor 1999; Figure 15–17). Females then left the nest more often to feed themselves, reducing their own attentiveness. In further support of the hypothesis of sensitivity, males of open-nesting species that experienced high rates of nest predation reduced their rate of visitation more than did males of species that experienced low rates of nest predation (Ghalambor and Martin 2002).



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DATA FROM MARTIN AND GHALAMBOR 1999

Figure 15–17 Males of hole-nesting bird species (blue and red circles), which are subject to low nest-predation rates, feed their incubating mates on the nest more frequently than do males of open-nesting bird species (orange and green circles), which are subject to higher predation rates. Because of the lower rates of feeding by their males, female open nesters are less attentive during incubation than are female hole nesters.

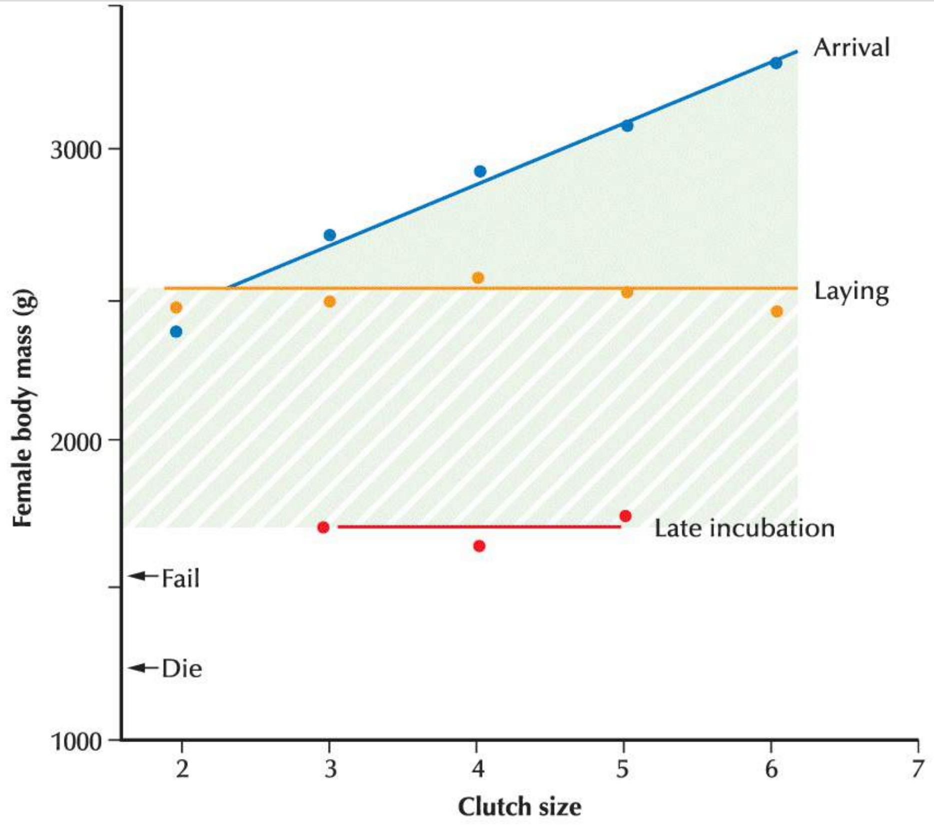
Changing shifts may be surreptitious or highly animated. Most small land birds lack conspicuous relief ceremonies, slipping on and off the nest surreptitiously to prevent detection by predators. Meadowlarks land some distance from the nest and sneak back to it through the grass by using one of several indirect routes. Bearded Reedlings pretend to look for food as they get near their nests and then enter rapidly if they perceive that the coast is clear. The female Long-tailed Hermit, a tropical hummingbird, behaves similarly. On returning from foraging, she searches intensively for spiders on the buttresses of large trees before quickly slipping onto her nest and sitting very still.

Other birds have highly ritualized relief ceremonies. When changing the guard, Pied-billed Grebes touch bill tips lightly. Least Bitterns erect their crown feathers and rattle their bills. Some herons present a stick for the nest to their mates, and terns offer a freshly caught fish. Penguins have elaborate changeover rituals that facilitate individual recognition and reinforce the pair bond, as described here for one species:

> As a Yellow-eyed Penguin approached his incubating partner, she broke into an “open yell.” He ran up with arched back and beak to the ground. Then both put their heads together to perform a hearty welcome ceremony, in which a great volume of sound issued from their widely opened mouths as they faced each other, standing erect close together. After several less-intense displays of mutual affection and three repetitions of “welcome,” the

> female resumed her position on the eggs, then rose to relinquish them to her mate. [Skutch 1976, p. 171, from Richdale 1951]

Because their foraging time is limited, incubating birds sometimes must fast and depend on their fat reserves for supplementary food. A nesting, female Snow Goose, for example, must subsist on the reserves remaining after egg production. Inadequate reserves cause some females to desert their eggs during incubation and others to die of starvation (Figure 15–18). Similarly, male Emperor Penguins and King Penguins start incubation with substantial reserves that allow them to fast for as long as four months (in the Emperor Penguin’s case). They lose substantial weight in the process. Male King Penguins depend on relief from their mates before they lose too much weight. If their mates fail to return on schedule, the males fast an extra eight days and metabolize body protein before abandoning their eggs in the interest of self-preservation (Robin et al. 2001).



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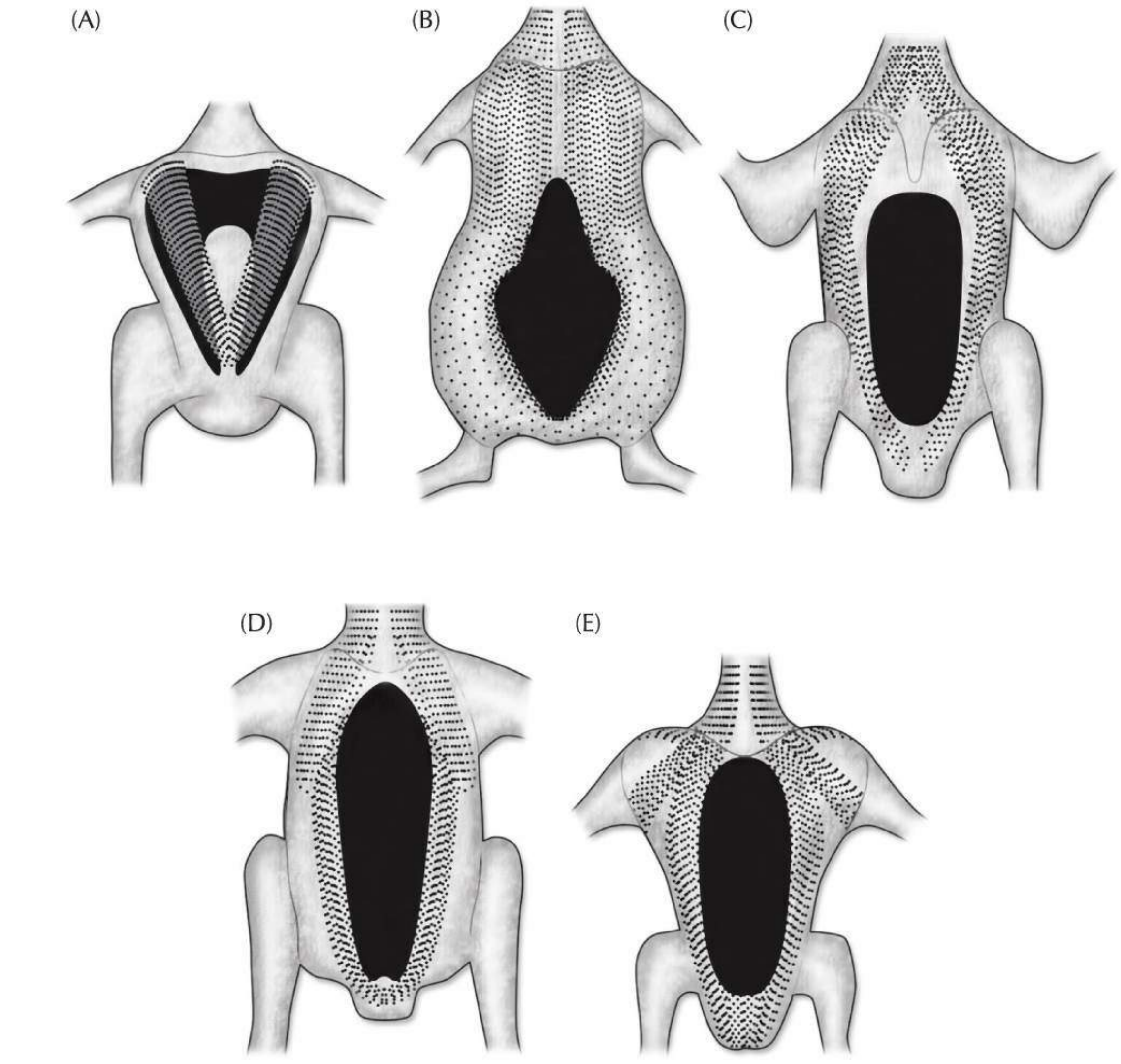
DATA FROM ANKNEY AND MACINNES 1978, DRENT AND DAAN 1980

Figure 15–18 Relation of fat reserves of the female Snow Goose arriving on Arctic breeding grounds to its projected clutch size. Females use some reserves (measured by loss of body mass, shaded area) to produce eggs and then use more reserves during incubation (hatched area). The number of eggs that a female lays is directly related to its reserves. Most females finish laying and start incubating with approximately the same body mass and, hence, similar reserves. It takes the same amount of energy to incubate a clutch of any size. Females that start incubation with inadequate reserves may abandon their eggs to prevent starvation, but sometimes they do not do so in time. Data are mean values of body mass.

Brood Patches

Birds transfer body heat to their eggs through **brood patches,** or incubation patches, which are bare, flaccid sections of skin on the abdomen or breast that are swollen like a blister. This area may be a single median patch, as in most birds, or two lateral patches, as in most shorebirds, gulls, and quails (Figure 15–19). Most birds lose feathers to form an incubation patch for the purpose of brooding. Pigeons and doves use a normally bare apterium, or featherless region (see Chapter 4).



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DATA FROM LEA AND KLANDORF 2002

Figure 15–19 Incubation patches (in black) of (A) California Quail, (B) Red-necked Grebe, (C) White-crowned Sparrow, (D) Rook, and (E) Northern Harrier. Stippling indicates feather tracts. Clear areas indicate areas without feathers—called apteria.

The accumulation of fluids—edema—and the infiltration of white blood cells swell and soften the skin, allowing better contact between the surfaces of the incubation patch and the egg. The epidermis itself thickens into a callused surface that is not damaged by sustained contact or friction with the eggs. Finally, blood vessels proliferate throughout the patch to efficiently deliver body heat to the eggs. The arterioles in the network of blood vessels have well-developed musculature that directs the flow of warm blood to the skin surface during incubation and stops the flow when the parent is not actively incubating.

Incubation patches develop just before the incubation period under the direct control of the hormones estrogen and prolactin. The patches regress after hatching. If both parents incubate, then brood patches develop in both sexes.

Prolactin or estrogen or both, depending on the species, stimulate defeathering and vascularization of the incubation patch. Progesterone stimulates the thickening and increased sensitivity of the epidermis. Most birds develop brood patches in response to experimental hormone treatment, except brood parasites, such as Brown-headed Cowbirds and many cuckoos, which never incubate (Lea and Klandorf 2002).

Some birds lack incubation patches. For example, gannets and boobies, lacking brood patches, incubate with their feet instead. They grasp a single egg in their well-vascularized, webbed feet or even hold two eggs, one in each foot. Murres and penguins incubate their eggs on the top surfaces of their feet. Some penguins have a muscular pouch of belly skin that holds a single egg in this position.

Incubation Periods

The **incubation period** is the time required by embryos to develop in freshly laid eggs that receive normal attention by incubating parents. It is defined as the interval between the laying of the last egg of a clutch and the hatching of that egg.

Most birds delay the onset of incubation until the clutch is complete. This behavior ensures that the embryos begin to develop and later hatch at roughly the same time, even though some eggs are laid earlier than others. Pigeons and doves, for example, sit on the first egg before the second is laid but do not bring it up to the temperatures required for incubation. Owls and raptors, on the other hand, begin incubation before the clutch is complete, with the result that young hatch at intervals. To maintain the viability of the eggs in their large clutches, female ducks increase attendance as laying progresses. The development of embryos starts slowly after the second egg is laid. Increased warming by the hen then accelerates the development of later embryos. As a result, the ducklings hatch together at about the same time (Loos and Rohwer 2004).

Incubation periods vary from as short as 10 days for some woodpeckers, cuckoos, and small songbirds to as long as 80 to 90 days for albatrosses and kiwis. Longer incubation periods increase the risk that a predator will find the nest.

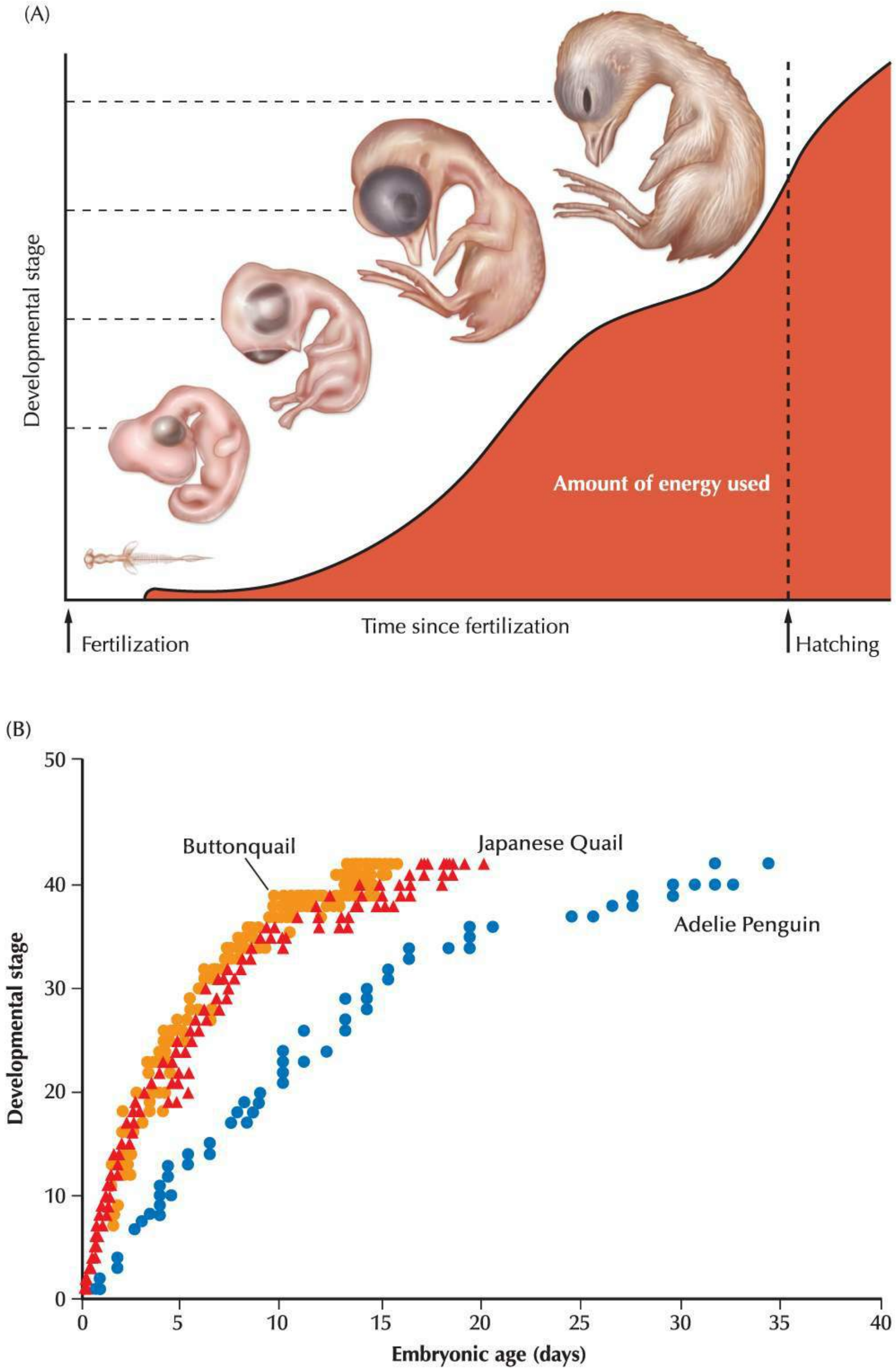
Embryos

The growth of avian embryos is regulated by adaptive, genetically controlled developmental programs. Growth rates of embryos vary with egg size and with incubation period, but they have little to do with a developmental stage and activity of the newly hatched young—a spectrum ranging from altricial to precocial modes of development

(Chapter 16). Similar-sized eggs of different taxa differ greatly in the amount of time that they take to hatch and in the chick's state of development at hatching.

A broad survey of 47 families and subfamilies of birds revealed that incubation periods relate directly to how long adult birds live (Ricklefs 1993). Incubation periods also correlate with the probability of predation. Species that nest in holes tend to have longer incubation and nestling periods than do species that nest in less safe, open sites. Long incubation periods produce active, precocial chicks with advanced muscular and sensory development.

From fertilization to hatching, the avian embryo undergoes a standard sequence of stages of development regardless of the length of the incubation period (Ricklefs and Starck 1998a; Figure 15–20). The sequence includes 42 stages that experts distinguish by the morphology of the embryo. The first 33 stages vary little among different species from songbirds to penguins. The body plan develops, tissue begins to differentiate, and organs begin to form. The basic systems of life are established, including a feathered integument, a skeleton made first of cartilage and then gradually calcified, a brain that may continue to enlarge and build internal neural networks, and a digestive system that will set limits to energy intake.



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(A) DATA FROM STARCK 1999. (B) DATA FROM RICKLEFS AND STARCK 1998A

Figure 15–20 (A) The development of the avian chick proceeds through a well-defined sequence of morphological stages from fertilization to hatching. (B) Although the sequence of stages is similar among species, the rate of morphological change, the amount of energy used, and the length of each stage vary among species.

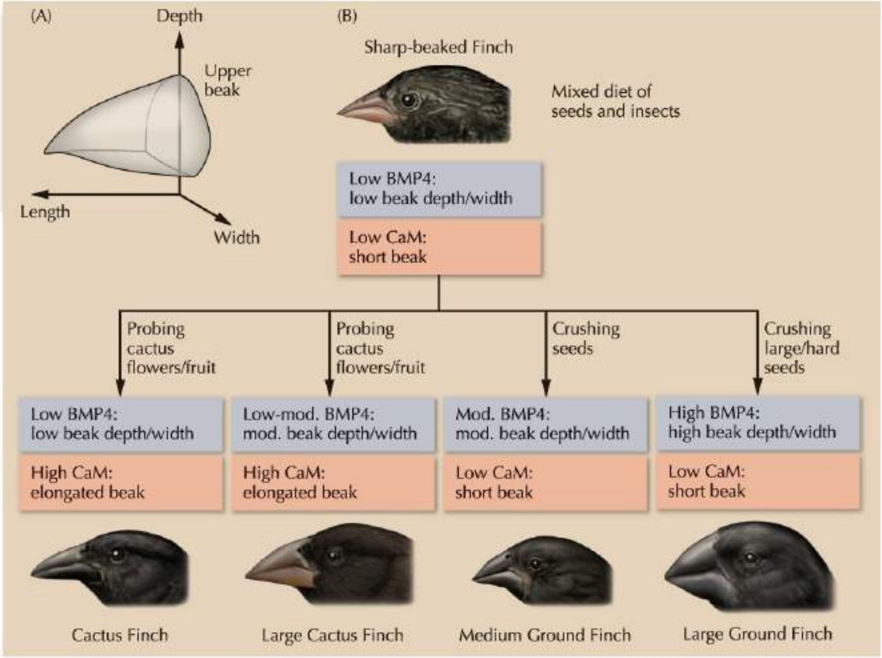
The lengths of the final stages of development vary with features that are specific to different species (Box 15–4). Stage 39, for example, is prolonged in species such as the megapodes and penguins, which hatch in advanced physical condition. The same stage (39) is abbreviated in birds as different as buttonquails and songbirds.

Box 15–4

Ecologically Important Traits Can Develop in the Egg: Evolution of Finch Bills

Embryonic development controls many ecologically important characters of birds, including beak shape. The well-known Galápagos finches, for example, differ dramatically in their bill shapes and sizes, which evolved in response to different food choices (see Chapter 1; see also photos below). The size and shape of the beak is influenced by the expression of extra-cellular signaling molecules by the cells in the cartilaginous plates of the embryonic avian face. Changes in the expression of bone-morphogenetic protein 4 (Bmp4) are associated with the diversification of beak shape among Galápagos finch species (Abzhanov et al. 2004; Pennisi 2004). Earlier and greater activity of this Bmp4 protein results in the larger bills of ground finches, compared with the slender bills of cactus finches. Among different species of ground finches, Bmp4 activity starts earliest to produce the large grosbeak-like bill of the Large Ground Finch. Meanwhile, higher expression of the calmodulin gene results in an elongate bill and is greatest in the Cactus Finch and least in the Large

Ground Finch (Abzhanov et al. 2006).



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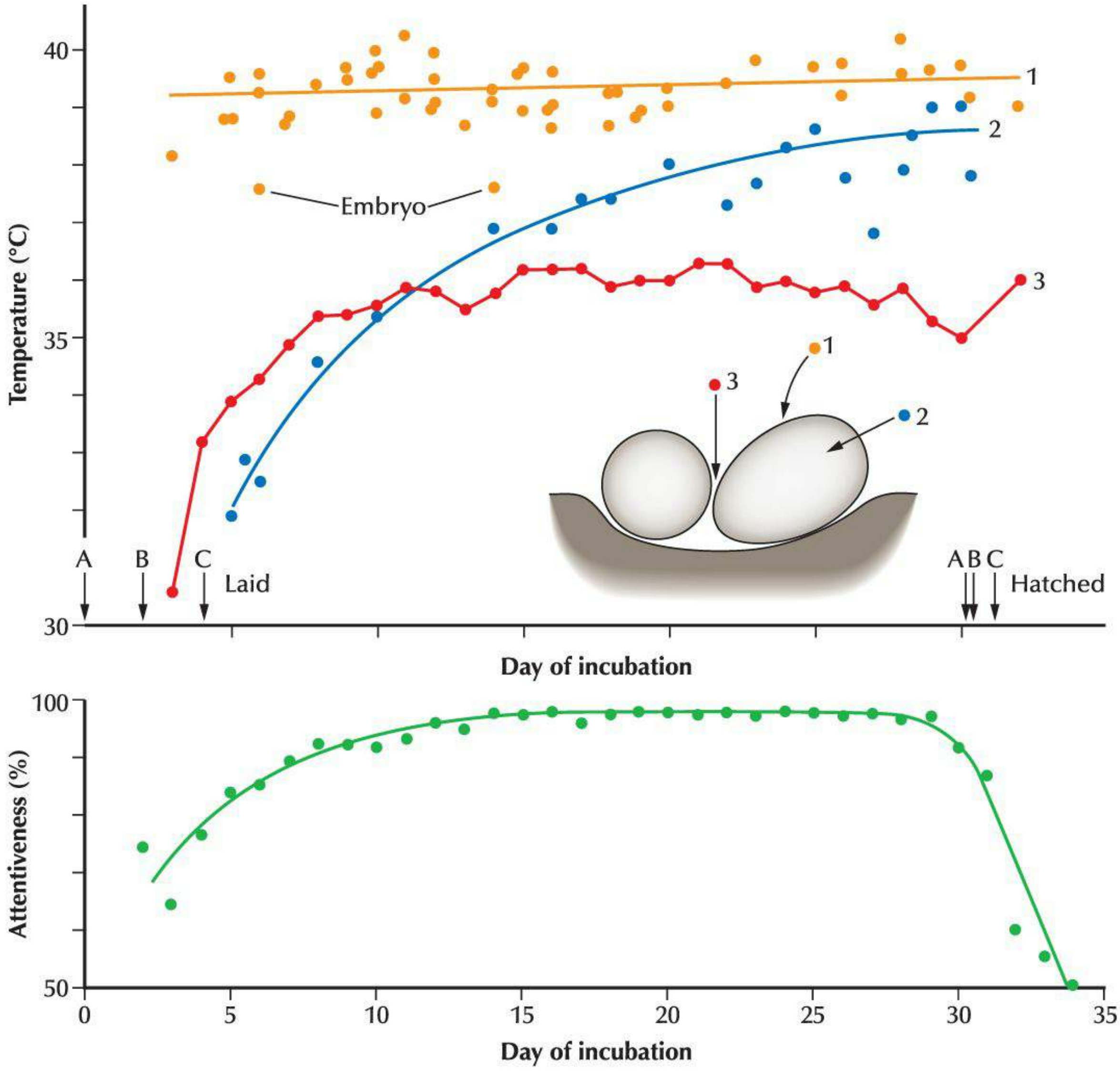
DATA FROM ABZHANOV ET AL. 2006

The variation in beak shape among Galápagos finch species (top row) have evolved through natural selection for ecological specialization on different diets. These ecologically important bill shape variations are produced by differences in the timing and magnitude of expression of developmental regulatory genes—Bmp4 and Calmodulin (CaM)—during embryonic development.

Keeping Eggs Warm

The first priority of incubation is to keep the eggs close to the optimum temperature for development—that is, from 37°C to 38°C. Internal egg temperatures are low at first, but they increase steadily due to both parental incubation and to heat generated internally by the growing embryo’s own metabolism (Figure 15–21).



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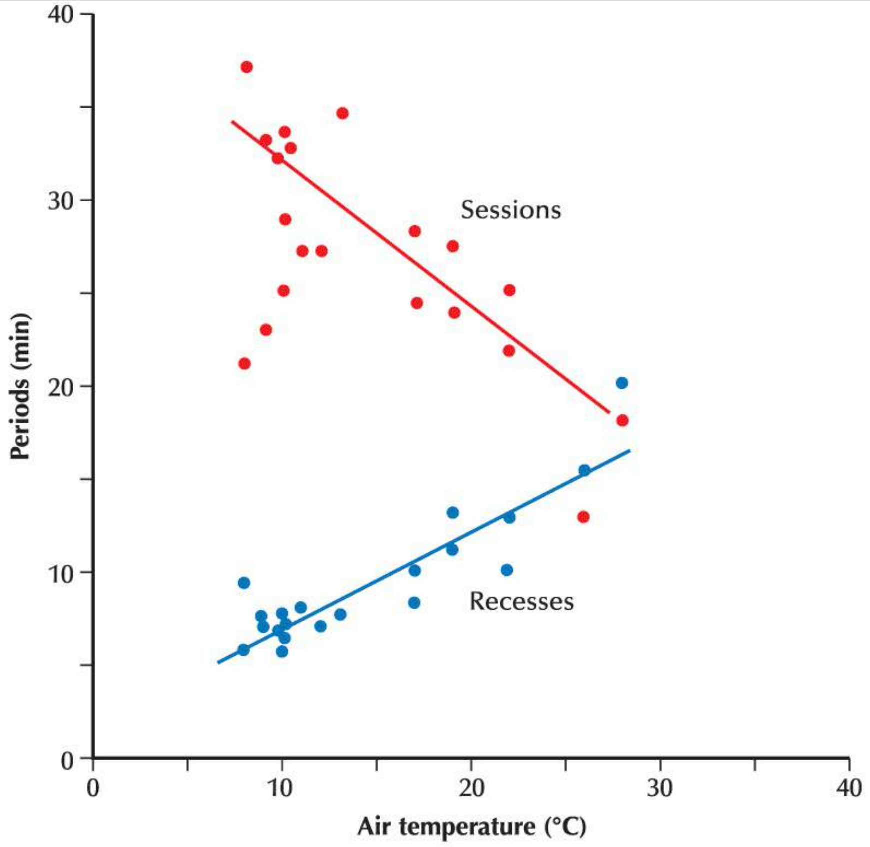
DATA FROM DRENT 1975

Figure 15–21 (*Top*) Egg temperatures during natural incubation by a Herring Gull. The three lines represent measurements taken at different sites: (1) the egg surface, (2) inside the egg, and (3) air between eggs A, B, and C. Points labeled “Embryo” indicate measurements taken inside the egg near the embryo on days 6 and 14. (*Bottom*) The constancy of incubation (attentiveness) of adults increased steadily in the first two weeks of incubation.

Serious problems result if the embryo is exposed to temperatures outside the range of 35°C to 40.5°C. Exposure to higher temperatures is lethal, and even a short exposure to lower temperatures between

26°C and 35°C can disrupt normal development. Below 26°C, the development of young embryos simply stops. For these reasons, frequent or continuous warming is necessary unless ambient air temperatures are very high. Embryos in the later stages of development—of American White Pelicans, Ring-billed Gulls, and Herring Gulls—detect temperature changes of the egg within one minute and vocalize faster, signaling their need for heat. Parents then respond with increased incubation (Evans 1994; Brua 2002).

Incubating parents keep the internal temperatures of their eggs remarkably stable despite the conflicts that incubation behavior itself presents. The natural incubation rhythm of a species is geared directly to the maintenance of critical egg temperatures (Figure 15–22). At lower air temperatures, sessions on the eggs are longer, and recesses for food and drink are shorter. Experimental heating of the nests of the Common Starling reduced the costs of incubation, including energy expenditure to keep the eggs at the temperature required for the development of the embryo (Reid et al. 2000). The parents reallocated the energy that they saved to later stages of that nesting attempt (feeding the young) and to a second nesting attempt. Compared with controls, starlings that were helped by the heating pad during their first brood incubation fledged more young from that brood and were more likely to hatch all the eggs in their next brood.



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DATA FROM KLUIJVER 1950, DRENT 1972

Figure 15–22 Incubation rhythms of the Great Tit are directly related to the air temperature in the nest box. Time on the eggs (sessions) decreases and time off the eggs (recesses) increases when the air is warmer.

Some (but not all) male Common Starlings help their mates incubate (Reid et al. 2002). Incubation time by the male supplements that of the female, leading to increased total nest attendance. Although they do not maintain the eggs at quite as high a temperature as do females, males rewarm cool clutches faster than females and thereby increase the pace of embryo development, leading to improved breeding success. This extra help leads to shorter incubation periods, greater hatching success, and larger nestlings.

Keeping Eggs Cool

Birds that nest in hot places face the opposite challenge: keeping eggs cool. The temperatures of unprotected eggs quickly rise to lethal levels. Just leaving the nest to chase predatory gulls, for example, can cause the temperature of a Forster's Tern's egg to rise to 46°C in 10 minutes and to 50°C during a 25-minute absence (Grant 1982). Shading the eggs, therefore, is a critical part of incubation behavior. Gray Gulls that nest in the extreme deserts of northern Chile incubate their eggs at night, when it is cold, but shade them during the day, when air temperatures reach from 38°C to 39°C (Howell et al. 1974).

Conservationists, beachgoers, and research scientists should be aware of the dangers of egg exposure. The unwitting disturbance of nesting colonies of island seabirds or vulnerable beach-nesting species such as the Piping Plover and Least Tern causes the parents to leave their nests and expose their eggs to the sun. Direct exposure to the hot sun, caused merely by brief disturbances, kills the sensitive embryos. At risk is the potential failure of entire nesting colonies. Human disturbance also increases the risk of predation or desertion.

Wetting the nest or eggs counteracts extreme heat with evaporative cooling. This practice is common among shorebirds, gulls, and terns. Killdeer, for example, cool their eggs by transferring water from wet belly feathers (Jackson and Jackson 2000). The Egyptian Plover, which nests on the hot sandbars of the Nile River, cools its eggs by covering them with a thin layer of sand and then sprinkling water on top of the sand. The nest temperature holds near 37.5°C as a result (Howell 1979).

Heat and water problems stress the parent itself while it tends its eggs in a hot environment. To protect eggs from the hot sun, the incubating parent must absorb and dissipate enormous amounts of radiant energy without overheating itself. Sooty Terns dissipate that heat by extending their legs fully, erecting their feathers, and panting (see Figure 6–10). The breeze removes the heat absorbed by their black backs. The more sunlight that incubating Herring Gulls absorb, the more they must pant. The stress on a bird’s water balance is so great and the consequences of even temporary absences are so severe that gull mates must take turns providing continuous egg coverage.

Turning Eggs

An incubating bird rises periodically to peer sharply down at its eggs. It then draws each egg backward with a sweeping motion of the bill, rearranging its clutch and turning the eggs. Parents rearrange their eggs so that those that have been on the outside of the clutch are moved to the center, where the temperature is several degrees higher.

Unlike other reptiles and dinosaurs, the turning of bird eggs is crucial for the normal embryonic development of most species. Regular turning of eggs in early incubation also prevents the chorioallantois from adhering prematurely to the inner shell membranes. Species differ in how often they turn their eggs: eggs rich in albumen get turned more often than yolk-rich eggs (Deeming 2002b). The turning of eggs optimizes the growth of the extra-embryonic membranes and the fluid dynamics needed to absorb the albumen. Premature adhesion interferes with albumen uptake by the embryo and obstructs its ability to attain the tucking position essential for hatching.

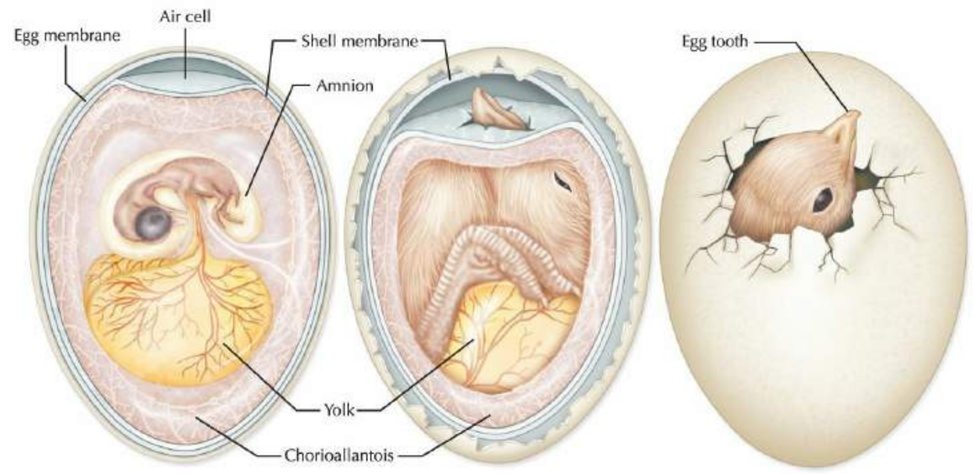
Not all species turn their eggs. Palm swifts use their special saliva to glue their eggs to their simple nest made on the palm fronds, where they remain fixed for the full period of incubation. Perhaps the movement of the palm frond prevents the adhesion of the membranes to the eggshell.

Successful incubation culminates in hatching, itself a challenging but sometimes cooperative and closely orchestrated event.

15.3 Hatching

Hatching—breaking the eggshell and emerging from it—is a physical challenge. In its final stages of development, the chick is folded and compact and fills the space inside the egg that was once occupied by yolk and albumen. The chick barely seems to fit inside the tight confines of the shell. By this time, the chicks communicate both with their siblings in the other eggs and with their parents. Calls by the developing embryo engage parents in the hatching process and help to synchronize hatching in precocial species (Brua 2002).

How exactly does a chick break out of the egg? The hatchling-to-be withdraws its head so that its bill passes between its body and its right wing. This so-called tucking position increases the efficiency of pipping, or breaking the eggshell, and therefore the chances of hatching successfully. To hatch, the chick first punctures the membrane that encloses the air chamber at the large blunt end of the egg. Then the chick pecks feebly but regularly at the shell while slowly rotating in a counterclockwise direction by pivoting its legs. After one to two days of "bumping," the chick leaves a circular series of fractures on the eggshell and finally penetrates through the eggshell to the world outside (Figure 15–23). The power for the first pecks comes from the hatching muscle on the back of the neck (Figure 15–24). The hatching muscle withers when its task is done.



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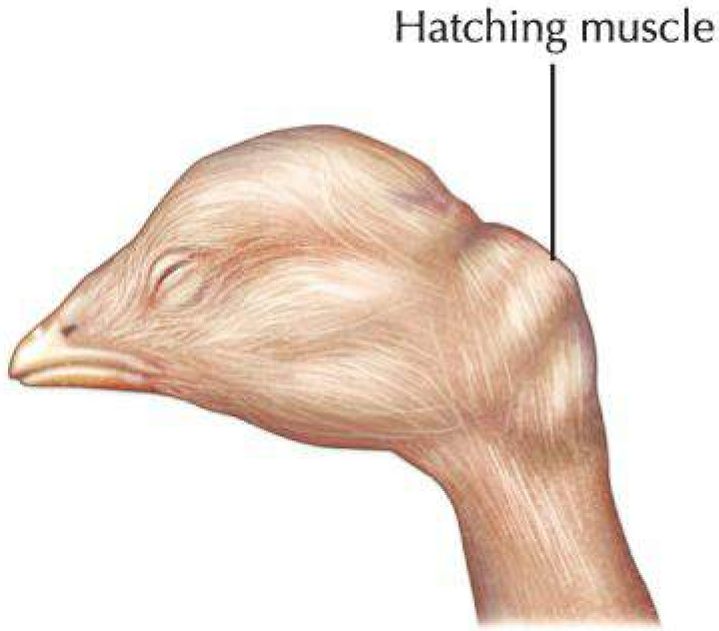
DATA FROM RAHN ET AL. 1979

Figure 15–23 Avian development inside the egg. (A) The developing embryo grows capillary networks into the yolk to absorb energy and around the chorioallantois to exchange oxygen and carbon dioxide through the shell. (B) Shortly before hatching, the chick shifts into the tucking position, breaks into the air chamber with its beak, and inflates its lungs for the first time. (C) The chick chips its way through the eggshell with the aid of an egg tooth.

A special, calcified **egg tooth** on the tip of the bill (not a real tooth) helps the chick to break the shell. The hard, sharp-edged egg tooth is generally located just before the bill tip where the tip curves downward. The sheath of the egg tooth includes the lower mandible in loons, rails, bustards, pigeons, shorebirds, auks, hornbills, and woodpeckers. Egg teeth drop off the bills of most baby birds soon after hatching: in one to three days in shorebirds and fowl and in as much as three weeks in petrels (Clark 1961). Songbirds gradually absorb the egg tooth.

Most birds chip a big hole out of the eggshell toward the blunt end of the egg and finally shatter it with their body movements. Emerging



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DATA FROM BOCK AND HIKIDA 1968

Figure 15–24 The hatching muscle is a short-lived feature of chick anatomy that helps the chick break out of the egg.

woodcocks and Willets, however, split the eggshell longitudinally, ripping open a seam rather than breaking the eggshell into pieces (Wetherbee and Bartlett 1962). After hours or even days of struggling, ostrich chicks virtually explode from their thick-shelled eggs, shattering the shell into many pieces (Sauer and Sauer 1966). Sometimes, a parent ostrich will help crack the shell by pressing its breastbone down on the egg and then pulling the chick out by the head. A parent may also help its chick to hatch by enlarging the initial hole.

Prompt removal of eggshells after hatching protects the camouflage of a nest site. Parents may eat the shell, feed it to their chicks, or take it away from the nest for disposal. In a classic early experiment, Niko Tinbergen (1963) demonstrated that the removal of eggshells from the nests of Herring Gulls reduced predation by crows from 65 percent to only 22 percent.

Eggs in a clutch may hatch almost synchronously or asynchronously at intervals that range from a few hours to more than a week. Staggered, asynchronous hatching is due to the onset of incubation before the clutch of eggs is complete. The first-hatched young often have an advantage over their younger siblings, which succumb first to shortages of food and sometimes to physical abuse by the oldest sibling (Stoleson and Beissinger 1995; Chapter 16). In many species, the second chick rarely survives. The parents focus their investment on the first individual to hatch but lay a second egg as insurance. Different egg provisions (see section 12.2) can overcome some of these handicaps, as can different embryonic development rates for the two sexes. For example, even though female Common Kestrels are the larger sex by 20 percent, female embryos grow faster and have a shorter embryonic period than male embryos (Blanco et al. 2003). The female chicks hatch earlier than male chicks and assume higher ranks in the brood-size hierarchy.

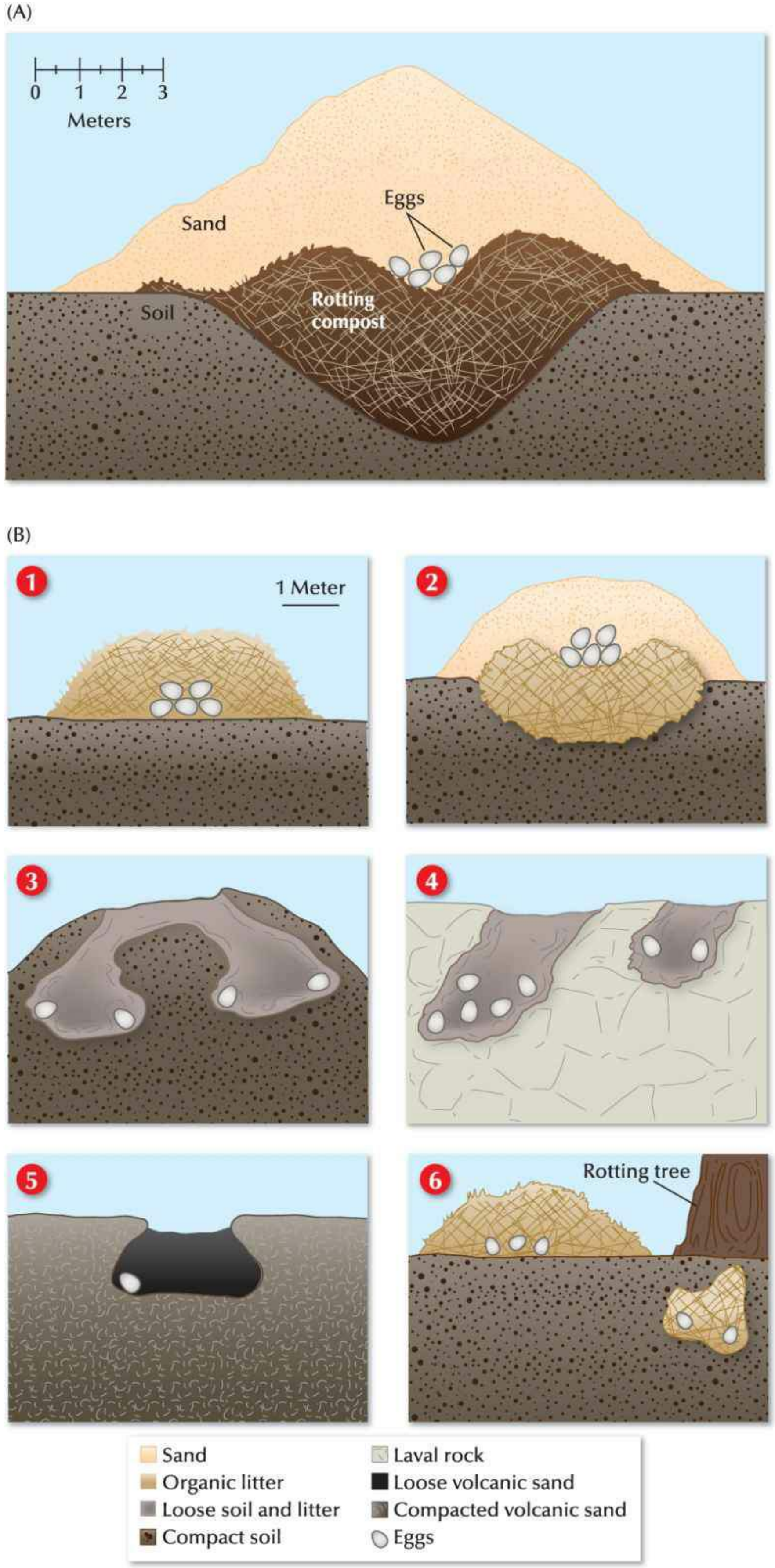
Highly synchronized hatching is characteristic of waterfowl and quails, which have large broods of active young that move from the nest to safer sites soon after hatching. For example, the 11 to 13 eggs in the clutch of a Mallard Duck all hatch within two hours despite having been fertilized and laid over a two-week period. Differences in their rates of development bring early and late eggs closer together in the stages of embryo development.

Coordinated adjustments orchestrate the final synchrony of hatching. First, chicks inside the eggs communicate with each other. Older chicks that are ready to hatch "click" slowly (from 1.5 to 60 times per second), causing younger siblings to accelerate their hatching effort. Conversely, younger chicks unable to catch up click rapidly (more than 100 times per second), causing their older siblings to delay emergence as long as 33 hours (Brua 2002). The jarring of adjacent eggs by the first hatchling is the final signal, stimulating nest mates to make their final hatching moves and to break out together from 20 to 30 minutes later.

New hatchlings vary in their ability to run, thermoregulate, and feed. A species' mode of development frames the challenges that start for both parents and their offspring after the chicks hatch—sibling competition, parent-versus-offspring conflicts, and strategic brood reduction. The spectrum of modes of development from helpless (altricial) to mobile (precocial) is the central theme of Chapter 16. The extraordinary incubation and hatching feats of the extremely precocial megapodes, however, are a fitting climax for this chapter.

15.4 Megapodes

The megapodes, or mound builders, are fowl-like galliform birds from Australia, New Guinea, and eastern Indonesia that use heat from decomposing vegetation, geothermal springs, or the sun to incubate their eggs (Booth and Jones 2002; Figure 15–25). Although it may seem rather reptilian, this behavior evolved secondarily from normal avian incubation behavior. Regulation of the incubation temperature stems either from the thermal stability of the nesting site or from active manipulation by the birds. Two species, the Australian Brushturkey and the Malleefowl, regulate the internal temperatures of their nest compost heaps with great sensitivity.



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(A) DATA FROM FRITH 1959. (B) DATA FROM BOOTH AND JONES 2002

Figure 15–25 (A) Cross section of a Malleefowl incubation mound with eggs. Underneath the egg chamber is a pit full of decaying vegetation. Sandy soil covers the eggs. (B) Structural diversity of megapode nests: (1) Australian Brushturkey—a mound of organic litter material raked together by parents is the most widespread system; (2) Malleefowl—the most sophisticated mound consists of a sand blanket atop a bed of decaying organic material; (3) Dusky Megapode—tunnels containing loose soil and litter inside a larger mound of compacted soil; (4) Tongan Megapode—tunnels filled with loose soil and organic material in solid, geothermally heated lava rock formations; (5) Maleo —simple pits in geothermally heated sand; (6) Philippine Megapode—tunnel dug between rotted tree roots and filled with loose soil and organic litter as well as mounds of organic litter material as in the Australian Brushturkey structure (1).

The great nest mound of the Australian Brushturkey is a giant compost pile that weighs 6,800 kilograms and maintains a stable equilibrium temperature of 33°C (Seymour and Bradford 1992; see Figure 15–25B1). The male brushturkey keeps the mound at this temperature by adding and removing litter and by making sure that there is enough water to keep the decay process going at the right level. The rate of heat production (200 watts) through microbial decay is 10 times that of a resting bird. It allows the megapodes to incubate many more eggs simultaneously than they could in the traditional way. Little maintenance is required after a large nest mound has been established with a critical mass of fresh litter (about 3,000 kilograms), sufficient water content, and occasional mixing of the litter. One or more hens will lay eggs in the male’s nest, but on average more than 25 percent of the eggs in a nest are fertilized by some other male (Birks 1997).

The “nest” of the Malleefowl is a large sandy mound, as large as 11 meters in diameter and five meters high, made of decaying vegetation and sand (see Figure 15–25B2). The hen lays her large eggs deep into the nest at intervals throughout the nine-month breeding season. Incubation temperatures inside the mound remain at 32°C to 35°C as external air temperatures range from 0°C to 38°C. The decomposition of litter placed under the eggs produces most of the incubation heat in the spring.

The male Malleefowl tends the mound alone. He spends five hours a day manipulating the amount of material covering the eggs to regulate heat loss or retention. He regularly checks the temperature inside the mound by testing the soil in his beak. In the spring and summer, he cools the mound by opening it (to release accumulated heat) and by replacing hot sand with cooler sand. In the fall, when there is less sun and less decay, he manipulates the covering of a shallower pit that takes advantage of daytime solar heating. He spreads sand to warm it by day and then piles it over the eggs at night, adding extra insulation to seal in the heat.

Megapode eggs are two to three times larger than eggs of other birds of comparable size. The chicks hatch after 42 to 99 days within incubation mounds, the longest incubation period of any bird. They do so unaided and ready for independent living without parents. David Booth and Darryl Jones (2002) provide an excellent review of mound-builder chick biology and hatching.

Briefly, the megapode embryo has an egg tooth early in its development but loses it by hatching time. Rather than pecking its way out of the egg, the hatchling kicks and shoulders its way out by causing the thin shell to shatter. Whereas most birds require from one to two days to switch from respiration through the chorioallantois membrane to breathing air, mound-builder chicks do so in minutes. After they’re hatched, they rest for an average of 16 hours, clearing their lungs before starting to dig their way upward and out of the nest. That work takes another 24 to 55 hours of effort, in which short bursts of digging alternate with longer rests. Residual yolk provides the energy required to fuel this effort. The chick first scratches out an air chamber around it and then scratches down the ceiling above it, molding the loose material underneath it. Its plumage dries out as it climbs slowly upward, enabling it to thermoregulate when it finally reaches the surface. Finally, it emerges:

> Suddenly the back of its neck appears at the mound’s surface. After the neck is free, the head quickly follows. The chick opens its eyes for the first time and rests briefly. Then it resumes its struggles, freeing one wing and then the other. Soon the whole body follows. Temporarily exhausted, the young Mallee-Fowl may lie exposed on the surface for some time, an easy prey to predators; but more often it tumbles down the side of the mound and staggers to the nearest bush to collapse in the shade, where it recuperates its strength after such prolonged exertion. Its recovery is swift: within an hour it can run firmly; after two hours it runs very swiftly and can flutter above the ground for thirty to forty feet. Twenty-four hours after its

> escape from the mound, it flies strongly. [Skutch 1976, p. 234]

Most other hatchlings enter a more dependent, temporary period of parental care, the topic of the next chapter.

REVIEW KEY CONCEPTS

15.1 Nests

Nests provide a location and structure for the incubation of eggs and, often, the care of altricial young. Nests must provide protection from the elements and predation. The diversity in nest materials, placement, and architecture are evolved solutions to natural selection on nesting and fledging success. Bird nests vary from precarious constructions on bare branches to enormous communal apartments, from burrows dug into the soil to cavities excavated in trees, and from simple scrapes on the ground to elaborate stick castles. Birds construct their nests from a wide variety of materials, ranging from sticks, pebbles, and plant fibers to mud, spiderwebs, and even their own gluey saliva. Birds inherit behavioral preferences to seek out particular sites and materials in their environments and manipulate them in specific ways to build their nests. The results are strong phylogenetic patterns in nest evolution. Some of the most important adaptations in nest architecture and nesting behavior provide protection from predation. Nest placement often takes advantage of appropriate microclimates for successful incubation and nestling care.

Key Terms: extended phenotype, secondary cavity nesters

15.2 Incubation

Almost all birds incubate their eggs with direct contact with their endothermic bodies. In the majority of birds, the incubation is shared by the male and the female, but in some species, incubation is performed by the female only or the male only. When incubation is shared, the members of the pair take shifts to maintain a consistent incubation temperature. Incubation is made more efficient by the development of brood patch—a fluid-filled swelling of belly skin that improves body contact with the eggs. Birds delay the onset of incubation until the clutch is complete. The length of the incubation period varies from 10 to 90 days, depending on the size of the eggs and the stage of development at hatching. Long incubation periods increase the risk of predation but provide more time to for the young to develop. Incubating parents keep the internal temperatures of their eggs remarkably stable (37°C to 38°C), but some birds face the challenges of keeping their eggs sufficiently cool (below 40°C). In addition to incubation, bird eggs must be turned periodically to ensure proper development.

Key Terms: brood patches, incubation period

15.3 Hatching

Breaking the egg shell and emerging from it pose a physical challenge to the avian embryo. The hatching movements involve piercing the membrane that encloses the air pocket and then fracturing the egg shell nearer the blunt end of the egg. These movements are made possible by a calcified egg tooth on the tip of the beak and strong hatching muscles in the neck. Hatching often occurs synchronously within a few hours but can be staggered over days. Older chicks often have survival advantages.

Key Terms: hatching, egg tooth

15.4 Megapodes

The megapodes, or mound builders, of Australasia are fowl-like galliform birds from Australia, New Guinea, and eastern Indonesia that use heat from decomposing vegetation, geothermal springs, or the sun to incubate their eggs. The male constructs the nest in a cavity in the ground and maintains the egg temperature by creating a pile of composting vegetation or (near geothermal springs) by the thermal stability of the sand itself. The females visit a male at his nest, lay an egg, and leave. The fledglings hatch asynchronously, dig their way out of the nest, and are immediately independent. The megapodes are one of the few birds with no posthatching parental care.

APPLY YOUR KNOWLEDGE

1. How does the presence of predators affect nest construction and the behavior of parents?
2. Explain how the features of habitats and ecosystems determine the distribution and sites of nest construction.
3. What observations lead to the conclusion that nest building is innate and/or learned?
4. What are the hormones and their actions that contribute to the successful incubation and protection of a clutch of eggs?
5. How do parents adjust the timing of hatching of eggs in a clutch?
6. What are the advantages of successive and simultaneous hatching?
7. Explain the unique incubation method of the incubation of Malleefowl mound nests and how incubation temperature is regulated.

8. What are the factors contributing to a male Malleefowl’s fitness, and what factors diminish it?

CHAPTER 16 *Parents and Their Offspring*

Nelson, Alan G./Animals Animals

A Western Grebe carries its chick during a sustained period of parental care that includes learning how to catch fish on its own.

> The selfish interests of young birds inevitably

> conflict with those of their parents. [Trivers 1985]

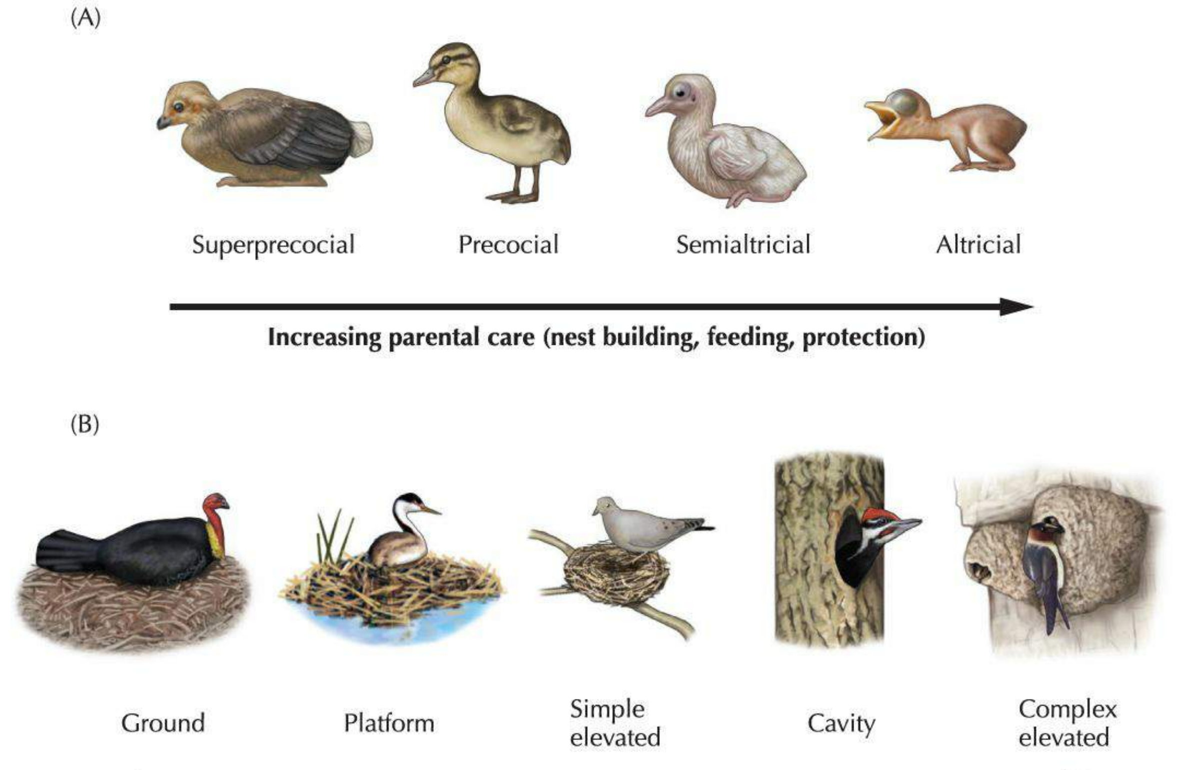
Parents should try to raise as many, equally vigorous young as possible. But chicks demand care that exposes their parents to increased predation risk and to physiological stress. Chicks also vie with one another for parental attention, protection, and extra portions of food. The conflict between the costs of parental care and those required for self-maintenance constrains solo parenthood in birds.

This chapter follows the life of a bird from hatchling to fledgling and beyond. A central theme is the contrast between the altricial and the precocial modes of development. In these different modes, chicks hatch with very different degrees of physical maturity. First, we examine the major features of the physical growth and development of hatchlings. As the chicks grow, sibling rivalry and competition increase, sometimes leading to siblicide, especially when eggs hatch at different times, producing nest mates of different ages and abilities. Then we examine the challenges and solutions of parenting in birds, which include favoritism. The chapter concludes with the fledging of young birds from their nest, followed by their behavioral growth, including the central process of imprinting.

16.1 Modes of Development

The development of an individual bird begins with embryonic cell divisions and ends with the learning of the complex behavioral skills of a capable adult. Baby birds undergo part of their development inside the egg, then hatch from the egg, leave the nest, join flocks, and sometimes migrate to distant places. They learn to fly, to feed, and to sing. They distinguish predators from prey and potential mates from potential rivals. Fundamentally different paths of development guide the dramatic transformations of chicks to adults.

The dichotomy between precocial and altricial development is the single most striking feature of postnatal growth in birds (Ricklefs 1983). These alternative modes of development start subtly with the yolk provisions of the egg, as described in section 12.6, and emerge overtly when the chick hatches. The terms *altricial* and *precocial* refer to the states of physical maturity of the hatchling and its dependence on parental care (Figure 16–1; Table 16–1). The different modes of development affect not only the way in which fledglings leave the nest but also their subsequent growth and, ultimately, the patterns of care and the mating systems of the parents themselves.



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DATA FROM DIAL 2003B

Figure 16–1 (A) A spectrum of developmental categories of hatchling birds, from independent (superprecocial) mound builders to helpless (altricial) songbirds that require the most parental care. (B) A spectrum of nest types, from simple ground nests to complex elevated nests, corresponds to birds' increasing flight proficiency, with reliance on wings (forelimbs) rather than legs for locomotion. The development of increased flight abilities requires increased parental care before dependent young master flight.

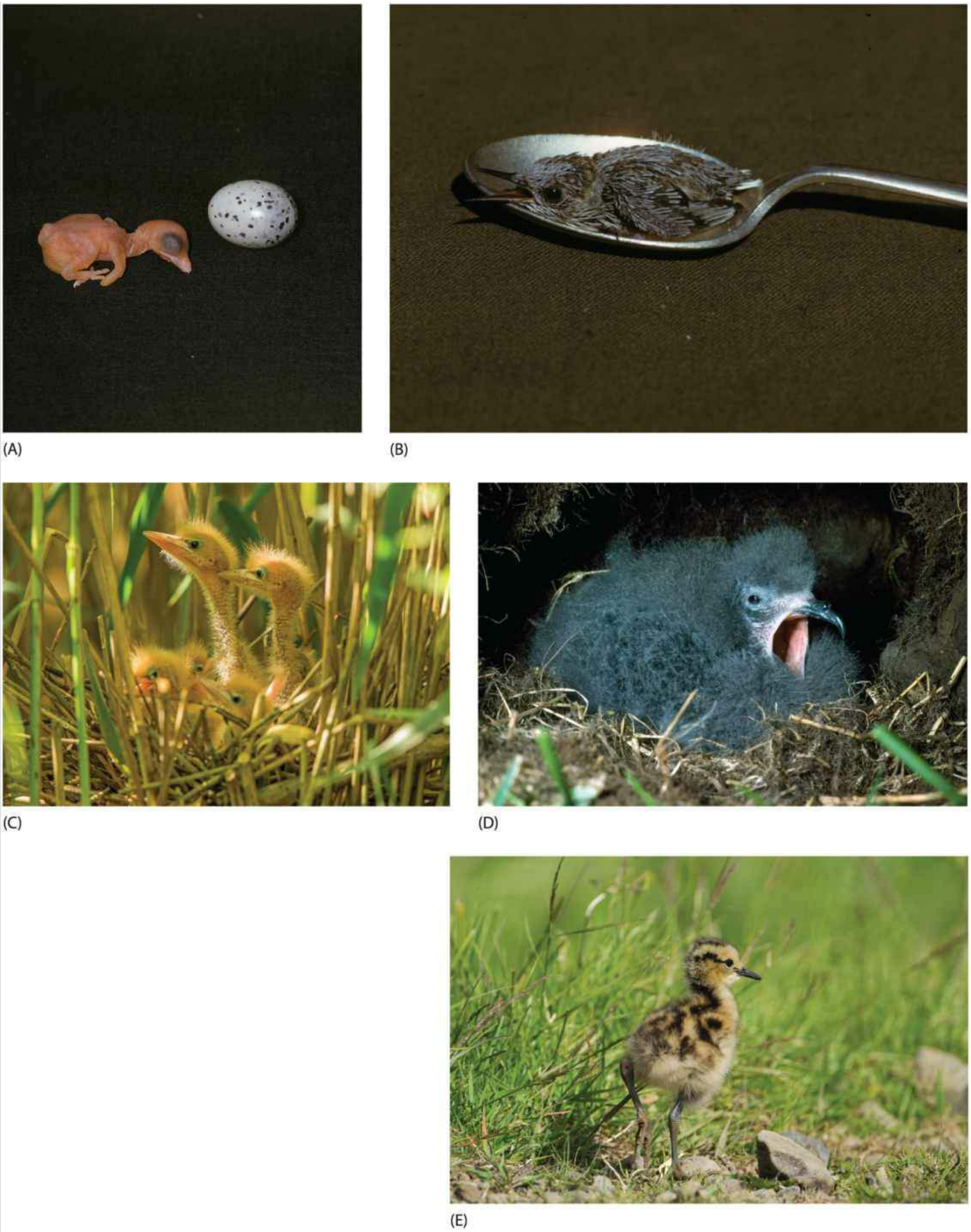
Table 16–1 *Comparison of Altricial and Precocial Modes of Development*

Character	Altricial	Precocial
Eyes at hatching	Closed	Open
Down	Absent or sparse	Present

Mobility	Immobile	Mobile
Parental care	Essential	Minimal
Nourishment	Parents	Self-feeding
Egg size	Small (4%–10%)[a]	Large (9%–21%)[a]
Egg yolks	Small	Large
Brain size	Small (3%)[a]	Large (4%–7%)[a]
Small intestine	Large (10.3%–14.5%)[a]	Small (6.5%–10.5%)[a]
Growth rate	Fast (3–4 times precocial rate)	Slow

[a] Brain size at hatching as a percentage of adult weight.

Altricial birds are naked, blind, and virtually immobile when they hatch. They stay in the nest (are **nidicolous**) and depend on their parents for food (Figure 16–2A–C). The helpless, grublike nestlings of altricial birds look as if they have hatched prematurely. Altricial hatchlings have huge bellies and large viscera that support fast growth.



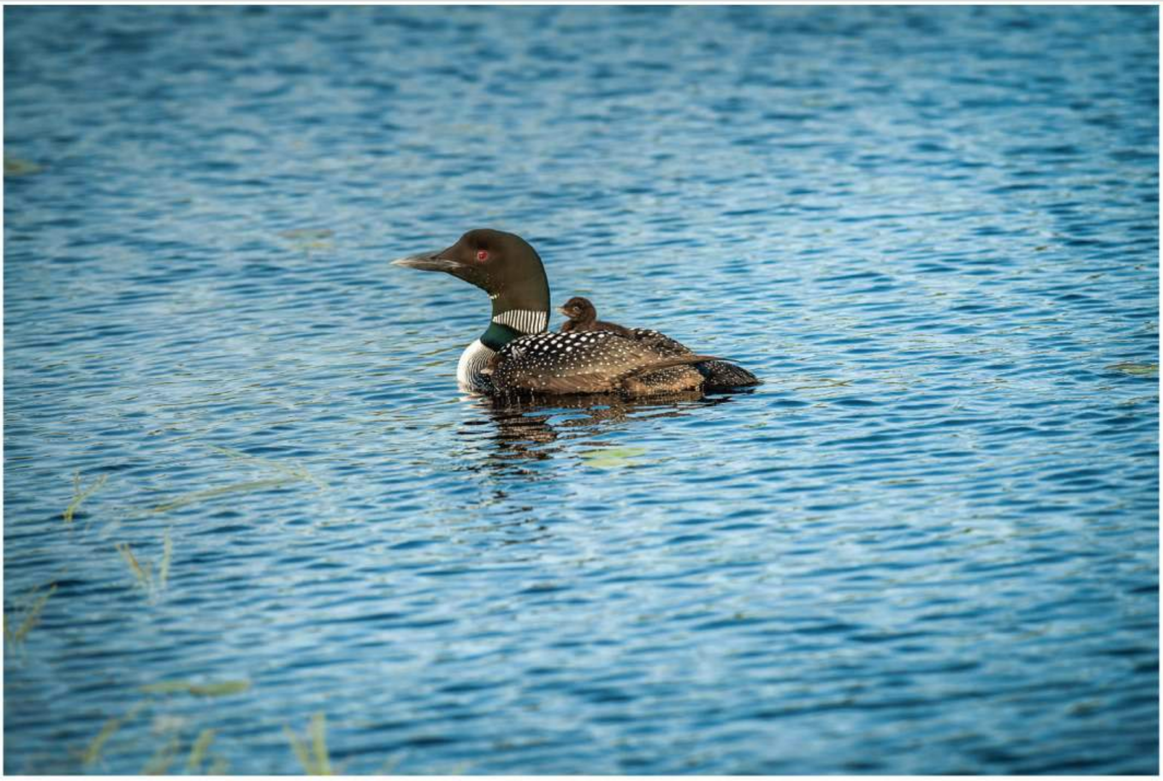
(A, B) © O. Pettingill, Jr./VIREO. (C) A. Hartl/AGE Fotostock. (D) © Richard Vaughn/ardea.com/AGE Fotostock. (E) Astrid Kant/AGE Fotostock.

Figure 16–2 Baby birds and their state of development at hatching: (A) Cedar Waxwing, altricial; (B) Ruby-throated Hummingbird, altricial; (C) Little Bittern, semialtricial; (D) Leach’s Storm Petrel, semiprecocial; and (E) Whimbrel, precocial.

Compared with altricial chicks, **precocial** chicks hatch from larger eggs in a relatively advanced physical state and are soon mobile. Precocial chicks are usually covered with fuzzy natal down. They leave the nest (are **nidifugous**), run about, feed themselves, and regulate their body temperature soon after they hatch (Figure 16–2D, E). A three-day-old Lesser Scaup duckling, for example, can dive, catch a minnow, and return to the surface. Precocial chicks have large food stores that increase their initial chances of survival outside the egg. They absorb their substantial yolk reserves as a supplement to their feeding for several days after hatching.

Precocial development was the original mode among birds. It is typical of many basal groups of modern birds, including the ratites, waterfowl, and chickenlike birds. The ancient enantiornithine birds of the Mesozoic era also were precocial: a well-preserved avian embryo (in egg) from the Lower Cretaceous of China was distinctly feathered and precocial in its state of development (Zhou and Zhang 2004).

How did altricial development evolve? There is no simple evolutionary sequence from precocial to altricial. The altricial condition evolved independently in unrelated groups of birds. Although most birds are clearly precocial or altricial, intermediate categories also exist. The diversity of hatchling abilities sorts into at least six major categories of hatchlings based on classical criteria of mobility, open or closed eyes, the presence or absence of down, and the extent of parental care (Box 16–1; see Table 16–1). Semiprecocial chicks of gulls, terns, auks, and petrels are fed at the nest. The subprecocial chicks of grebes and loons cannot dive or chase prey skillfully. Their parents carry them on their backs, often under their wings, and so dive and feed relatively undisturbed (Figure 16–3). Semialtricial or semiprecocial modes of development evolved secondarily from altricial or precocial modes of development.



BARRY SPRUCE PHOTOGRAPHY

Figure 16–3 Adult Common Loon carrying subprecocial young on its back.

Box 16–1

Development Categories of Hatchlings

Ornithologists recognize six development categories of hatchlings:

Superprecocial Wholly independent. Examples: mound builders and Black-headed Ducks

Precocial Hatchlings leave the nest immediately (nidifugous) and follow their parents; pick up their own food soon after hatching, although parents help to locate food. Examples: ducks and shorebirds; quail, grouse, and murrelets; also ostriches and kiwis

Subprecocial Hatchlings leave the nest immediately and follow their parents; are fed directly by their parents. Examples: rails, grebes, cranes, and loons; also guans and some pheasants

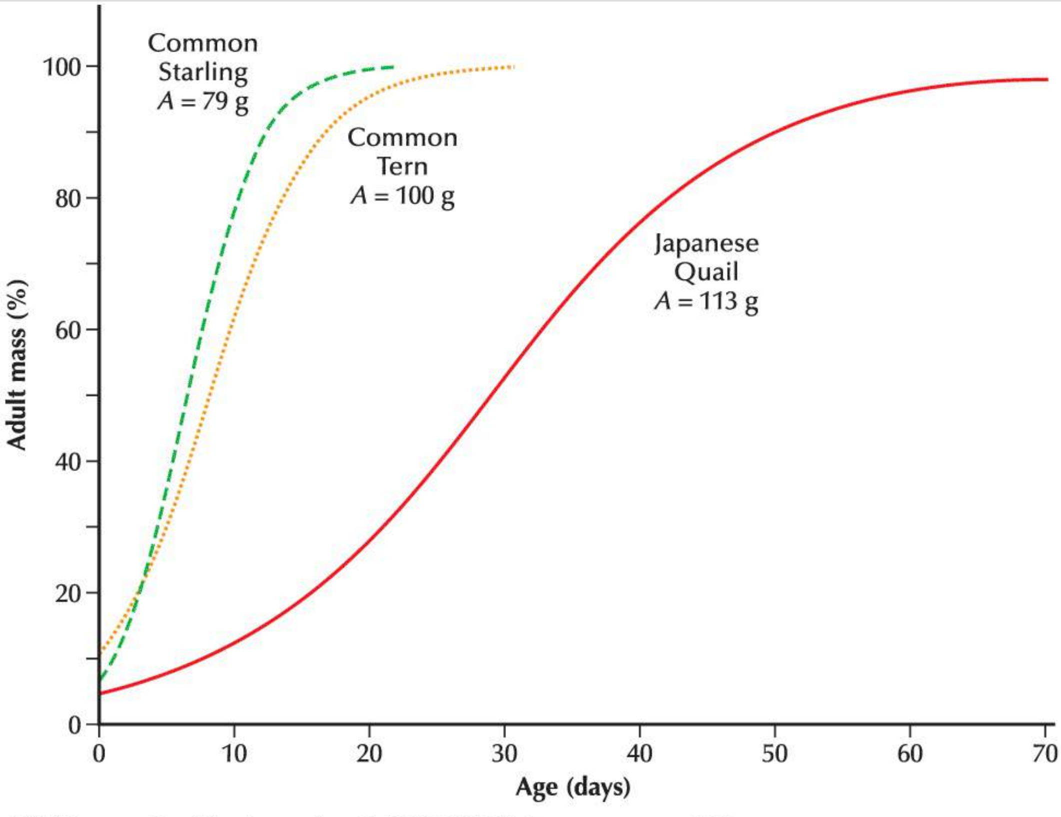
Semiprecocial Hatchlings are capable of body-temperature regulation; mobile but stay in the nest; fed by their parents. Examples: gulls, terns, auks, petrels, and penguins

Semialtricial Hatchlings stay in the nest (nidicolous), although physically able to leave the nest within a few hours or the first day; fed and brooded by parents. Examples: herons and hawks; also nightjars, albatrosses, and seriemas

Altricial Naked, blind, and helpless at hatching. Examples: songbirds, woodpeckers, hummingbirds, swifts, trogons, kingfishers, pigeons, and parrots

Rapid growth is a primary feature of altricial development and perhaps its driving evolutionary advantage. Altricial nestlings grow three to four times faster than precocial chicks. The evolution of such different growth rates is a major research topic. Although energetic efficiencies contribute to the fast growth rates of altricial birds, they cannot explain the difference in growth rates between altricial and precocial birds (Ricklefs 1983).

Instead, growth-rate differences between precocial and altricial chicks channel limited resources into either increased tissue mass or into the maturation of tissue functions required for survival (Ricklefs and Starck 1998b). The so-called **tissue-allocation hypothesis** suggests that the growth of tissue mass and the maturation of tissue functions (such as muscle contraction) are mutually exclusive. Altricial chicks grow fast by channeling resources efficiently into growth and by postponing tissue maturation. Fast growth rates enable them to pass quickly through the early, most vulnerable stages of development. A comparison of the altricial Common Starling, the semiprecocial Common Tern, and the precocial Japanese Quail illustrates the interaction between the precocity of tissue maturation and the overall growth rate (Figure 16–4).



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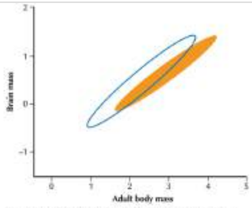
Data from Ricklefs 1979

Figure 16–4 Growth curves for an altricial bird (Common Starling), a semiprecocial bird (Common Tern), and a precocial bird (Japanese Quail). *A* is the bird's mass at the top of the growth curve. Of these three species, the starling grows fastest, the tern grows nearly as fast as the starling, and the quail grows relatively slowly. The rapid maturation of the quail's large leg muscles, essential for precocial locomotion, detracts from the quail chick's potential growth rate. The tern's legs also develop rapidly, but the material and energy needed for the growth of its tiny legs are only minor investments relative to its overall growth. The starling puts energy into growth before tissue maturation.

The different modes of development correspond to progressively mature functions of chicks at hatching. Increasing maturity is evident in the tissues of a hatchling as well as in its external appearance and behavior. The fraction of tissue that is fat free and dry, called its lean dry weight, increases as tissue matures. A low index of tissue maturity at hatching distinguishes altricial development from all other modes.

Also related to the trade-off between tissue growth on one hand and maturity of function on the other hand is the increased reliance of altricial species on the wings, or forelimbs, for locomotion (Dial 2003b; see Figure 16–1). Precocial chicks have well-developed legs when they hatch, enabling them to leave the nest, start to find food for themselves, and hide from predators. Precocial species also emphasize bipedal locomotion as adults. In contrast, the initial dependence of immobile altricial hatchlings on their parents corresponds directly to these species' predominant use of their wings rather than their legs. Altricial chicks first delay the maturation of wings and flight muscles, and then they channel resources into their development. Swifts and hummingbirds, with their advanced flight abilities but diminutive legs and feet, represent the extreme of this shift of emphasis to forelimb locomotion.

Differences in brain development are another distinction between



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Data from Ricklefs and Starck 1998b

Figure 16–5 Logarithmic relation of brain size to adult body size. The brains of altricial species and semialtricial species (white oval with blue outline) average larger than the brains of precocial bird species (orange oval).

altricial and precocial bird species (Figure 16–5). In general, the brains of altricial birds are smaller (relative to body size) at hatching than are the brains of precocial birds. Parental care of altricial chicks substitutes for early functional differentiation of the brain. After hatching, the brains of altricial birds then undergo greater growth to an adult brain size that ultimately averages larger than that of precocial species of the same body size. This growth pattern allows the control functions of their enlarged forebrains to differentiate at a later stage than they do in the brains of precocial birds. Accordingly, altricial chicks learn active feeding skills and social skills at a later stage of development.

Temperature Regulation

Homeothermy—the ability to generate metabolic heat (**endothermy**) and to maintain a high, constant body temperature—is a major step of early development. Homeothermy releases a chick from its absolute dependence on parental brooding and enables it to tolerate exposure.

The process of hatching initiates the development of homeothermy as hatchlings undergo rapid changes in their metabolism and temperature responses. Pipping through the shell membranes gives a chick access to oxygen, which supports increased metabolism. Emergence from the shell itself allows increased movement as well as ventilation and shivering. Once out, the chick's down dries to form functional insulation. The stage is then set for the development of endothermy and the refinement of homeothermic thermoregulation through the maturation of muscular tissue and endocrine control systems. The advanced muscle development and natal down of hatchling precocial birds enhances their ability to thermoregulate. Precocial and semiprecocial chicks, such as those of quail, gulls, and terns, achieve 90 percent of their adult thermoregulatory capability within one week (Dawson and Whittow 2000).

Regulation of temperature by both precocial and altricial chicks improves in the course of development as they gain mass relative to surface area, increase metabolic heat production, and develop improved control by the nervous and endocrine systems. An altricial chick's ability to retain metabolic heat improves later as its feather coat thickens. Experimental shaving of nestling Great Tits and Eurasian Pied Flycatchers, for example, increases their oxygen consumption by 25 and 15 percent, respectively (Shilov 1973).

Skeletal muscle activity is the main source of heat production. The large leg muscles of a young precocial chick are of primary importance in early thermogenesis, followed by the pectoral muscles. Early development of large pectoral muscles in chicks of the Willow Ptarmigan and Leach's Storm Petrel facilitates their heat production (Aulie 1976; Ricklefs et al. 1980). Supporting their function in early thermogenesis, the pectoral muscles of nestling Leach's Storm Petrels mature by two weeks of age, even though the chicks do not fly for nine to 10 weeks. The naked hatchlings of altricial songbirds with little skeletal muscle cannot regulate their body temperatures outside ambient temperatures of 35°C to 40°C. They take a week to develop just the initial stages of thermogenesis by shivering.

Energy and Nutrition

Baby birds require energy for maintenance, temperature regulation, activity, excretion, and growth. Growth itself accounts for a major fraction of total energy expenditures early in development. The energy channeled into growth constitutes from roughly 21 to 40 percent of a chick’s energy budget for the entire developmental period. Total energy expenditures peak late in development. Important as it is, however, energy may be less important in determining rates and patterns of development than is nutrition. There are no fundamental distinctions between altricial and precocial species in this regard.

The production of new tissues requires nutrients such as certain amino acids that the body cannot manufacture. The sulfur-containing amino acids cysteine and methionine, for example, are essential for feather keratin production. To provide the calcium for bone growth, parents feed their chicks fragments of teeth, bone, snail shells, and eggshells as dietary supplements. The bone growth of Lapland Longspurs, for example, requires more than the meager amount of calcium (0.1 percent by dry weight) in the crane flies and sawflies that they eat. Accordingly, their parents feed them lemming bones and teeth (Seastedt and Maclean 1977).

Chicks also require lots of protein, especially in the early stages of their development. The parents of many species of songbirds supply mostly small, soft-bodied insects at first, especially spiders, caterpillars, and katydids (in the tropics), and then increase the proportion of fruits and seeds. But fruits alone do not usually provide an adequate diet for nestling growth (Foster 1978). The chicks of Bearded Bellbirds, which eat only fruits, grow half as fast as those of other tropical birds. The Resplendent Quetzal, a spectacular fruit eater, feeds its young only insects for the first 10 days to support a more normal growth rate.

Pigeons, flamingos, and Emperor Penguins feed nutritious esophageal fluids to their young (Table 16–2). Pigeon milk, the best known of these fluids, is full of fat-laden cells sloughed off the epithelial lining of the parent’s crop. Like the milk of marine mammals, this fluid is rich in protein (23 percent) and fat (10 percent). It also includes essential amino acids. Flamingo milk, the sole initial source of nutrition for the chicks of Greater Flamingos, has more fat and less protein than does pigeon milk. The esophageal fluid of the Emperor Penguin is rich in both fat and protein, and their chicks double their body weight in the first week of life (Figure 16–6).

Table 16–2 *Nutritional Composition of Avian Esophageal Fluids*

Bird	**Protein (%)**	**Lipid (%)**	**Carbohydrates (%)**
Pigeon	23	10	0.0
Flamingo	8	18	0.2

Penguin	59	29	5.5

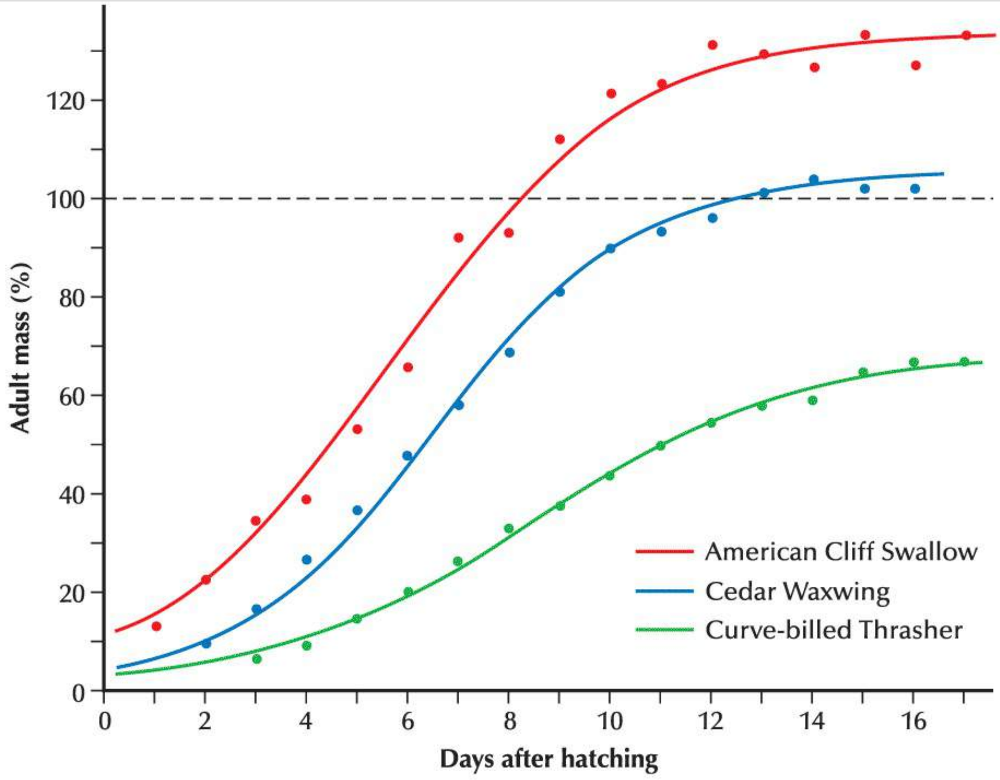
DATA FROM FISHER 1972.

ROGER CLARK/ALAMY

Figure 16–6 Emperor Penguin chicks double their body weight on an initial diet of rich esophageal fluid from their parents.

Growth Rates

The growth of body mass of a baby bird during development follows an S-shaped curve, or **sigmoid curve** (Figure 16–7). At first, the chick grows slowly, then the growth rate accelerates, and mass increases rapidly. Finally, growth slows as the chick approaches its adult weight. The sigmoid curve allows a comparison of species that differ in size and growth strategies because it is defined mathematically by only a few variables: initial size, growth rate, and final maximum value.



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Data from Ricklefs 1968

Figure 16–7 Sigmoid nestling growth curves of three altricial birds: the American Cliff Swallow, the Cedar Waxwing, and the Curve-billed Thrasher. Data are standardized to the maximum values of the growth curve to directly compare birds of different species size.

The growth rates of chicks of different bird species vary 30-fold. More than half of the variation in growth rate relates directly to adult body weight: big birds grow more slowly than little birds. The growth rate decreases roughly as the cube root of adult body weight increases. The slow-growing Wandering Albatross (Figure 17–3B), one of the largest seabirds, has the longest-known nestling period of any bird—as long as 303 days. They have long waits for meals from parents that return from great distances. In contrast, fast-growing small songbirds have short nestling periods of 10 to 12 days.

Growth rates of individual birds in a species are affected by the quality and quantity of food, temporal pattern of feeding, and temperature, all of which vary according to locality, season, habitat, and weather. For example, the average fledging weights of Rhinoceros Auklets in British Columbia vary from 266 grams in bad years to 361 grams in good years (Gaston and Dechesne 1996). The effects of food supply on growth rate are perhaps best known in swifts and martins. The maturation of Common Swifts, for example, varies from 37 to 56 days, depending on feeding conditions. Chicks of these swifts can survive for as long as 21 days of starvation by becoming hypothermic and ceasing to grow (Koskimies 1948).

Chicks of some bird species store excess energy as fat as insurance against poor food delivery by parents or as reserves for the days just after fledging when the chick learns to feed itself (Box 16–2). Aerial passerines, such as swallows, deposit more fat than do other species as insurance to the irregularity of their food supply (O’Connor 1977). The accumulation of fat is most striking in petrels. Their obese chicks reach masses twice those of the adults.

Box 16–2

Obesity for a Purpose

Young Oilbirds raised on the oily lipid-rich fruits of palms and other tropical trees accumulate large lipid stores. These stores are mostly excess energy that must be sidelined and stored in order for the chicks to extract adequate amounts of protein from their specialized, protein-poor and lipid-rich foods. Such excess lipid supplies also act as reserves for bad times.

RICK & NORA BOWERS/AGEFOTOSTOCK

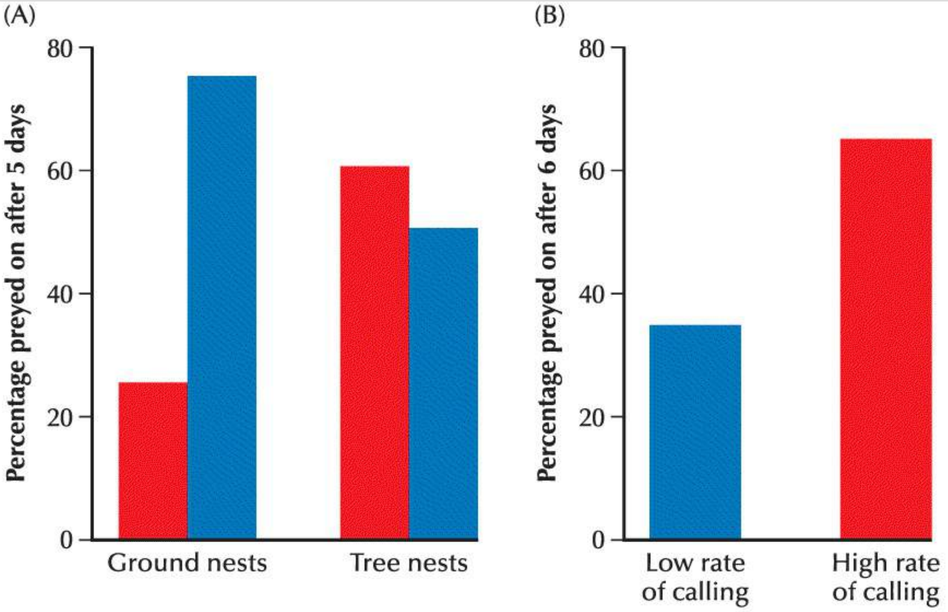
Baby Oilbirds at their cave ledge nest await the return of their parents.

16.2 Begging for Food

Hungry nestling birds make their needs known through begging behavior, which includes both exaggerated body movements and loud calls. The young's begging cries stimulate parents to deliver food to the nest. Experimental changes in the volume and continuity of begging cries at the nest prompt greater activity. In a classic experiment, Lars von Haartman (1953) hid extra young Eurasian Pied Flycatchers behind the wall of a nest box. In response to their cries, the parents brought more food to the nest than was required for their nestlings. Recall also the simulation of host warbler calls by nestling cuckoos (see Chapter 14). Blue Tit parents immediately reduce their provisioning efforts when the chicks do not beg (Grieco 2001). As soon as the chicks resume their begging, the parents resume their normal provisioning effort.

Siblings coordinate their begging behavior to their own benefit. Nestling Black-headed Gulls, for example, extract more regurgitated food from their parents by begging together (Mathevon and Charrier 2004). Parent gulls react to the total intensity of begging rather than to the chick that is begging the loudest. Compared with single chicks, three siblings beg less often and not separately. They save their begging for an intense joint bout for a returning parent, which then dumps a full load of food on the ground in front of the chicks.

Birds at a nest, whether parents or young, risk discovery and death from predators. That risk increases with activity at the nest (see Chapter 15). Under discussion for years has been whether begging calls themselves attract predators to the nest. They do, at least for ground-nesting species (Figure 16–8). In a clever experiment, David Haskell (1994) monitored predation rates at artificial nests outfitted with miniature two-way radios that broadcast begging calls (of Western Bluebirds) or that were silent. Predators found most (75 percent) ground nests with begging calls within five days but found significantly fewer (23 percent) of the silent ground nests. In a second experiment, predators found significantly more of the ground nests that broadcast begging calls at a high rate compared with a low rate.



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DATA FROM HASKELL 1994

Figure 16–8 Begging calls by nestlings increase predation. (A) Predators found most artificial ground nests with begging calls (blue bars) within five days, but they found significantly fewer of the silent ground nests (red bars). Tree nests with or without begging calls did not differ in the risk of predation. (B) Predators found significantly more of the artificial ground nests that broadcast begging calls at a high rate (red bar) compared with a low rate (blue bar).

Counteracting the increased risk of predation due to begging calls, many nestling birds scream loudly. These screams frighten an approaching predator, incite parents to come to the rescue, and stimulate nest mates to flee or hide (Roulin 2001). Nestlings of screaming species also have more conspicuous begging calls than do nestlings of nonscreaming species—which strongly suggests that screaming evolved as an antipredator strategy. Higher predation rates have favored the addition of screaming to their survival kit.

The gaping mouths of nestlings serve as visual stimuli that facilitate or, in some instances, allow food delivery by the parents (see Figure 14–6). The chicks of some cavity-nesting species have brightly colored mouth markings that attract parental attention and serve as targets for food delivery. The mouth colors of nestling Great Tits, for example, make them easier for their parents to detect in dark nest cavities and hence affect the rate at which their parents feed them. Nestlings with (painted) yellow mouth gapes and side flanges are fed more frequently than are nest mates with (painted) red gapes and flanges, but only at low light intensities (Heeb et al. 2003). In well-illuminated nest cavities, there is no difference between red- and yellow-painted nestlings.

Mimicry of the color pattern and behavior of caterpillars is perhaps one of the most unusual known defense adaptations of nestling birds (Londoño et al. 2015). Specifically, the bright orange color and white filoplumes of the nestlings of the Cinereous Mourner of Amazonia resemble the warning colors of toxic hairy caterpillars. At six days of age, when disturbed, the nestlings move their heads slowly from side to side in a caterpillarlike motion. The slow growth rate of these nestlings combined with high rates of predation favor their extreme defense system.

16.3 Sibling Rivalry

Growth rates of altricial nestlings tend to decrease as brood size increases. The smallest chicks starve when food is insufficient. These observations suggest that parents cannot deliver enough food to all nestlings to ensure the maximum growth and survival of all. For this reason, nest mates compete with one another for food. In its extreme form, competition among nest mates results in death or **siblicide.**

Vicious rivalry seems to be normal among the chicks of some birds, especially if the eggs hatch at staggered intervals. A small delay in hatching time places a younger chick at a competitive disadvantage with respect to its nest mates, particularly when food is in short supply (Box 16–3). Larger siblings tend to bully their nest mates to get the first choice of food delivered by their parents. For example, the younger of two South Polar Skua siblings has a good chance of surviving if it is nearly the same size as the older chick, but it has a poor chance of survival if it is only eight grams (10 percent) lighter than its older nest mate (Procter 1975).

Box 16–3

Laughing Kookaburras: Last to Hatch Loses

The Laughing Kookaburra is the source of a famous laughing call heard in the background of many old movies. This large, terrestrial Australian kingfisher typically lays three eggs, but the third chick to hatch often doesn’t survive to leave the nest (Legge 2002). Typically, its older two siblings kill it within a few days of hatching. They do so aggressively—tearing it apart with a specialized siblicide hook on their upper bills. Those that survive the physical abuse of their first days are then likely to starve to death in the weeks that follow as competition for food increases.

(A) © NHPA/Photoshot/Avalon. (B) John Carnemolla/Getty Images

Kookaburra (A) nestlings and (B) juveniles.

The probability of being torn apart by older brothers and sisters depends on the intensity of their own aggression toward one another. That intensity is greatest when the two older siblings are opposite sexes of similar size with the male hatching first. They fight with each other, hurting the third sibling in the process, especially if it is much smaller. Extra male helpers tend to reduce strife by increasing food deliveries to the nest. Their absence adds to what Sarah Legge has dubbed the “kookaburra siblicide syndrome.” Getting rid of junior early has a significant effect on the growth and health of the senior brood mates. Those that kill their youngest nest mate attain higher final weight, larger skeletons, and better feather development than do those that let junior starve to death. These attributes lead to better survival and more likely recruitment into the breeding population in future years.

Different egg provisions can offset the disadvantages of being last to hatch when there are sibling rivalries (see Box 12–1). In particular, mothers of some species add more testosterone (androgen) successively to later eggs of a clutch. The experimental addition of testosterone to eggs of Black-headed Gulls demonstrates this effect (Eising and Groothuis 2003). Chicks hatched from eggs with extra testosterone are initially more active and beg more frequently, thereby getting a larger share of the food than chicks from control eggs.

Siblicide is a standard practice in the nests of some eagles, skuas, herons, and boobies (Mock and Parker 1997). As a rule, parents react passively to the deeply rooted, destructive behavior of their offspring. In the well-studied Verreaux’s Eagle, for example, only once in 200 records did both siblings survive to the fledging stage. In most cases, the older sibling deliberately killed the younger eaglet (Gargett 1978).

Many raptors exhibit reversed sexual-size dimorphism; that is, males are smaller than females. Why should this reversal be so? The topic has been discussed without consensus. Keith Bildstein (1992) shifted the focus of discussions on the roles of adult raptors to the possible advantages of smaller-sized male nestlings. His **head start hypothesis** is based on observations of fledgling Northern Harriers, in which males develop faster and leave the nest earlier than their sisters. They gain flight and hunting experience ahead of their sisters and so hone skills that they will need as the primary provisioner of food to their mates and young. They are also less likely to overpower and injure their sisters by being smaller and leaving the nest early. The survival of sisters then adds to a young male’s inclusive fitness.

Sibling rivalry is a way of life in some colonial herons (Mock 1984). Elder chicks of the Great Egret often kill their siblings, but siblicide is rare in the Great Blue Heron. Why should two such similar species differ in this way? The type of food brought by the parents to their nestlings is part of the answer. Great Egrets bring small fish, which are easily monopolized by an aggressive older sibling, whereas

Figure 16–9 Great Blue Heron. In this species, parents bring their chicks large fish, which are not easy for individual chicks to monopolize.

Great Blue Herons bring larger fish, which cannot be easily monopolized (Figure 16–9). When placed in Great Egret nests, young Great Blue Heron broods adopt the siblicidal tactics typical of the egret, in response, it seems, to the opportunities presented by the smaller food (Table 16–3). Surprisingly, the converse result does not take place. Great Egret broods cross-fostered in Great Blue Heron nests do not become more tolerant of their nest mates. Sibling aggression in the Great Egret is a deep-seated, obligatory behavior similar to that of raptors.

Table 16–3 *Fate of the Youngest Chick in Natural and Experimental Foster Broods*

Brood[a]	**Number Alive by Day 25**	**Number of Siblicidal Deaths**	**Number of Other Deaths**	**Number of Broods Studied**[b]
Great Egret chicks				
Natural	5	8	4	17
Foster	4	6	0	10
Great Blue Heron chicks				
Natural	8	1	10	19
Foster	1	6	2	9

[a] Natural broods were raised by parents of the same species. Foster broods were experimentally switched so that they were raised by parents of the other species; for example, foster Great Egret chicks were raised by Great Blue Heron parents.

[b] Typical brood size in all cases was three or four chicks.

DATA FROM MOCK (1984).

Location, location, location: a nestling's position in the (open-cup) nest affects whether the nestling is fed by its parents. The center of the nest is best (Ostreiher 2001). When deprived of food, first-hatched nestling Arabian Babblers take over and control that prime spot to preempt incoming food. Eliminating the central spot with a barrier evens the odds of feeding for all nestlings. When the parent babblers access the nest from only one direction, dictated by experimental fencing, the senior nestling takes over the prime (nearest) location and garners 52 percent of all feedings.

Rather than compete for food, Barn Owl chicks queue up and minimize competition by using begging calls to communicate with one another for position when their parents are away hunting for the next mouse (Roulin et al. 2000). One mouse for a chosen chick per visit is the routine. Chicks in small broods become more vocal after being fed, but in larger broods, they quiet down in the absence of a parent. The hungriest chick then tunes up and gets first rights to the next mouse.

16.4 Parenting

Raising young is one of the most energetically expensive periods of a bird's annual cycle. Peak breeding activity, for example, increases total daily energy expenditures by as much as 50 percent. Rearing chicks consumes 31 percent of an adult Little Penguin's total annual expenditures of energy (Gales and Green 1990). Daily food consumption by hardworking penguins exceeds 60 percent of their body mass when the chicks reach full size. The high costs of parenting cause females of many bird species to lose body mass in the first days of the nestling period. The fueling of these extra costs, therefore, requires some combination of increased foraging time for food supplies, the use of accumulated reserves, or help by mates or fully grown offspring.

In their first week of life, most baby birds need protection from extreme temperatures and from predators. Parents routinely brood their young by sitting on them, usually in the nest. Brooding parents not only protect their young from the rain and predators but also keep them warm. Parents of seabird chicks shade them from the hot sun (Figure 16–10). Protecting young from predators also requires constant parental vigilance. Males and females of four species of large plovers called lapwings, for example, face major time constraints while taking care of their mobile young. They alternate "tending" behavior in order to feed themselves (Walters 1982).

(A) © Claudio Contreras/naturepl.com. (B) Roberta Olenick/Getty Images

Figure 16–10 Thermoregulation of nestlings. (A) Heermann’s Gulls tend to their young in the hot desert sun. (B) Laysan Albatross chicks can thermoregulate at an early age by dissipating excess heat from their large feet, which they expose to the breeze by leaning back on their ankles. Still, dehydration and poor thermoregulation are the primary causes of death among young Laysan Albatross chicks on Midway Island in the Pacific Ocean.

The stresses of parental care also affect the immune systems of breeding birds, mediated by glucocorticosteroid stress hormones (see section 9.3). Recall that prolonged surges of stress hormones dampen a bird’s immune response, making it more susceptible to disease and parasites. Increasing parental care by male Barn Swallows by manipulating brood sizes, for example, reduces their immune response (Saino et al. 2002c).

Parent birds can manage the trade-offs between parental care and self-maintenance. The time spent by female House Sparrows in brooding their young nestlings decreases as brood size increases

(Chastel and Kersten 2002). Smaller broods produce less total heat and lose heat faster than larger broods do. As a result, females tending experimentally reduced broods experience a sharp drop in body condition when their young hatch and when brooding is most intensive. In contrast, females tending experimentally enlarged broods lose weight only gradually during the nestling period. Males are not affected because they spend much less time brooding (about one-third of that spent by females) and thus have ample time to take care of themselves.

A parent's options for adjusting its investments also include choosing among rival nestlings, reducing risks of nest predation, favoring one sex over the other, and even sacrificing some of their young if necessary. Usually, the largest nestling or the biggest mouth seems to get most of the food (Box 16–4). Favoritism actually starts with different provisioning of the eggs and then extends to begging nestlings of different ages or at different stages of development (Lessells 2002).

Box 16–4

Feeding Nestlings

How do nestlings get fed? Altricial nestlings receive food by direct insertion, sometimes deeply into the digestive tract. Young hummingbirds receive an injection of nectar and insects through their mother's long, hypodermic-like bill (see photographs (C) and (D)). Commonly among seabirds, parents regurgitate a meal either directly into a nestling's mouth or onto the ground for the nestling to pick up. Young penguins and pelicans plunge their heads deeply into their parents' gullets. Spoonbills and albatrosses cross their large bills with those of their young, like two pairs of open scissors, so that the chicks' mouths are in position for food transfer.

How often do parents feed their nestlings? Food delivery rates to nestlings range from every second or third day for albatrosses to once or twice daily for seabirds, swifts, and large raptors to once per minute for some small land birds with large broods. Normal rates of food delivery by small- and medium-sized land birds average from four to 12 times per hour. Trogons bring food to the nest once per hour, Bald Eagles four to five times per day, and Barn Owls 10 times a night. Recorded extremes of rapid food delivery to large broods include 990 trips per day by the Great Tit and 491 trips per day by the House Wren.

Food delivery rates vary according to the age of the young. Hatchlings require only small amounts of food but, as they develop, their appetites grow. The Eurasian Pied Flycatcher brings food to the nest every two minutes, making about 6,200 feeding trips to nourish its young from hatching to fledging. In general, parents must gather two to three times as much food as they need for themselves to cover the energy needs of their nestlings (Walsberg 1983). To meet such demands, the Common Swift of Europe flies 1,000 kilometers a day, scooping insects from the sky.

(A) Per-Gunnar Ostby/Oxford Scientific/Getty Images. (B) Arthur Morris/Corbis Documentary/Getty Images. (C) © W. Greene/VIREO. (D) William Leaman/Alamy stockphoto

Parent birds feeding young: (A) Anhinga young begging for food, (B) parent Anhinga feeding one of the young, (C) Ruby-throated Hummingbird nestlings begging for food, and (D) parent hummingbird feeding one of the nestlings.

Females of some species prefer to feed runt nestlings (Gottlander 1987). American Coots favor not only the smaller, late-hatched chicks in their broods but also the chicks that are most colorful. In their natal plumage, these coot chicks sport bright orange, waxy-tipped filaments on the front half of the body, enhanced by brilliant red papillae of the skin around the eyes and base of the bill. Lacking the cryptic downy colorations of most precocial chicks, conspicuous coot chicks actually hide their heads when parents give alarm calls, doing their best to prevent detection by predators. Bruce Lyon and his colleagues (1994) trimmed back the orange plumes of some coot chicks and compared parental attention to them with that paid to control chicks in mixed broods. Parents favored the more brightly colored control chicks, which grew faster and survived better than their trimmed experimental brood mates.

What is best for a parent often conflicts with what is best for some of the offspring. First and foremost, parents should value their own survival over that of their offspring, particularly for species with high annual survival and few chicks per nest. That is, we would expect parental risk taking to be sensitive to life expectancy. We would expect long-lived species, which can nest repeatedly in the future, to take fewer risks than short-lived species, which have limited opportunities to nest.

Supporting this prediction are comparisons of matched pairs of species from Argentina (which have higher adult survival and a smaller clutch size) and from Arizona (which have lower adult survival and a larger clutch size). To assess risk to the nestlings, Cameron Ghalambor and colleagues (2001, 2013) recorded the rate at which parents fed them in the presence of a model of a nest predator (jay). To assess risk to the parents themselves, they recorded the parents’ own feeding rates in the presence of a hawk. As predicted, southern (Argentine) parents took less personal risk than northern (Arizona) parents, even if by taking less risk they sacrificed their young. Conversely, northern (Arizona) parents assumed greater personal risk to increase the probability that their young would survive.

Underlying what may seem to be their spirited and cooperative parental effort, the sexes themselves may have different agendas and different best levels of investment of their time and energy. The parental tactics of differently colored male House Finches correlate with alternative breeding strategies (Duckworth et al. 2003). Bright red males (with low prolactin levels) provide almost no parental care, whereas dull-colored males (with high prolactin levels) actively participate in the feeding of nestlings. By holding back on parental care, bright red males are less likely to die after the breeding season than are dull males. But the dull males achieve higher pairing success that compensates for their higher mortality. Apparently, females prefer males that help, leaving males with the “choice” between being a good dad now or living longer and breeding more times.

In general, the costs of parental care are less when rearing offspring of different ages than when raising offspring that are the same age. It’s easier to raise children spaced apart at different ages than it is to raise twins or triplets. Nevertheless, female Blue Tits do better and survive better to the next breeding season when they care for same-age (hatched synchronously) broods of young than when they care for young of different ages, experimentally produced by hatching them asynchronously (Slagsvold et al. 1994).

Male Blue Tits fare oppositely. They survive better when parenting asynchronous broods than when parenting synchronous broods. The reason? Synchronous broods stimulate males to higher rates of provisioning effort at a cost to their survival. A female gains from this extra effort on the male’s part by coasting a bit more and reducing her own effort, with the result that females survive better. Female Blue Tits usually win this contest in nature because they alone incubate the eggs. They don’t start incubation until most of the eggs are laid and so will hatch them all at the same time.

Sexes of the Blue Tit on the island of Corsica also respond differently to their parental challenges—in this case, to infestations of blowflies that parasitize their nestlings (Hurtrez-Boussès et al. 2000; Banbura et al. 2001). In addition to feeding the young, females do almost all of the nest sanitation. They remove maggots, mend the nest, and remove fecal sacs (see section 15.1). The time spent by females on nest sanitation is higher in parasitized nests than in (experimentally) deparasitized ones. Males, however, just remove fecal sacs. Instead of spending time on nest sanitation, males concentrate instead on finding the best food for the nestlings—caterpillars. As a result, males deliver more and larger caterpillars than do females (Figure 16–11).

Morales/AGE Fotostock

Figure 16–11 Adult Blue Tit feeding its young.

Caterpillars are a prime food for the development of nestling Blue Tits and many other species. They are also a source of carotenoid pigments responsible for the yellow plumage color of adult Blue Tits. How bright yellow an adult is indicates its ability to find caterpillars and thus how good a parent it will be. Experiments have supported this prediction. Cross-fostered nestlings developed best when fed by stepfathers having brighter yellow plumage (Senar et al. 2002).

Sex Ratios of Offspring

Broods of nestlings don’t always yield equal numbers of males and females. Many departures from a 50:50 ratio of males and females in broods of birds are due to differences in the survival of male and female hatchlings. Brood sex ratios of the Red-winged Blackbird, for example, depend on the age of the breeding female. Young females fledge more daughters than sons, whereas old females fledge more sons than daughters. Although equal numbers of sons and daughters hatch in the broods of young females, starvation is common, and sons starve more often than daughters. Why? Young females lay poorly provisioned final eggs in the clutch, which causes the nestlings hatched from them to be most vulnerable to starvation. Young females also tend to lack the experience required to feed their nestlings adequately. A sex bias exists in the probability of starvation because male offspring need more food than their sisters do. They grow faster to a larger size and hence are more likely to starve. Older females, however, do not lay inferior final eggs, and they better provision their young. Hence, their large, fast-growing sons are less likely to starve.

The physical condition of both sexes and their ability to feed their young can bias the survival of the young according to their sex. Male chicks of the Lesser Black-backed Gull, for example, die more frequently when reared by parents in poor condition than when reared by parents in good condition (Nager et al. 2000). Female chicks, however, are not affected by the condition of their parents. The heightened mortality of male chicks is due to their greater sensitivity to poor egg quality and to the greater demands that they put on their parents in poor condition.

House Wrens in Wyoming provide another case study of the ways that females manipulate the sex of their offspring (Albrecht and Johnson 2002). The first female to mate with a polygynous male gets most of his help in raising her chicks. Second-mated females, which receive little assistance, fledge fewer and lower-quality young. Quality at fledging has a greater effect on the future reproductive success of male wrens than on that of female wrens. Conforming to prediction, second-mated females biased the sex ratios of their offspring toward females that could overcome a quality handicap. This result was not due to biased nestling mortality or biased feeding. Somehow, once again by unknown means, female wrens can control the sexual composition of their offspring in accord with theory.

Brood Reduction

One way that birds can cope with uncertainties about the number of young that they can raise in any particular year is to lay the number of eggs that should be successful in good years and then to sacrifice some of these eggs or young if necessary. Brood reduction protects parents against losing the entire brood should conditions for raising young be unpredictably poor. How is brood reduction accomplished? Starting incubation before the last egg is laid promotes asynchronous hatching, which in turn sets up options for brood reduction. Brood reduction itself ranges from overt siblicide, as in raptors and herons, to more subtle, selective elimination of some members of a brood.

More optimistically, smaller last-hatched chicks serve as “insurance” should one of the older siblings fail. The Masked Booby, a large, tropical seabird, lays one extra egg as insurance against the hatching failure of the first egg (Anderson 1989, 1990). Most gannets and boobies lay only a single egg and raise only one young. Asynchronous hatching of the two eggs ensures predictable siblicide in the Masked Booby: the first chick pushes the smaller, second chick out of the nest shortly after it hatches. Asynchronous hatching followed by siblicide ensures that the peak food demands of two growing young never compromise the parents’ ability to produce at least one chick. In good years, however, the last-hatched chick might supplement the parent’s reproductive success by fledging successfully despite its initial handicaps.

Experiments with Lesser Black-backed Gulls demonstrate that the last-hatched, or so-called marginal, chick can overcome its initial handicap to fledge successfully (Royle 2000). These gulls typically lay three eggs, with probable loss of the third, last-hatched chick. The youngest chicks channel their initial food into mass rather than growth, buffering themselves against starvation, buying as much time as they can, and postponing the ultimate sacrifice of brood reduction as long as possible. Staying small initially compromises even further their ability to compete with their siblings and thus increases the chance that they will die in poor food years. Alternatively, in good food years, marginal surviving chicks then channel resources into accelerated skeletal growth and catch up with their siblings. The initial parental investment, hedging a parent’s own bets, and a chick’s growth options maximize success despite the unpredictability of food supplies.

16.5 Fledging

As a naked, blind hatchling transforms into a feathered juvenile, the young altricial bird approaches a pivotal event in its life—leaving the nest. Departure from the nest and then from parental care increases a chick’s vulnerability to predators and the weather. The mortality rate during this period is high. After the first dangerous days have passed, however, the fledgling chick is safer than it would have been back in a vulnerable nest. Fledglings respond to the warning calls of their parents by hiding or by staying still. Immobility combined with camouflaging plumage can render chicks extremely difficult to find.

Technically speaking, the **nestling period** is the interval between hatching and departure from the nest, and the **fledging period** is the interval between hatching and flight (Skutch 1976). The nestling and fledging periods may be the same for altricial birds, such as hummingbirds, but different for subprecocial and precocial birds, which have short nestling and long fledging periods. The moment of departure from the nest by altricial birds is commonly termed “fledging” even though the young birds may only flutter and scramble about for a few days before their first flight.

Long before they are ready to leave the nest or to fly, young birds develop essential strengths through exercise. Young pelicans jump up and down and flap their growing wings with increasingly effective strokes. Young hummingbirds grip nest fabric with their feet as they practice beating their new wings, anchoring themselves so as not to take off. When first airborne, some young birds respond to the new experience with astounding ability and control. When a young Osprey launches itself on its first flight over a northern lake, it wobbles and flaps uncertainly, loses altitude, and seems certain to splash into the lake. In the last possible moments, it flaps more effectively and gains altitude, climbing steadily and safely high above the lake. It then glides in circles and practices steering and control. Even more impressive are newly fledged Common Swifts, which spend their first night out of the nest on the wing (Tarburton and Kaiser 2001).

Mobile young birds move with their parents closer to good feeding grounds, a tactic that reduces the strain on the parents. The initial journey away from the nest is often a heroic one (Figure 16–12). One brood of Wood Ducks jumped two meters to the ground from their nest in a tree cavity and then followed their mother down a bluff and across a railroad track before swimming three-quarters of a mile across the Mississippi River to feeding grounds in good bottomland (Leopold 1951). More amazing still is the pair of Egyptian Geese that bred for several years on the roof of a three-story building in Johannesburg, South Africa. After the chicks hatched, the female herded them toward the roof’s drain outlet, and after a little pushing and shoving, they fell three stories down the drainpipe to be shot out parallel to the ground by the curved end of the drain pipe (P. Ryan, pers. comm.).

Under more natural circumstances, precocial chicks that leave nests in tall trees or high cliffs must leap to the ground below, bouncing off soft earth if they are lucky or off jagged rocks if they are not. Torrent Ducks, for example, live in the dangerous waters of fast-flowing streams high in the South American Andes. To leave their nests in cliff

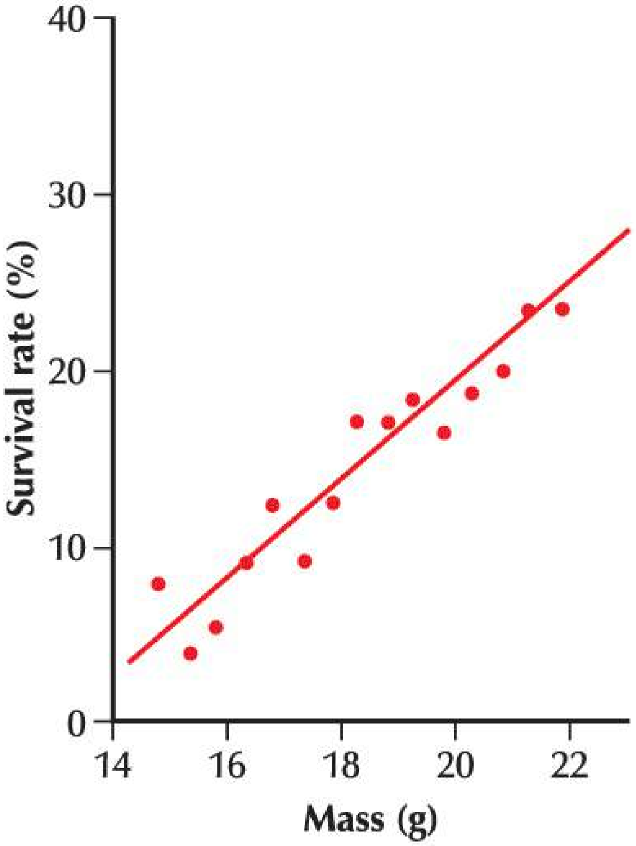
McDONALD WILDLIFE PHOTOG./ANIMALS ANIMALS

Figure 16–12 A Wood Duck baby leaves the nest.

crevices or holes above the streams, ducklings plunge as much as 20 meters into the turbulent water of the rocky streams below. Only rarely do they hurt themselves. Their light weight, buoyancy, and downy cushioning protect them from severe impact.

Nevertheless, mortality in the first few weeks out of the nest is typically high and relentless, especially in the first days out of the nest. Only 19 percent of fledgling Hooded Warblers survived the 28-day fledgling period prior to independence, and fledglings' daily survival probability was lowest in the first four days after they left the nest (Rush and Stutchbury 2008). Predators take about 50 percent of fledgling Yellow-eyed Juncos incapable of extended flight in the initial nine-day risk period (Sullivan 1999). Survival then improves for three weeks while parent juncos care for their mobile fledglings. With independence, however, comes a second episode of high mortality due to starvation. Newly independent young find insects slowly and inefficiently and spend almost all day feeding. Approximately half of them die, most by starvation. These juveniles take about two weeks to develop essential foraging skills.

A fledgling's chance of survival (measured by the number of future recaptures by field researchers) increases in proportion to its mass at fledging (Figure 16–13). In general, a young bird's chances of survival increase with the state of its physical development when it leaves the nest. This more advanced development is one of the advantages of longer nestling periods and of faster growth in altricial nestlings. The availability of food, the quality of parental care, the number of siblings competing for that care, and the timing of departure from the nest all affect a fledgling's physical condition.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company

DATA FROM PERRINS 1980

Figure 16–13 The probability of a young Great Tit's survival (and hence recapture by ornithologists) increases directly in relation to the mass attained by the bird before it leaves the nest.

16.6 Behavioral Growth and Development

Both heritage and experience affect the behavior of birds. Ended now are the intense debates of past decades about whether a particular behavior is innate or learned. The dichotomy was a false one. Instead, behavioral patterns of birds range continuously from those modified only slightly by experience to those derived entirely from experience. The embryonic growth patterns of the brain tied to length of the incubation period, for example, set the stage for later cognitive abilities required for foraging innovation and social interactions (Ricklefs 2004). Both brief imprinting exposures and prolonged learning experiences link a bird's genetic heritage of nerves, hormones, muscles, and bones to its social and ambient environments.

Innate responses to certain objects and color patterns guide a chick's solicitation of food from its parents. As soon as they are physically able, for example, hatchling Herring Gulls peck at the red spot on the bill tip of a parent to receive food (Tinbergen and Perdeck 1950). The apparently simple stimulus of red near the end of the bill is in reality quite complicated. It includes several ingredients, such as shape and color contrast. Experiments with the use of color-patterned bill-like sticks with this species and with the Laughing Gull revealed that the most effective stimulus for eliciting pecking was a red or blue, nine-millimeter-wide, oblong rod, held vertically at a chick's eye level and moved horizontally 80 times a minute (Hailman 1967). The Laughing Gull chick's accuracy in pecking increases with age as its depth perception, motor coordination, and ability to anticipate the parent's position improve. Older, more experienced chicks restrict their pecking to stimuli most similar to the head and bill of a real adult.

Predator Recognition

How do baby birds avoid danger? The natural and clearly beneficial escape responses of young birds to predators are both innate and learned. Baby domestic chickens innately avoid eating black and yellow prey, the warning coloration of many caterpillars. They then refine their choices with experience (Schuler and Hesse 1985). Similarly, hand-raised Turquoise-browed Motmots are frightened by sticks painted with black, red, and yellow bands to look like coral snakes (Smith 1977). Such a reaction is clearly adaptive—coral snakes are dangerous. Rather than having to learn to associate this color pattern with danger by direct experience, birds are genetically predisposed to avoid the risk, and then they learn refinements. Like other megapodes (see section 15.4), hatchling Australian Brushturkeys are independent as soon as they emerge from the compost mound. They respond innately to the alarm calls of Australian songbirds by becoming more alert (Göth 2001). They also react to real predators by crouching or running.

Learning about predators is important, too. Naïve, young Great Tits fail to distinguish between a model of a predator and a model of a nonpredator, even though older, wild-caught juveniles and adults do so (Kullberg and Lind 2002). In part, young birds learn to recognize predators or to improve their recognition by observing the mobbing behavior of other birds. Adults scold and attack owls and snakes that they discover (Figure 16–14). Inexperienced birds quickly associate potential danger with this commotion. Eurasian Blackbirds will mob a harmless stuffed songbird or even a Clorox bottle if, in experiments, they have seen other birds appear to mob them (Curio et al. 1978).


Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company

Figure 16–14 Crows congregate to mob a Great Horned Owl as it roosts during the day.

Imprinting

The process of imprinting is fundamental to the development of behavior in many birds. **Imprinting** is a special kind of learning that takes place during a well-defined time period called the critical learning period, and it is irreversible. Something once learned during this period persists. Recall that passerine birds, for example, develop songs by using innate templates to filter experience during critical periods (see Chapter 8). Imprinting determines adult mate preferences and habitat preferences. Imprinting also determines the prey-impaling behavior of the Loggerhead Shrikes and the selection of nest materials and sites by adult Zebra Finches (ten Cate et al. 1993). Successful captive propagation of endangered bird species requires careful attention to the early visual experiences of hand-reared chicks (Box 16–5).

Box 16–5

Endangered-Species Projects Accommodate the Sexual Preferences of Hand-Reared Birds

Courtesy of the Zoological Society of San Diego

Feeding California Condor chicks. A model condor head serves as the surrogate parent for a hand-raised California Condor chick, preventing it from imprinting on its human keepers.

When hand-raised by humans, captive baby birds tend to imprint on their human keepers and then to orient their adult sexual interests toward them. Disguises and models of parent birds are essential proxies for rearing California Condor chicks so that they will later exhibit proper species-recognition behavior (see photograph). Improper recognition behavior, however, sometimes has scientific advantages. Captive birds that have imprinted on their human keepers will ejaculate onto the keeper’s hand, providing sperm for artificial insemination. This technique has been used for the captive propagation of endangered species, such as the Peregrine Falcon.

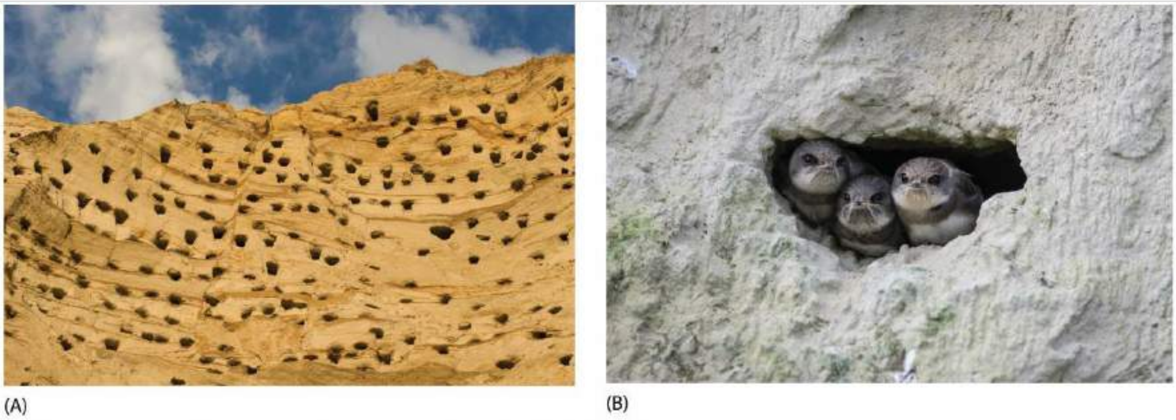
An early sensitive period enables young precocial birds to establish the critical concept of “parent,” on which their survival depends. The young of species that leave the nest shortly after hatching must learn to distinguish their parents from inanimate or inappropriate objects. Ducklings, for example, imprint most strongly on a moving and calling object when they are from 13 to 16 hours old. The objects that ducklings follow define their future acceptance of comrades and mates. They start with their parents.

Two particular stimuli help define a parent to ducklings: movement and short, repetitious call notes. Imprinting is enhanced when both stimuli are present, but movement alone is sufficient. Chicks, ducklings, and goslings will follow and imprint on a human, a moving box containing a ticking alarm clock, or even a moving shadow on a wall. The strength of imprinting increases with the conspicuousness and variety of stimuli that a parent presents.

The next step in the behavioral development of a chick is to learn to distinguish its parents from other adults. The parents' visual appearance alone may be an important distinguishing factor. When exposed to different breeds of hens, baby chicks follow the one that looks most like their mother, on which they had imprinted initially (Collias 1952). Aggressive rebuffs by adults other than their parents may reinforce this process, quickly teaching chicks to avoid menacing adults of all kinds.

A baby bird may also imprint quickly on a parent's voice—one of the first sounds that it hears, perhaps even while it is in the egg. Common Murre chicks exchange calls with their parents before hatching and recognize their parents' voices on hatching (Ainley et al.

2002). Accurate parent–chick recognition is most important in birds that gather in large colonies and have chicks that require parental attention. In large colonies, young Sand Martins (also known as Bank Swallows) in large colonies, for example, are apt to wander into the wrong burrow and perish because they are not fed. The adult Sand Martins learn to recognize their own young by their distinctive individual calls and do not accept strange young (Beecher et al. 1986; Figure 16–15). In contrast, Northern Rough-winged Swallows, a related but solitary nesting species, do not discriminate between their own offspring and those of others placed in their nests. They feed whichever young occupy their nest.



(A) VISHNEVSKIY VASILY/SHUTTERSTOCK. (B) HANS LANG/IMAGEBROKER /AGE FOTOSTOCK

Figure 16–15 (A) Colonies of Sand Martins riddle dirt embankments with their nesting tunnels. (B) A brood of three young Sand Martins, almost ready to fledge, waits for food at the entrance to their burrow.

Sexual Identity and Species Recognition

A chick’s early visual experience with its parents typically affects its reaction to alternative color patterns, its social interactions and identity, and its eventual choice of a mate. Face- or head-color patterns, including skin colors of the face and bill, differ among related species. These patterns enable rapid identification by the birds themselves as well as by bird-watchers.

Sexual imprinting, as it is called, is widespread among birds. It has been documented in more than half of the orders of birds and in many families (ten Cate et al. 1993). The process starts with the specific signals of a parent, either visual or vocal, then generalizes more broadly and, finally, adjusts to exclude the signals of other species. The process of sexual selection based on early imprinting experiences has likely played a major role in the evolution of distinctive plumage color patterns of bird species.

The white and dark "blue" color morphs of the Snow Goose of the Canadian Arctic exhibit how sexual imprinting works (Mowbray et al. 2000; see Figures 4–22D, E). The different plumage colors of this species have a simple genetic basis. As a rule, white geese pair with other white geese, and dark geese also pair with each other in what is called **assortative mating.** Early visual imprinting on family color is the force behind these mating preferences. Young Snow Geese choose mates of the same color as that of their families, mainly that of their parents. Regardless of their own color morph, geese raised by white parents later choose white mates, and geese raised by dark parents choose dark mates. Geese raised by mixed pairs choose either white or dark mates.

Much more complex is the role played by imprinting in the early development of young obligate brood parasites, which are raised by host parents. Village Indigobirds imitate the songs of their host fathers, including dialect variations (see section 14.4). Host vocalizations enable female indigobirds to recognize potential mates with the same host heritage as well as to lay eggs in the appropriate host nest. Brood parasites still need to shift from social affinity with the host parents to social affinity with others of their own species. One possibility is that they use a species-specific "password" to do so (Box 16–6).

Box 16–6

Password Access to Cowbird Society

If sexual identity starts with a process of imprinting on parents and socializing with siblings, then how do brood parasites develop a sense of identity different from their host species? After fledging, young Brown-headed Cowbirds, for example, shift their affinities to other cowbird fledglings and to adults of their own species (Lowther 1993).

Mark Hauber and his colleagues (2001) discovered that one call, the "chatter," may serve as a kind of identity password for entry into cowbird society. The chatter is an innate, spontaneous, and invariant vocalization of young cowbirds. Its development requires no social experience. Nestling cowbirds are highly responsive to playback of this chatter. After they leave their host parents, fledglings and then later juveniles instinctively approach other chattering cowbirds or experimental broadcasts of the chatter. After they have reunited with others of their species, triggered by one or the other of the vocalizations, young cowbirds begin to have social experience with flock mates, learning and refining vocalizations, including dialects and other cultural traits, and ultimately their mating preferences.

Cross-fostering experiments, in which young are raised by parents of another species, illustrate the effects of early imprinting on a bird's sexual response to species-specific color patterns. Cross-fostering causes the sexual interests of many species to shift to the foster species. For example, male Zebra Finches raised by Bengalese Finches (a domesticated form of the White-rumped Munia) prefer to court Bengalese Finch females instead of Zebra Finches. When Zebra Finches are doubly imprinted on Zebra Finches and Bengalese Finches, they prefer to court hybrids with visual features of both species (ten Cate 1987).

Learning Essential Skills

After chicks leave the nest, they enter a period of intense learning and practicing essential skills, including foraging and avoiding predators. Fledglings of most small passerines stay with their parents for two to three weeks after they have left the nest. In the Tropics, where long apprenticeships also seem necessary to develop feeding skills, some young passerines stay with their parents for 10 to 23 weeks. Young boobies and terns depend on their parents for as long as six months after they have fledged—until they have mastered the art of plunging after fish.

The **postfledging period** is a final period of parent–offspring conflict. Fledglings should prolong this period of postfledging parental care as long as possible. Parents, however, should encourage independence of their young as soon as their investment is secure, which enables them to start incubating another clutch. In Montagu's Harriers, as the fledglings' flying and hunting skills improve, parents terminate the postfledging dependence by decreasing the amount of food that they provide (Arroyo et al. 2002). They hold back on food provisions despite increased and more aggressive solicitations. In years of low food availability and tougher hunting, the fledglings try even harder to extend parental care.

Other essential skills also develop with age and social experience. Orientation and navigation skills require calibration of compasses and definition of goals. Young songbirds acquire their vocal repertoire and learn to communicate through social interactions. The extraordinary Gray Parrot named Alex (see Box 7–5) required social exchange with his tutor to learn words and concepts; he could not learn from a television video program (Pepperberg 1991).

Social skills and dominance also improve with age. Some birds play. Young crows, ravens, jackdaws, and their relatives, for example, frequently play and even create elaborate social games similar to “king of the mountain” or “follow the leader.” Stick balancing and manipulation or the exchange of sticks, sometimes while upside down, and taking turns sliding down a smooth piece of wood in a cage are among the many games that these intelligent birds play (Gwinner 1966).

Gulls often drop clams onto hard surfaces to break them open for food. Sometimes, they swoop down to catch them before they hit the ground, a game of “drop–catch” that looks like play behavior (Gamble and Cristol 2002). Detailed studies of drop–catch behavior in Herring Gulls rejected the alternative hypotheses that (1) a gull was testing the probability of theft by other gulls before actually letting the clam smash open or (2) the gull was trying to reposition the clam in its bill for a better drop (like a tennis player catching the ball to do a better serve). Most telling were observations that young birds played drop–catch more than older birds and often did so with objects other than clams. What looks like "play" is usually a form of practice for developing essential locomotory and social skills (Smith 1983).

Peregrine Falcons develop their hunting skills through playful practice and social interactions. After they fledge, young Peregrines depend on their parents for food for one to two months. They develop their flying and hunting skills through aerial interactions when playing with their siblings. In aerial dogfights, they chase and dive at each other, called stooping, and roll over to grapple each other's talons. Programmed to chase, juvenile Peregrines can develop good hunting skills without much help from their parents. Initially, they chase anything large that flies nearby, including herons and vultures as well as one another. Their first captures almost seem to be accidental, surprising contacts. Kills soon become more deliberate, usually directed initially at large easy-to-catch insects, such as butterflies and flying beetles, which they may eat on the wing. The adolescent Peregrines then graduate to taking birds as prey, killing them with increasing efficiency.

REVIEW KEY CONCEPTS

16.1 Modes of Development

Most hatchlings fall into one of two categories, altricial or precocial, which represent different trade-offs between tissue growth and maturation, including wings for locomotion and temperature regulation. The 30-fold variation in the growth rate of chicks of the various species relates directly to precocity of development and adult body proportions, including brain size.

Key Terms: altricial, nidicolous, precocial, nidifugous, tissue-allocation hypothesis, homeothermy, endothermy, sigmoid curve

16.2 Begging for Food

Baby birds manipulate food delivery by their parents through advanced begging behavior and colorful mouth markings. Begging calls can attract or thwart nest predators.

16.3 Sibling Rivalry

Sibling rivalry for limited food deliveries is often intense. Asynchronous hatching fosters siblicide by fights or control of food between chicks of unequal size and strength.

Key Terms: siblicide, head start hypothesis

16.4 Parenting

Peak breeding activity adds substantial daily energy costs, leading to loss of weight and increased hormonal stress. A parent’s options for adjusting its investments include choosing among rivaling nestlings, reducing risks of nest predation, and even sacrificing some of their young if necessary. Parents can manipulate their investments into male or female offspring by provisioning eggs differently and by biasing their care of the sexes.

16.5 Fledging

Young birds show extraordinary skill and daring when they leave the nest, a period of high mortality due to predation and starvation. How long they stay with their parents depends on the difficulty of skills that must be acquired.

Key Terms: nestling period, fledging period

16.6 Behavioral Growth and Development

Play behavior enables young birds to practice the essential locomotory and social skills that they need to survive on their own. Maturation experiences vary from brief imprinting exposures during critical sensitive periods early in life to prolonged learning and cultural exchanges of information. Imprinting affects many aspects of avian behavior from recognition of species to choice of nest sites and habitats.

Key Terms: imprinting, sexual imprinting, assortative mating, postfledging period

APPLY YOUR KNOWLEDGE

1. Differentiate the strategies of growth and development of

precocial versus altricial young in terms of the tissue-allocation hypothesis.

2. What selective forces would favor producing naked, blind, and mostly helpless young?
3. Describe the head start hypothesis and the value of male young being smaller than female young for the success of the entire brood.
4. Explain the differences between producing large broods and small broods considering the success of the brood in fledging and the personal risk and success of the parents.
5. When incubation begins with the production of the first egg, hatching of eggs in the clutch occurs sequentially (asynchronously), and the last to hatch is smaller and more likely to die of starvation or siblicide. What factors might contribute to the success of the last hatched chick?
6. Describe the correlation between brood size and annual adult survival. Consider the contrasting behaviors of adults in protecting themselves and their young of different brood sizes and adult annual survival.
7. Delaying incubation until the last egg is laid leads to all eggs hatching simultaneously (synchronous brood). Using Blue Tits as an example of birds producing synchronous broods, explain the trade-offs between males and females and the fitness of the pair.
8. How is the production of an asynchronous brood or a synchronous brood adaptive under different environmental conditions, such as tropical and temperate habitats and in habitats that suffer the

vagaries of high and low food availability during different years?

9. Define the spectrum of innate and learned behaviors and the position of imprinting in this spectrum.
10. Describe the following in terms of the innate–learned–imprinting behavior spectrum:
    a. sibling rivalry in Great Egrets and Great Blue Herons
    b. mate selection in Snow Geese
    c. begging by Laughing Gull chicks
    d. color and pattern recognition of Turquoise-browed Motmots
    e. predator recognition in Great Tits and domestic chickens

CHAPTER 17 *Life Histories*

CHARLIEBISHOP/E+/GETTY IMAGES

The life history strategies of the Great Tit of Europe, including costs and benefits of family size, are among the best studied of all birds.

> In the end, an individual’s lifetime reproductive success is what counts.

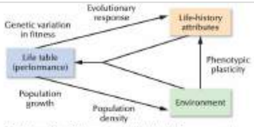
[CHARLES DARWIN IN MODERN TERMS]

Each bird proceeds through a series of life-history stages from early development to the annual cycles of adults. Compounding the challenges of survival through each stage of the annual cycle are the trade-offs between the short-term costs of reproductive effort and future breeding opportunities.

The rates of reproduction and annual survival of individual birds combine to measure an individual bird's lifetime reproductive success relative to that of its competitors—that is, its evolutionary performance. The reproductive successes of all individuals in a population together define the dynamics of that population's growth or decline. More broadly, the study of avian life histories integrates behavior, ecology, population biology, and evolution into a broad concept of the responses of birds to the environment (Ricklefs 2000b).

This chapter reviews the trade-offs between survival and reproduction by birds. It starts with an overview of the main life-history patterns of birds. It then explores in detail the two central life-history traits, longevity and fecundity, to set the stage for a discussion of the trade-offs between annual reproduction and age-specific survival. The final part of the chapter deals with the premier topic of avian life-history research—the evolution of optimal avian clutch sizes, or how many chicks a bird should attempt to raise at one time.

17.1 Life-History Patterns



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Data from Ricklefs 2000a

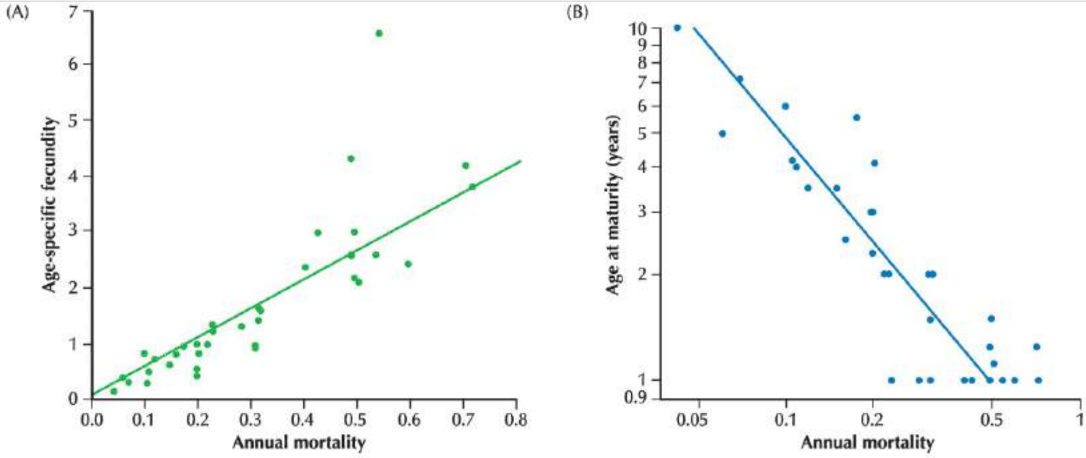
Figure 17–1 Influenced by the environment, the life-history attributes determine the lifetime reproductive success and relative performance of individual members of a population. Genetic variation in performance, called fitness, establishes an arena for natural selection and an evolutionary response in the population to variation in the environment. Variation in the environment also affects population growth and density-dependent feedback on individual attributes and performances.

Life histories are sets of evolved traits or attributes. Woven together, individual life-history attributes interact with environmental variables to determine the performance of an individual member of a population (Figure 17–1). In turn, each member's performance relative to that of others defines the selective advantage or disadvantage of that member's traits. In this way, the life-history attributes of a population evolve toward a particular optimum. The diverse life-history patterns of birds are the products of this evolutionary process.

Trade-offs between longevity and fecundity are the traditional focus of life-history theory. The substantial trade-offs between them lead to different solutions or optima for different species. Central to longevity is the probability of living to a particular age, called **age-specific survivorship.** As a whole, birds are long-lived, warm-blooded animals that age slowly. Studies of the life spans of birds have potential application to the treatment of human aging and fertility (Holmes and

Ottinger 2003).

Annual fecundity—the number of young successfully fledged in a year—increases directly with annual adult mortality. This relation is the central theme of avian life-history theory (Figure 17–2). Short-lived (high-mortality) species, such as ducks and small songbirds, tend to have high fecundity. Long-lived (low-mortality) species, such as albatrosses and eagles, tend to have low fecundity.



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DATA FROM RICKLEFS 2000A

Figure 17–2 (A) Age-specific fecundity (number of fledglings per year) increases in short-lived species, graphed here as annual adult mortality (percent). The greater the annual adult mortality, the more short lived a species is. (B) Age at maturity (first breeding) decreases in short-lived species, again graphed here as annual adult mortality (percent).

A Song Sparrow, for example, has a short life span, but it starts breeding without delay, after just one year. It then concentrates high annual output—from three to five nestlings twice a year—into a few consecutive years. At the other extreme is the Wandering Albatross, which takes a long time to start breeding—at eight to 11 years of age—and reproduces slowly. It produces one chick every two years for as long as 50 years (Figure 17–3). A single axis spans the short and fast sparrow life history and the long and slow albatross life history. This “fast–slow” axis captures most of the variation in life histories among birds (Ricklefs 2000a).

(A) Enrique R. Aguirre/AGE Fotostock. (B) Chantal Steyn Photography/Moment/Getty Images

Figure 17–3 (A) The Black-browed Albatross and related species are long-lived birds that raise only one offspring at a time. (B) The Wandering Albatross produces one chick every two years for as long as 50 years.

Included in the sweep of life-history features tied to life span are behavioral traits of cognition and intelligence. Families of birds known for their intelligence and advanced social behaviors, such as crows, parrots, and woodpeckers, have large brains in relation to their body sizes (see Figure 7–15). Relative brain size is also linked to innovative foraging behaviors and, especially, play behavior (see section 7.6). Underlying this nexus of traits is the length of the incubation period; longer incubation periods enable the development of capacities for more advanced behavior.

Few avian life histories depart from the tight correlation between annual fecundity and life span. No long-lived bird produces large numbers of young each year, as, for example, a maple tree produces seeds, or waits to the end of its life to produce lots of young, as a salmon does. Why would this be so? The evolution of avian life-cycle options may be constrained by the physiology of birds (Ricklefs and Wikelski 2002; Box 17–1). Endocrine control systems, in particular, must undergo delicate transitions between life-history stages, managing stress and the risk of alternative and incompatible behavior while minimizing damage from prolonged overdoses of hormones. In addition, early developmental patterns—particularly, long incubation periods—relate directly to long life spans in birds. Such correlations suggest a high level of evolutionary integration of life-history traits in birds from fledging to old age.

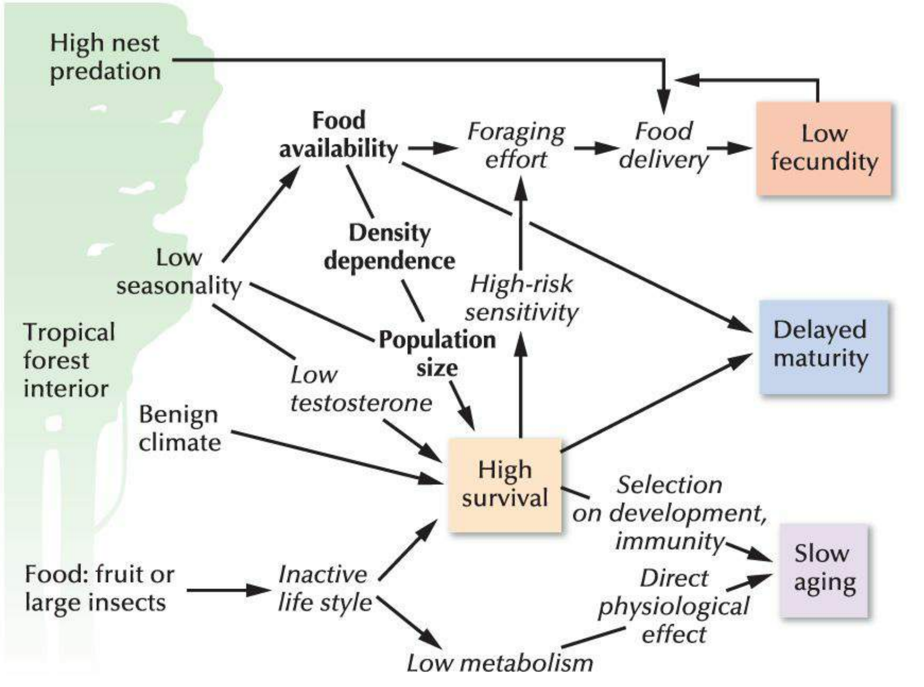
Box 17–1

Physiological Constraints Shape Avian Life-History Traits

The study of avian life histories includes physiological trade-offs and constraints (Ricklefs and Wikelski 2002). These trade-offs and constraints help us to understand the ways that selection pressures—such as food availability, seasonality, and predation—shape a species’ life-history traits.

The diagram illustrates a model of the network of interactions that potentially connect environmental features of the tropical forest interior (shaded area) to the life-history traits (boxes in unshaded area) of a small tropical forest bird, such as a manakin. Shown are direct connections of behavior and physiology (in italics) as well as indirect connections of ecological feedbacks (in boldface).

Physiological responses such as metabolic rates and hormones, especially testosterone, mediate the interactions. Incompatible hormone controls of different behaviors and time-limited hormone responses to stress are likely to constrain fecundity, parental effort, and life span.



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DATA FROM RICKLEFS AND WIKELSKI 2002

Model of the role of physiological processes (italics) and population processes (boldface) in the evolution of the life-history traits (boxes) of a bird species that lives in the interior of a tropical forest (shaded area). These species typically have long life spans, small clutch sizes, and delayed maturity. A manakin is such a species.

The primary life-history attributes—survival and fecundity—change with age. **Life tables,** like those used in the insurance industry, integrate the vital measures of age-specific survivorship and also age-specific fecundity. These statistics help us to project rates of population growth and future population trends, whether up or down. Population trends, which are critical to the sound conservation management of healthy, stable populations of birds, are the subject of the following chapter.

17.2 Longevity and Life Span

Birds are remarkable for their longevity. Compared with mammals, they are long lived both for their sizes and for their high metabolisms, which average from 1.5 to 2.5 times those of similar-sized mammals. Birds expend five times as much energy or more throughout their lifetimes as do mammals of the same size. Some birds live about as long as humans. The long lives of birds challenge current understanding of the aging process through cellular degeneration due to the oxidative by-products of metabolism (Box 17–2).

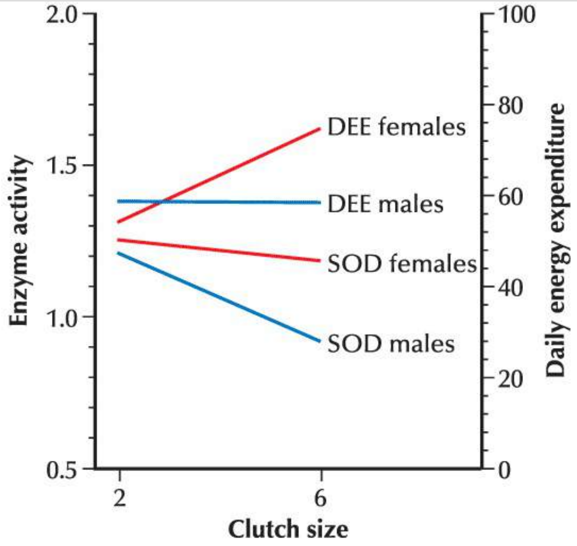
Box 17–2

Antiaging Mechanisms in Birds?

The long life spans of birds interest biogerontologists, the biologists who study the aging process (Holmes and Ottinger 2003). What is responsible for aging? Aerobic metabolism generates by-products known as reactive oxygen species (ROS) that damage cells, cell organelles (such as mitochondria), DNA, lipids, and proteins. Damage from ROS by-products is thought to be the major cause of aging, or senescence. For this reason, we get plenty of encouragement to include antioxidants in our diets by eating such foods as blueberries, Brussels sprouts, and tomato salsa.

High metabolic levels and reduced antioxidant activity increase ROS damage. Reproductive effort reduces antioxidant activity and thereby damages health and reduces longevity. Experimental doubling of the clutch sizes of Zebra Finches, for example, caused antioxidant activity to decrease by 24 to 28 percent in the male Zebra Finches but not their mates (see graphs).

The long life spans of birds suggest that despite their high metabolisms and major energy expenditures, they have interesting ways of prolonging life by reducing ROS damage through oxidative protection. The mechanisms responsible for slow aging may be linked to the evolution of flight because bats show similar trends of life span and aging. However, we don’t yet know exactly what these antiaging mechanisms are or whether they directly increase the life spans of birds by neutralizing ROS activity.



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DATA FROM WIERSMA ET AL. 2004

Larger clutch sizes cause a reduction in the activity of the major antioxidant enzyme superoxide dismutase (SOD) in male Zebra Finches but not significantly in female Zebra Finches. Daily energy expenditure (DEE) did not increase with the larger brood size in males, but females exerted additional effort.

The maximum ages recorded in wild birds average between 10 and 20 years for songbirds and between 20 and 30 years for seabirds and raptors. Records of long-lived individual birds abound. Included are a 51-year-old Laysan Albatross, a 36-year-old Eurasian Oystercatcher, and a 34-year-old Great Frigatebird. A female Royal Albatross named “Grandma” banded at her nest in New Zealand disappeared at age 53.

Another record-holding seabird is a Manx Shearwater banded on North Wales as an adult on May 22, 1957, and recaptured again 45 years later on April 3, 2002, having flown an estimated 800,000 kilometers on annual migrations between Wales and South America, a distance equal to flying to the moon and back (Bhattacharya 2003).

Captive birds tend to live even longer than their wild relatives. Some parrots live to be 80 years old in captivity (Flower 1938).

Annual survival rates accrue to define life span. The survival rates of adult birds range from as low as 30 percent per year for Blue Tits and Song Sparrows to highs of more than 95 percent for Royal Albatrosses, Bald Eagles, and Atlantic Puffins. In general, large species survive better than small species, and seabirds survive better than land birds.

The risk of death is strongly seasonal for most adult birds. Survival rates of songbirds strongly correlate with seasonal changes in average monthly temperatures, which indicate the harshness of the lean or winter season. Annual survivorship of American Redstarts, for example, corresponds in part to the quality of their winter habitats (Marra and Holmes 2001). Whether a seasonal environment is warm–cold or wet–dry, the shortage of food for several months in that environment increases mortality due to starvation.

Migration itself may impose substantial mortality that is difficult to separate from winter mortality. Scott Sillett and Dick Holmes (2002) tracked seasonal survival in the Black-throated Blue Warbler. This handsome species migrates between wintering grounds in the

Caribbean and breeding grounds in New England. Annual survival rates were estimated to be 51 percent for males and 40 percent for females. Month-to-month mortality, however, was negligible (for both males and females) from May to August in New England and from October to March in Jamaica. Instead, most of the annual mortality (85 percent) was during migration.

Tracking birds in real time with geolocators will likely revise overestimates of mortality based on recaptures of banded birds (Hoover 2003; see also Karr et al. 1990). The primary reason is that breeding birds may relocate after a poor breeding season and thus not be found the following year, even though they are alive and well outside the study area.

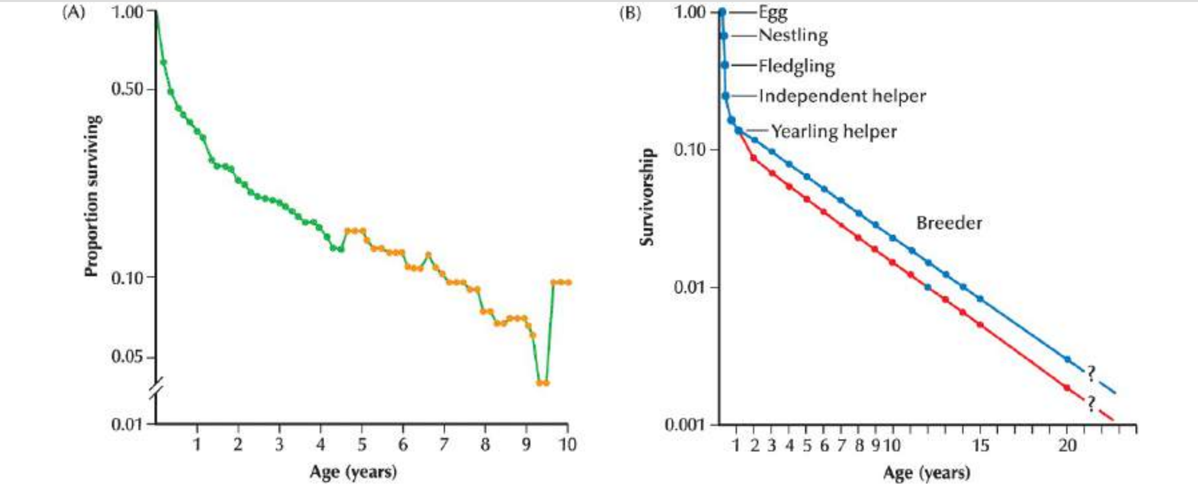
Age-Specific Mortality

Rates of annual survival change conspicuously with age in the first years of life and may also differ between the sexes. A young bird's annual chance of survival (from fledging to breeding) typically is about half that of an adult. Only 13 to 30 percent of fledgling Great Tits survive their first year, but 48 percent of adult females and 52 percent of males survive each year until the age of five years. After that age, mortality rates increase (Cramp and Perrins 1993). Small land birds are especially vulnerable in their first year, starting when they leave the nest and then their parents (see Chapter 16).

Revealing the high levels of predation on young birds are the metal bands, or "rings," that accumulated with songbird carcasses in the nests of Eurasian Sparrowhawks in Wytham Wood at Oxford, England

(Perrins and Geer 1980). These raptors fed intensively on the marked research populations of Great Tits and Blue Tits. The sparrowhawks took 922 ringed tits in 1976, 759 in 1977, and 1,220 in 1978. Most were juveniles. Each year, the sparrowhawks ate from 18 to 34 percent of all Great Tit juveniles in that population and from 18 to 27 percent of the Blue Tit juveniles in that population.

After birds have reached adulthood, their chances of survival increase and stay essentially constant. Survivorship in juvenile Florida Scrub Jays, for example, is extremely low during the first few months after they leave the nest (Woolfenden and Fitzpatrick 1996; Figure 17–4). Only 33 percent of Florida Scrub Jays survive their first year, after which they “graduate” to the higher survival rates of (breeding) adults, which average 78 percent per year.



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DATA FROM WOOLFENDEN AND FITZPATRICK 1984

Figure 17–4 (A) Survivorship of Florida Scrub Jays (males and females combined) observed in a population in central Florida, from fledging through age 10 years. Green symbols indicate sample sizes of cohorts containing more than 100 potentially surviving birds. Data become more irregular and unreliable at the end because of small sample sizes. Note that the proportion surviving drops sharply in the first year of life to about 40 percent of the initial cohort. (B)

A complete survivorship curve from beginning of incubation through possible age of senescence (question marks). Males (blue circles) and females (red circles) diverge slightly after age one year because of the greater mortality of females, which disperse from their natal territory. Survivorship of breeders is identical between sexes.

A death rate that increases with age is called **actuarial senescence.** Evidence of senescence in ducks, songbirds, and albatrosses challenges the traditional view that mortality in adult birds is independent of age (Holmes and Austad 1995; McDonald et al. 1996). A carefully controlled analysis of the life spans of adult Florida Scrub Jays, for example, revealed that their rate of mortality doubles in 6.4 years. Whether the increasing death rate in jays is due to the degenerative effects of their old age or other causes is not known.

One potential cause of **senescence**—age-related declines in immune function—has been documented in wild populations of the Collared Flycatcher (Cichon et al. 2003). Older female flycatchers (five to six years of age) produce fewer antibodies against a nonpathogenic vaccine of sheep red blood cells. They also produce smaller fledglings compared with young females (one year old) and middle-aged females (three years old). Recall that female birds transfer immunoglobulins to their young through the egg, which suggests that weakening immune capacities of older females could directly impair their young’s health.

17.3 Fecundity

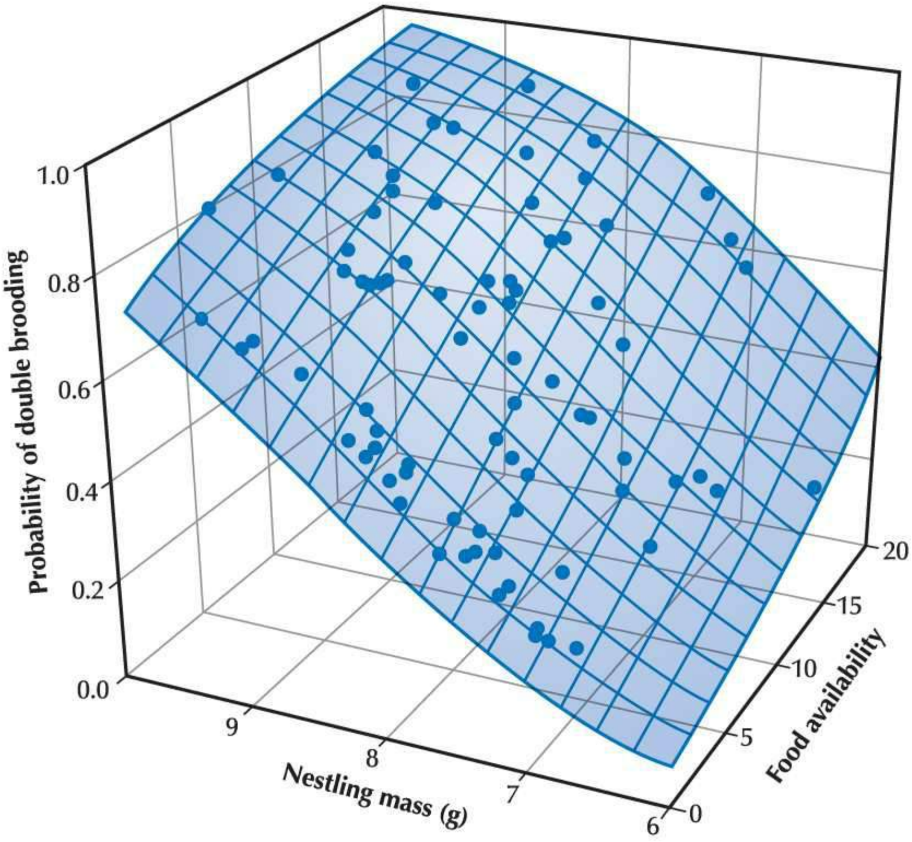
Fecundity—the number of young raised successfully—is a measure of an individual bird's reproductive success. Total lifetime reproductive success depends on the age at which a bird starts to breed, on how long it lives, and on the cumulative result of the bird's annual reproductive performance, both successes and failures. Annual fecundity, in turn, depends on the number of nesting attempts and the success of each attempt, the number of eggs laid each time (clutch size), and the age and experience of a breeding bird. Linked to these key elements of fecundity is a complex web of variables governing the relationships between parents and their offspring.

Single and Multiple Broods Compared

The number of broods that a pair can raise depends, in general, on the length of the breeding season. Predation early in the cycle also can stimulate multiple renesting attempts. Tropical birds generally attempt more broods than do temperate birds, in part because of prolonged breeding seasons. From two to six successive clutches are not unusual in the Tropics. The White-bearded Manakin, for example, typically lays from three to five clutches per season in Trinidad. Conversely, long nesting cycles or restricted breeding seasons, such as those in Arctic latitudes (mid-June to July) tend to preclude extra broods. Hence, many temperate and Arctic birds—Pileated Woodpeckers, Ruffed Grouse, and Snowy Owls, for example—attempt only one brood.

Long-term studies of the breeding dynamics of Black-throated Blue Warblers at Hubbard Brook in New Hampshire revealed that about half of the females laid a second clutch of eggs after successfully fledging their first brood (Nagy and Holmes 2005a). Double-brooded females maintained their physical condition: they exhibited no extra costs of mortality the following winter.

These females nested on high-quality territories with more food (Figure 17–5). The proportion of females that laid second clutches also increased when supplementary food was provided and declined when the availability of food was reduced (Nagy and Holmes 2005b). Both chicks and their double-brooded mothers benefited from higher food availability because the young fledged at heavier body mass, which likely increased their survival after fledging.



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COURTESY OF AMERICAN ORNITHOLOGICAL SOCIETY, FROM LAURA R. NAGY AND RICHARD T. HOLMES, (JUL., 2005) "TO DOUBLE-BROOD OR NOT? INDIVIDUAL VARIATION IN THE REPRODUCTIVE EFFORT IN BLACK-THROATED BLUE WARBLERS (DENDROICA CAERULESCENS)" THE AUK, VOL.122, NO. 3, PP. 902–914

Figure 17–5 Food availability on territories of the Black-throated Blue Warbler affected both the mass of nestlings when they fledged and the probability that female Black-throated Blue Warblers would attempt a second brood. High-quality territories with the most food produced larger nestlings. Females on these food-rich territories were more likely to attempt a second brood.

Overlapping successive small clutches can be a better way of increasing fecundity than enlarging a single clutch because it subdivides periods of peak parental care into smaller separate peaks. The male Goldcrest builds the second nest alone and then takes charge of the young in the first nest when the female shifts to incubate eggs in the second clutch. He shifts his attention to the second brood after the first has achieved independence.

Clutch Size

The number of eggs that a female bird lays in each nest, or clutch size, is an essential and heritable component of fecundity. Waterfowl, pheasants, rails, and many other precocial birds have clutch sizes of as many as 20 eggs. Passerines and other small land birds that feed their young lay clutches of two to six eggs, some as many as 19. The exact number varies among species. Within a species, it may also vary with latitude, climate, age, and quality of territory. Variation within a single species can be great. Northern Flickers lay from three to 12 or more eggs; Blue Tits lay from eight to 19 eggs. Other birds have virtually invariant clutch sizes: precocial shorebirds typically lay four eggs, and oceanic birds lay only one egg. Hummingbirds and doves normally lay two eggs.

A simplified and traditional hypothesis is that nutritional requirements of egg formation limit the clutch sizes of precocial birds, whereas the abilities of parents to feed their young limit the clutch sizes of altricial birds. This classic explanation, however, opens rather than closes the discussion. For example, why should the Ruby-crowned Kinglet lay from eight to 12 eggs, whereas the Yellow-rumped Warbler lays only three to five eggs? They are similar-sized species with similar life spans. They breed side by side in the boreal forests and eat similar insect foods. Food limitation cannot explain this difference. We will return to the question of food limitation and the evolution of clutch-size variations after first touching on some other aspects of fecundity.

Age and Experience

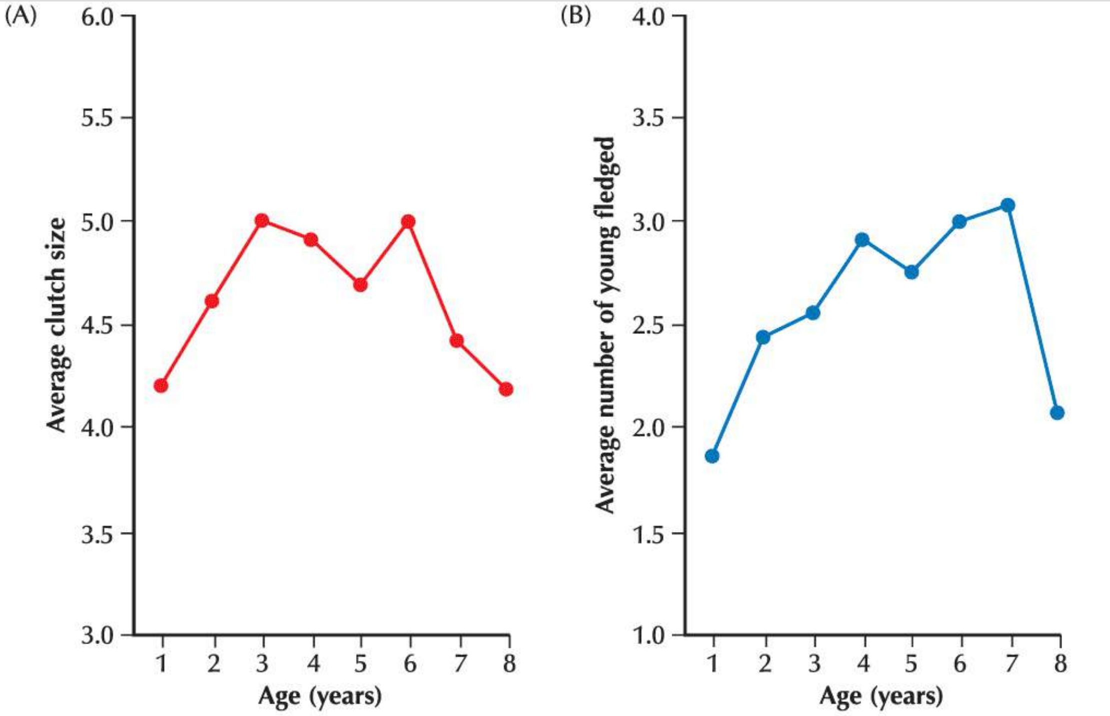
Birds that breed for the first time typically produce fewer eggs and raise fewer offspring than do older birds, primarily because competence and experience increase with age (Forslund and Pärt 1995). As yearlings, Peregrine Falcons are usually not good parents; they typically wait two to three years to breed (Figure 17–6). First-year pairs that try to breed usually fail (H. B. Tordoff, pers. comm.). One-year-old females, however, may nest successfully by pairing with an older mate. If they breed, young males may kill their own young. For example, a one-year-old male in Milwaukee fertilized his mate’s eggs and helped to fledge the young, but then he killed them by aggressively diving at them and accidentally breaking their wings. The next year, this male was less aggressive toward his offspring, which survived. In another case, a young female joined an experienced four-year-old male in Minnesota. She dropped her first egg into the nest box by accident while sitting on the front ledge and didn’t know what do with it. She was unable to roll it from the edge of the box where it was lodged to the central nest scrape for incubation. The older male came to the rescue and promptly rolled it expertly from the edge of the box to the middle of the scrape. When the egg was in its proper place, thanks to the male, the female settled on it right away and laid the rest of the clutch in the scrape. In this case, incubation was successful, but often young females are inattentive and haphazard in their incubation behavior, causing their nests to fail.

LUKE MASSEY/NATUREPL.COM

Figure 17–6 Peregrine Falcon nest on cliff ledges. More recently, they also nest on tall buildings or bridges in urban areas.

Feral Pigeons are prime prey for Peregrine Falcons. In addition to having a lowered risk of being caught, older pigeons increase their reproductive output by overlapping sequential clutches of two eggs each. The extent of overlap of clutches increases with a mated pair's combined experience as parents and their ability to, together, handle the different stages of parental care at the same time (Burley 1980).

As a general rule, reproductive performance increases in the first years to a middle-age plateau and then declines in older birds. Improved foraging skills, better access to prime resources, and enhanced knowledge of predators all improve parental abilities. After their first year, for example, female Eurasian Sparrowhawks increase both the average number of eggs laid and the average number of young fledged per nest (Figure 17–7). Seven- and eight-year-old females, however, exhibit reproductive senescence. Clutch size drops sharply at age seven, and the number of young that they fledge drops sharply at age eight.



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DATA FROM FORSLUND AND PÄRT 1995

Figure 17–7 Age-specific fecundity in Eurasian Sparrowhawks. Both (A) clutch size and (B) the number of young fledged per nest increase with age. Average clutch size grows to about five eggs in midlife but then declines in seven- to eight-year-old females. The average number of young fledged increases steadily with age and experience until age eight.

In another example, older California Gulls produce more young than younger gulls (Pugesek 1983). The oldest gulls (12–18 years old) produce 1.5 young per year, whereas middle-aged gulls and the youngest gulls (three–five years old) produce 0.8 young per year. Mature gulls feed their young more frequently, spend more time looking for food, and leave the nest unattended less often than do the younger members of the colony.

Delayed Maturity

Many birds wait a year or two or more to breed (Box 17–3). More generally, swifts breed at two years, parrots at two or three years, and raptors at three or more years. Waterbirds, except ducks, and seabirds generally take four or more years to breed for the first time, and large albatrosses and condors take from eight to 12 years. Among the species with late maturity, age at first breeding correlates strongly with longevity.

Box 17–3

Small Penguins Take Their Time

The factors favoring delayed maturity are well documented in Adelie Penguins (Ainley et al. 1983). First, breeding entails greater risk than not breeding. The mortality of breeders (39 percent) is greater than the mortality of nonbreeders (22 percent). The greatest mortality is found the first time that young Adelie Penguins try to breed. An amazing 75 percent of three-year-old females die in their first attempt to breed. The reason? They are less efficient at obtaining the food necessary to sustain the costly breeding effort. They may also be less wary or adept at escaping leopard seals lurking at the edge of the pack ice. Mortality then declines with age to 10 percent in 11-year-old breeding females.

Offsetting the risks of initial reproduction in Adelie Penguins are improved prospects for raising young in subsequent attempts. Adelie Penguins that breed for the first time at three to four years old (and survive that effort) are less likely to lose their eggs or young in subsequent nesting seasons than are those penguins that breed for the first time at a later age. Whether these early starters are inherently better breeders or the early start somehow enhances subsequent breeding success is not known.

MATTHIAS GRABEN/IMAGEBROKER/GETTY IMAGES

An Adelie Penguin and its young

Delayed maturation and acquisition of adult features are widespread among birds. A third of sexually dimorphic passerines of North America do not attain full adult male plumage in their first year. Male Baltimore Orioles, Scarlet Tanagers, and American Redstarts, for example, do not acquire their colorful adult breeding plumage in their first breeding season, even though they are capable of breeding. Delayed plumage maturation reaches extremes in the lek-displaying Long-tailed Manakin, whose young males wait five years to reach adult plumage and eight or more before reaching alpha male breeding status (see section 13.2). Some males never achieve alpha status.

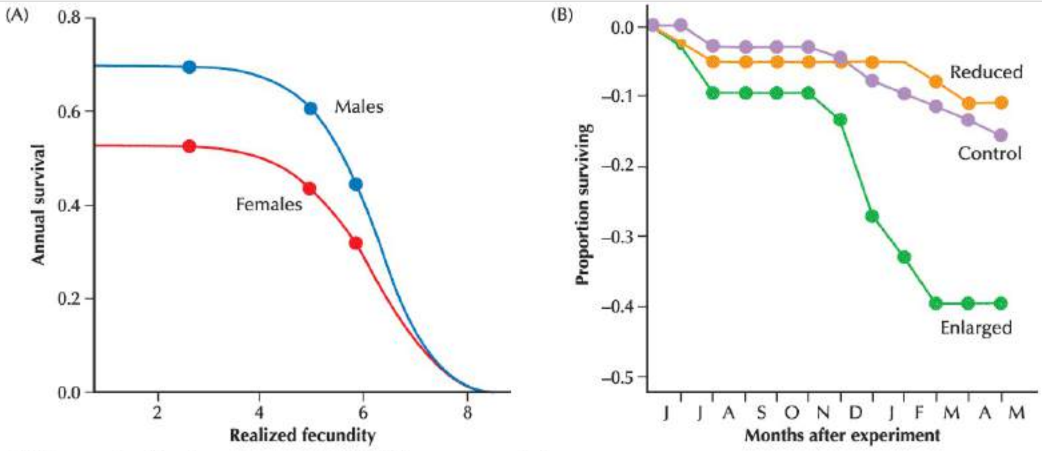
Why should a bird delay breeding? Every extra year of nesting would seem to increase its chances of leaving some offspring. Birds that can breed in their first year should soon replace others that delay breeding for several years unless the costs of early reproduction are too severe. In long-lived birds, however, delayed maturity may actually contribute to maximizing lifetime reproductive success. If competition for territories, resources, or mates is high and young birds are at a disadvantage, then it can be advantageous to delay breeding until later ages. Delayed dispersal and cooperative breeding, for example, are a special case of delayed maturity (see Chapter 14).

17.4 Annual Reproductive Effort

Increased investment into annual reproduction may take its toll on a parent's physical condition, on its reproductive potential the following year, and on its annual survival (see Chapter 16). The costs of breeding for young Adelie Penguins are just one of many examples (see Box 17–3). Experiments with sea ducks called eiders show costs, too, specifically in reference to the effect of current effort on future fecundity. Sveinn Hanssen and his colleagues (2005) compared the costs of incubation for female Common Eiders by giving some females a three-egg clutch and others a six-egg clutch. Female eiders fast during incubation. The effort of incubating the larger clutch size increased the loss of mass in those females and reduced their immune functions. But the consequences did not become evident until the birds nested the following year and produced significantly fewer eggs.

Eastern Bluebirds also experience a future consequence of their annual reproductive effort (Siefferman and Hill 2005). The experimental enlargement of brood sizes prompts an increased feeding effort by the parents, as compared with the efforts of parents with reduced broods. Males that fed reduced broods produced brighter plumage color the next year. Conversely, tending extra-large broods led to duller iridescence in the plumage of those males. The brighter-plumaged males that didn't overdo their effort the first year then mated with better females that laid eggs earlier in the next season.

The number of young fledged by Common Kestrels clearly affects their annual survival (Dijkstra et al. 1990; Figure 17–8). The reduction of brood size from the normal five chicks to just three increases the annual survival of both males and females. Increasing brood size from five chicks to six causes annual survival to drop sharply. Extrapolation of the curve fitted to these experimental data to even larger brood sizes suggested that trying to raise more chicks could be fatal. In fact, it is. Sixty percent of the kestrels that raised two extra nestlings were found dead before the end of the first winter, compared with only 29 percent of those that raised control or reduced broods (Daan et al. 1996).



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(A) Data from Ricklefs 2000a, Dijkstra et al. 1990. (B) Data from Daan et al. 1996

Figure 17–8 Trade-off between reproductive effort and life span in the Common Kestrel. (A) Costs of reproduction are higher in females (red) than in males (blue). Survival in both declined with experimental increases in brood size and in their realized fecundity (number of young actually fledged). (B) Enlarged brood sizes (green) caused a major increase in mortality in the following year compared with control (purple) and reduced (orange) brood sizes.

A long-held and strongly supported doctrine is that females suffer greater mortality and thus have higher costs of reproduction than males do. This outcome, too, is evident in the kestrels: annual survival of females is 55 percent compared with 70 percent of males, even when raising small broods. The better survival of male birds compared with females biases the sex ratio toward males in many bird populations.

17.5 Evolution of Clutch Size

No single topic has so occupied the attention of students of avian life-history patterns as has the evolution of clutch size. Clear patterns of clutch-size variation demand explanation. For example, average clutch sizes tend to be larger in the north temperate and in arid environments than those at lower, tropical latitudes and in wet environments. Why is this so?

The lively historical discussions about the reasons for such patterns continue, with increasing emphasis on nest predation and adult mortality. At work, however, are a host of factors ranging from phylogenetic history and constraints to age-specific trade-offs between fecundity and life span. Clutch size is only one trait in a complex network of interacting traits that guide the evolution of diverse life histories in a population context. Now broadening the discussion is the integration of physiological constraints that govern avian life cycles with the dynamics of population ecology that affect an individual bird’s lifetime reproductive success.

A formidable literature summarizes and interprets conspicuous patterns of clutch-size variation (Table 17–1). Clutch size is clearly an adaptation molded by selection over evolutionary time, but it is also sensitive to immediate environmental conditions. Some variations are due to genetic differences between individual birds, and others are due to a female’s physiological condition (see Chapter 12). The inheritance of egg-laying ability is well known to poultry farmers, who increase egg production by artificial selection. What number of eggs maximizes short-term or lifetime reproductive success for a particular species?

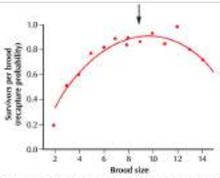
Table 17–1 *Conditions Correlated with Variations in Average Clutch Sizes*

Variable	**Conditions Correlated with Small Clutches (2–3 Eggs)**	**Conditions Correlated with Large Clutches (4–6 Eggs)**
Latitude	Tropics	Temperate/Arctic
Longitude	Eastern Europe	Western Europe
Altitude (temperate)	Lowlands	Highlands
Nest type	Vulnerable	Secure (cavity)
Body size	Large species	Small species
Habitat	Maritime, island, and wet Tropics	Continental, mainland, and arid Tropics
Feeding place	Pelagic seabirds	Inshore seabirds
Development mode	Altricial	Precocial

Theoretically, an optimal clutch size—for each bird in an average year—produces the maximum number of young capable of surviving to sexual maturity. Theoretically again, an average optimal clutch size should prevail in local populations. Understanding the evolutionary forces responsible for the evolution of a particular clutch size, however, remains one of the most controversial and unresolved challenges for ornithologists despite nearly half a century of intense research. The debate about the evolution of clutch sizes among birds centers on applications and extensions of David Lack’s original **food-limitation hypothesis.**

Food Limitation

The avian clutch size is adjusted by natural selection to the maximum number of nestlings that the parents can feed and nourish. Food availability limits clutch size. This fundamental postulate, which was championed with great force by David Lack (1947, 1948), guided research for more than half a century (Ricklefs 2000b). The hypothesis assumes that individual birds will be disadvantaged by natural selection if they lay fewer eggs each year than they can raise.



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Data from Perrins and Moss 1975

Figure 17–9 Lack’s hypothesis of optimal clutch size projects a maximum number of surviving young as a result of the balance between the number of young hatched and their probability of survival. In the population of Great Tits in Wytham Wood, broods of 10 to 12 chicks are the most productive. The average clutch size in this species is 8.5 (arrow).

The strongest support for Lack’s hypothesis comes from observations of the relative success of various sizes of clutches and from experiments designed to test the ability of parents to feed extra young. Some of these experiments were discussed in preceding chapters. In now-classic work, Christopher Perrins and Dorian Moss (1975) experimentally increased and decreased the clutch sizes of

Great Tits in Wytham Wood, near Oxford, England (Figure 17–9). Clutches of 10 to 12 eggs produced the most surviving young Great Tits. The probability of a chick's survival in a small brood was greater than in a large brood because the nestlings in a small brood are better fed and are heavier when they fledge, but the number of potential fledglings from small broods is, by definition, low. Above a brood size of 12, chicks tend to be underfed and to die, especially in "bad" years of poor food availability. In six of 13 consecutive years, the average natural brood size in the population was 10—that is, close to the most productive number—but the average brood size was slightly lower than predicted in other years, an outcome resulting in an overall average across years of 8.5.

Thus, birds seem to err on the side of caution. The vulnerability of large clutches in bad years favors moderate clutch sizes in the long run (Boyce and Perrins 1987). Conversely, the practice of brood reduction gambles on the bonus of the occasional survival of an extra egg or chick (see Chapter 16).

The strengths and weaknesses of Lack's hypothesis can be seen in its application to the increases in clutch size with latitude. The average clutch sizes increase with latitude for many passerines, owls, hawks, herons, terns, gallinules, some fowl, and some grebes. Lack (1947) proposed that this increase was due to the longer day length at high latitudes. Birds nesting during the long high-latitude summer have more time to find food for their young and themselves.

The potentially positive effects of increasing day length, however, do not explain why clutch sizes increase with latitude for owls that feed at night and thus have less foraging time, not more. Clutch sizes also increase not with day length but with longitude from east to west in Europe, with altitude in the temperate zone but not in the Tropics, and on the mainland compared with adjacent islands. Different day lengths can’t be the explanation for these trends. Finally, some species of birds can raise extra young that are added experimentally. Even some large seabirds, such as gannets, which normally lay only a single egg, can raise two young when an extra egg is added to the nest, without obvious short-term penalty (Nelson 1964).

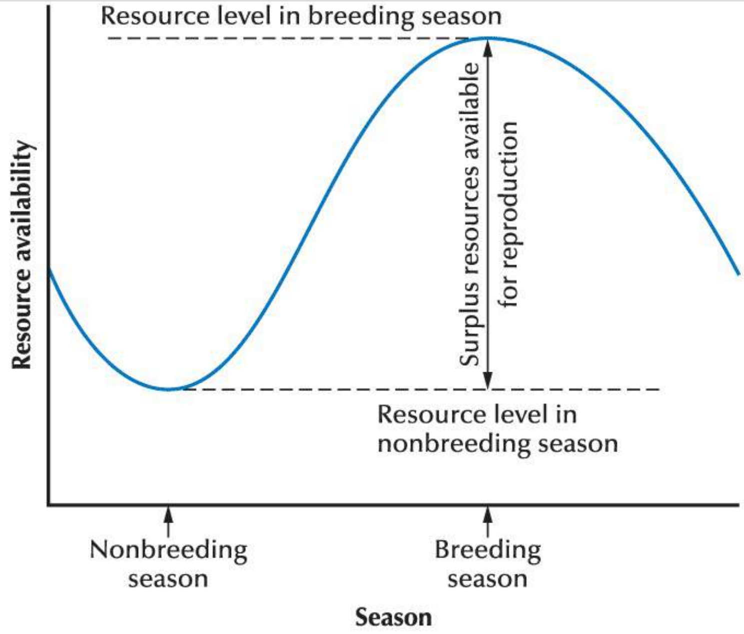
The inability of parents to care for fledged young is at least part of the reason why tropical birds tend to have small clutch sizes (Styrsky et al. 2005). Experimental manipulations of clutch sizes of Spotted Antbirds in Panama showed that parents could successfully feed nestlings in enlarged broods until they fledged. Postfledging mortality was not related to nestling mass two to three days prior to fledging or to predation. Instead, the inability of parents to care for the extra fledged young of enlarged broods reduced their survival.

Seasonality and Density Dependence

Lack’s hypothesis dominated the discussion of avian life histories for at least 20 years, from 1947 to 1967. In this period, two great ornithologists, Reginald Moreau and Alexander Skutch, led opposing, population-based viewpoints that emphasized the effect of population density on reproductive rate. They were, however, less forceful personalities than was David Lack (Ricklefs 2000b). As a result, their broader perspective did not prevail in their lifetimes. Their views were revitalized in a lucid challenge by Martin Cody (1966) and by new modeling approaches to population ecology.

From this work emerged the broader, modern population perspective of evolutionary ecology. This view recognizes the advantages of reducing the costs and risks of annual reproductive efforts to maximize lifetime reproductive success. The evolutionary ecology perspective also defined the effect of adult mortality, first on population density and then on reproduction rates through density-dependent effects on food availability.

Seasonality of food is the key to these relationships. Birds of seasonal arid habitats in both Africa and Ecuador have larger clutches than do those in habitats that are humid year-round at the same latitude. More generally, clutch sizes of birds relate directly to seasonal increases in food production rather than to absolute level of food production (Ashmole 1963b; Ricklefs 1980; Figure 17–10). This relationship exists because adult mortality in the cold or dry season of lowest food availability determines population density and baseline levels of food consumption in a habitat. The survivors as well as seasonal visitors then can benefit from increased per capita food availability in the spring.



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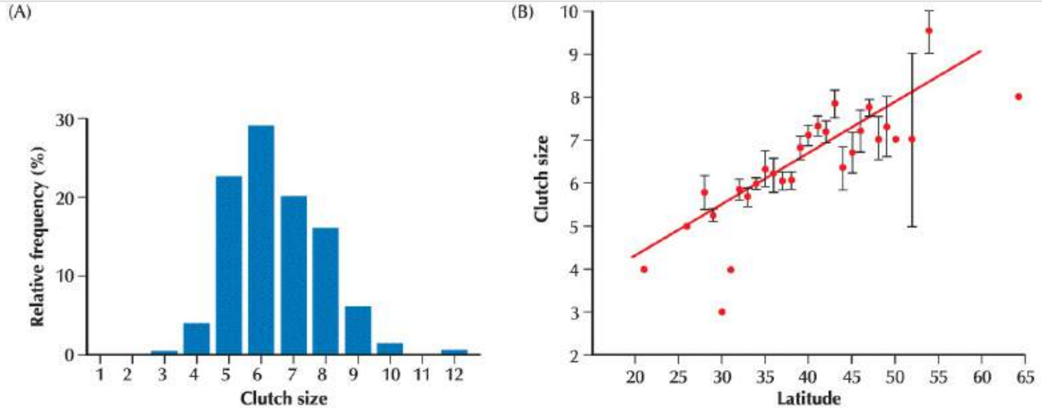
DATA FROM RICKLEFS 1980

Figure 17–10 The seasonality hypothesis for geographical variation in clutch size. Model of the seasonal increase in resources available for reproduction, measured in some months as the “surplus” above those resources that limit population size in the nonbreeding season. Clutch size varies in relation to the ratio of the breeding-season surplus to the adult population. Resources that are available during the breeding season depend on local demands by consumers, and these demands, in turn, depend on population density. The population densities of resident birds are regulated by low resource availability during the nonbreeding season. Seasonal increases above this baseline thus control the resources available for breeding on a per capita basis.

Through its control of adult mortality, variation in the seasonality of resources is the ultimate cause of geographical variations in clutch size, at least within a species. The pattern of clutch-size variation in the Northern Flicker, a widespread North American woodpecker, supports this “seasonality hypothesis” (Figure 17–11). Clutches of the flicker range from three to 12 eggs and increase by an average of one egg per

10 degrees of latitude. Variation in clutch size is directly correlated with the resources available to each breeding woodpecker. Walter Koenig (1984) estimated these resources as the ratio of local summer productivity (in terms of actual evapotranspiration, an index of plant productivity) to the breeding density of all woodpeckers. Local breeding densities of woodpeckers, in turn, are set by winter productivity, which determines how many woodpeckers survive until the breeding season.



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DATA FROM KOENIG 1984

Figure 17–11 (A) The clutch sizes of Northern Flickers vary from three to 12 eggs. Relative frequency equals the percentage of total sample that had *x* number of eggs. (B) The increase in average clutch size with latitude supports the seasonality hypothesis. Vertical lines on the graph represent local variation in clutch size.

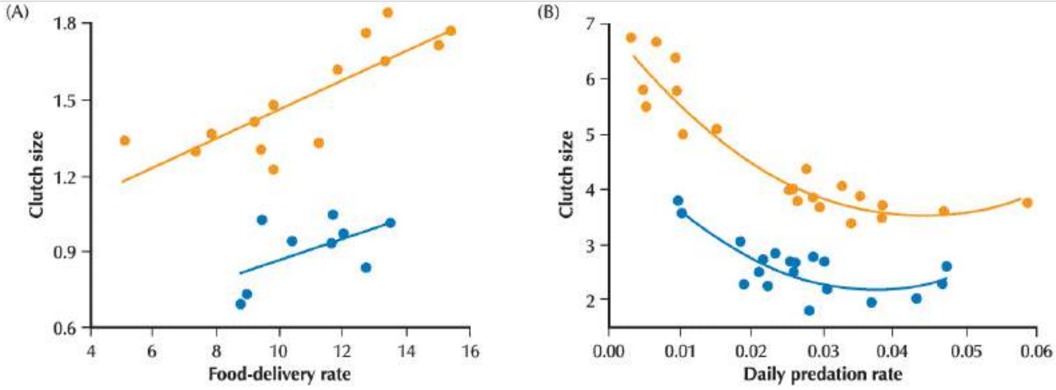
Predation

Adult mortality is one of the principal population processes that shape avian life histories. Nest predation is another. Nest predation is a major force in the evolution of avian life-history traits, ranging from nest construction and visitation (see Chapter 15) to clutch size and caring for young (Martin 2014).

In precocial birds, predation risk may limit clutch size by limiting the number of fledged young that parents can guard. Even though the parents of many shorebirds do not feed their precocial young, for example, they brood and tend them actively and guard them from predators. Physical distance between parents and their mobile young increases with brood size and potentially sets an upper limit on brood size (Safriel 1975).

Nest predation may favor smaller clutches of songbirds in several ways. First, small clutches take fewer days to complete, reducing the daily risk of their being found. Second, smaller numbers of young in a nest make less noise that might attract predators (see Chapter 15). Third, and perhaps most germane, reduced visitation by parents to feed smaller broods reduces the risk that nestlings (and parents, too) will be found and eaten. Selection, therefore, favors risking fewer eggs at a time and renesting as frequently as possible in (tropical) habitats with high nest-predation rates.

Support for this hypothesis about clutch size and renesting comes from comparisons of nesting pairs of matched bird species in Argentina and Arizona (Figure 17–12). Reduced visitation rates in the face of different levels of nest predation explain the variation in clutch sizes among bird species within Arizona and Argentina but not between the two regions. Instead, the difference between regions is best explained by differences in adult mortality and adult attentiveness during the incubation period, as already mentioned.



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DATA FROM MARTIN ET AL. 2000

Figure 17–12 Comparison of nesting pairs of matched bird species in Arizona (orange) and Argentina (blue) indicates that predation selects for smaller clutch sizes through rates of parental visitation. (A) Larger clutches produce larger broods that require more frequent parental visitation for delivery of food. (B) Clutch sizes are negatively related to the nest-predation rate within each locality. Lower adult mortality in Argentina selects for smaller clutch sizes, and predation rates play a significant but secondary role.

This chapter reviewed individual life-history attributes as they evolve in response to the environment mediated by population processes such as adult mortality. The dynamics of population trends themselves, including the nature of density-dependent regulation, are the subject of Chapter 18. The dynamics of bird populations based on the lifetime reproductive success of individual birds are also central to the themes of the final three chapters: the evolution of new species (Chapter 19), the coexistence of species in communities (Chapter 20), and the future viability of species, the heart of conservation of biodiversity (Chapter 21).

REVIEW KEY CONCEPTS

17.1 Life-History Patterns

Life histories are sets of evolved traits or attributes that interact with environmental variables to determine an individual bird’s lifetime reproductive success. The diverse life-history patterns of birds are the products of this evolutionary process.

Key Terms: life histories, age-specific survivorship, annual fecundity, life tables

17.2 Longevity and Life Span

Most small birds live from two to five years, whereas large birds may live from 20 to 40 years. Although many young birds die in their first year as a result of predation and starvation, the survival rates of adults are much higher and remain basically the same from one year to the next. Senescence has been demonstrated for several species of birds.

Key Terms: actuarial senescence, senescence

17.3 Fecundity

A fast–slow axis captures most of the variation among the diverse life-history patterns of birds. In general, short-lived species breed when one year of age and produce many young each year. Long-lived species tend not to breed until they are several years old and produce few young each year. Reproductive success and effort usually improve with age and experience.

Key Term: fecundity

17.4 Annual Reproductive Effort

A bird’s investment into annual reproduction affects its physical condition and its future reproductive potential. Trade-offs between the short-term costs of reproductive effort and the opportunities for breeding in the future compound the basic challenges of annual survival. Delayed breeding maturity increases lifetime reproductive success, especially in long-lived birds.

17.5 Evolution of Clutch Size

Lack’s original food-limitation hypothesis that birds raise as many young as they can feed is now amplified and informed by the integration of the population-density effects of adult mortality, seasonal food availability, and predation. High rates of nest predation favor smaller clutches.

Key Term: food-limitation hypothesis

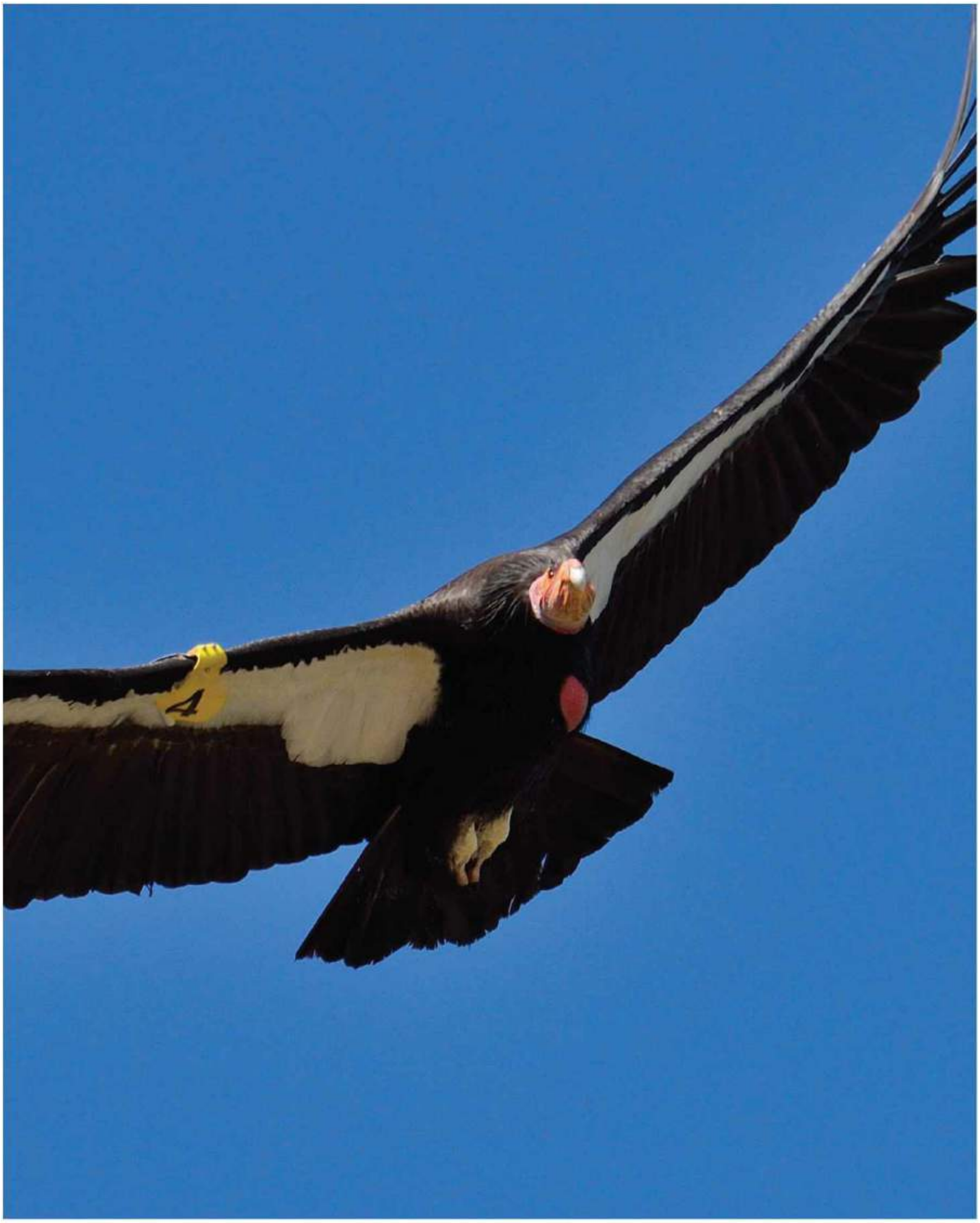
APPLY YOUR KNOWLEDGE

1. What aspects of life histories appear to be adaptations molded by natural selection that are inherited by descendants?
2. What factors are correlated with longevity across different species of birds?
3. Over time, what are the effects of increasing the number of eggs in a clutch above an optimal number? What factors define “optimal number”?
4. Describe the factors that best explain small versus large clutch

sizes for birds breeding in the same geographic area.

5. Describe the influence of seasonality, adult mortality, and food availability on life histories.
6. Describe the reasons that larger clutch sizes are produced by members of a species breeding at higher latitudes.
7. Describe possible reasons for clutch sizes of night-hunting owls increasing at higher latitudes despite the shorter nights during the breeding season.
8. Compare life histories of tropical and temperate birds in terms of the influences of seasonality.
9. How do the risks of predation influence clutch size and the number of clutches per year?
10. Consider annual survival rates and describe how delayed reproductive maturity increases the lifetime reproductive success.

PART V *Ecology and Conservation*



California Condor [Andriy Blokhin/Shutterstock.com]

CHAPTER 18 *Populations*

KLAUS NIGGE/GETTY IMAGES

Conservation management programs have increased the world population of the endangered Whooping Crane from 18 to over 400 in four free-living populations.

> The successful conservation of any threatened

> species requires knowledge of both its population biology and its ecological requirements. [Bourliere 1991, p. v]

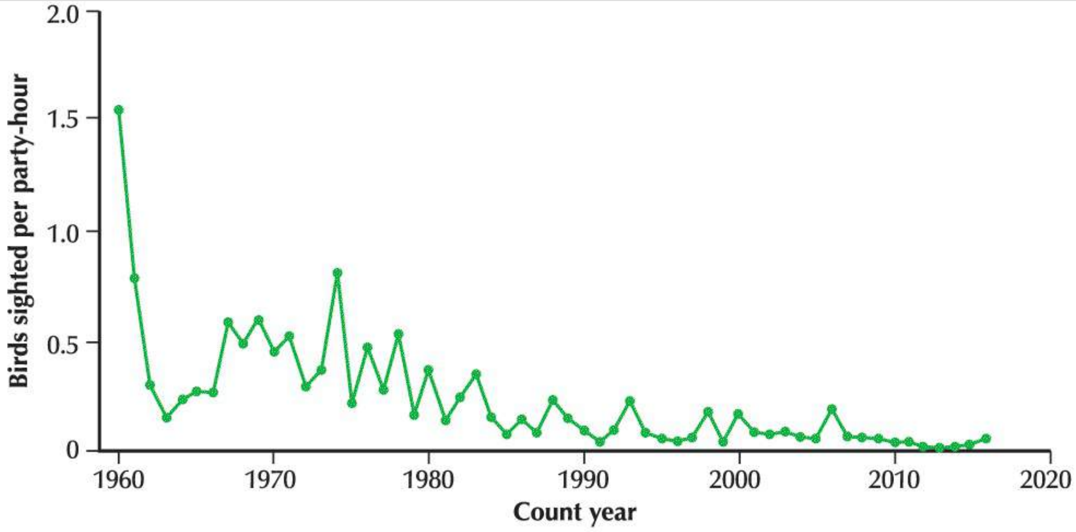
Bird populations fluctuate dynamically in their sizes and their distributions. Dramatic rebounds may follow worrisome declines, climate-induced bottlenecks, or local wipeouts due to disease or predation. Changes in population size, whether short term or long term, affect the genetic diversity of a population, the process of local selection, and the potential for speciation—the topics of Chapter 19.

The changes in local bird populations are the combined result of individual survivorship and fecundity augmented by immigration and emigration. Small-bird species with short generation times and large clutch sizes have high growth potential. They are able to respond opportunistically to environmental changes, including human-dominated landscapes. Large-bird species with long generation times, however, do not rebound as easily from their population setbacks.

This chapter on populations explores the dynamics of population sizes and distributions. We first consider the growth potential of populations and the factors that control or limit that growth. The next topic, population regulation, concerns the effects of density-dependent forces within populations, including social interactions. The final sections of this chapter summarize the value of long-term trends of bird populations as indicators of environmental quality. The population dynamics of a species are fully intertwined with their viability and their conservation needs, previewed here and then explored further in Chapter 21.

18.1 Growth and Declines

Some bird populations fluctuate dramatically in size from year to year. Others exhibit long-term stability, especially in the Tropics. Major storms or unpredictable climate shifts can affect local bird populations in the short term. Healthy populations, however, rebound from their short-term and sometimes severe setbacks (Box 18–1). For example, populations of Texas quail, especially the Scaled Quail, experience boom and bust years that correspond to rainfall (Figure 18–1). Bird populations also change slowly with the passage of time. Texas quail populations, both Scaled and Northern Bobwhite, are declining steadily due to habitat loss.



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DATA FROM NATIONAL AUDUBON SOCIETY 2016

Figure 18–1 Christmas Bird Counts document the long-term population decline of the Scaled Quail in Texas. A count year number reflects the year that the bird count ended (e.g., 2000 refers to the years 1999–2000). The total counts each year are standardized with respect to effort in terms of “party hour.”

Box 18–1

Rebound of the Short-Tailed Albatross

Although small populations of birds are vulnerable, they can be resilient. Most small populations have an intrinsic potential to rebound from severe reductions. A legendary case is that of the Short-tailed Albatross. It once nested in abundance in the western Pacific and congregated at the entrance to San Francisco Bay when whale slaughtering produced abundant food there.

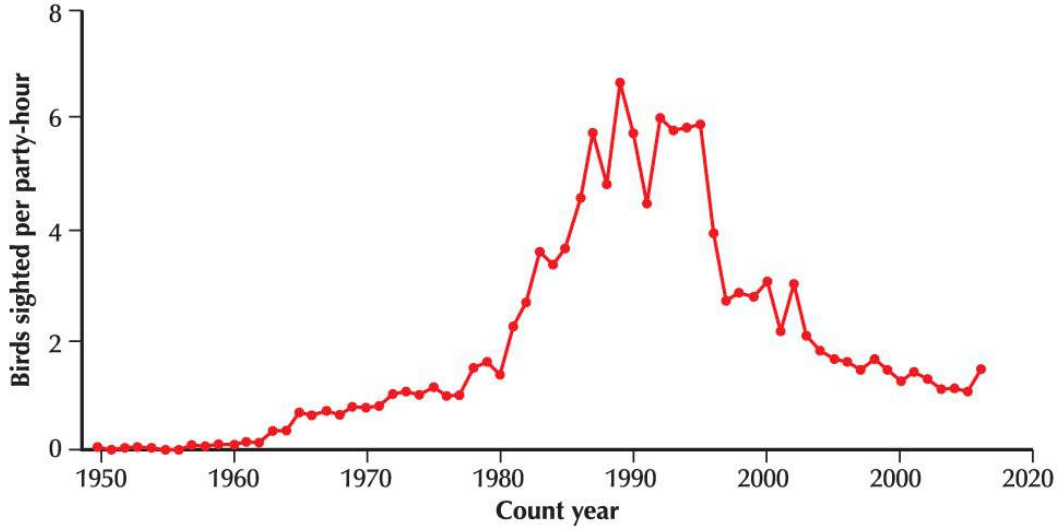
By 1929, feather hunters reduced this species to one population of 1,400 birds that bred at Tori-shima, an island refuge off southeastern Japan. Eruptions of the island’s volcano in 1939 and 1941 destroyed this remaining albatross colony. The species was declared extinct when no birds returned to the island to breed from 1946 to 1949.

Remaining, however, were some young birds that had been at sea. (Albatrosses wait 10 or more years before starting to breed.) In 1954, six pairs of these young survivors returned to Toroshima and produced a total of three young. Today, despite their low fecundity and delayed maturity, Short-tailed Albatrosses are recovering. The world population increased to 1,840 birds in 2005 and continues to rebound and to establish colonies on new islands.

BILL COSTER/ALAMY

The Short-tailed Albatross rebounded from near extinction.

Bird populations also have great growth potential. The 120 Common Starlings that were introduced into Central Park in New York City in 1890 multiplied into more than 200 million birds continent-wide in a century (Cabe 1993). More recently, but with similarities, the eastern population of the House Finch started when a few caged birds were released on Long Island in 1940. The population grew 21 percent per year from 1965 to 1979 (Figure 18–2). The range of the population expanded from Long Island throughout the eastern United States and Canada. The list of birds that have changed from scarce to abundant in recent times is long. Included on the list are waterfowl Canada Geese, Snow Geese, and Wood Ducks that have rebounded from overhunting in response to improved management practices.



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DATA FROM NATIONAL AUDUBON SOCIETY 2016

Figure 18–2 Exponential population growth and decline of House Finches introduced into New York State.

Some life-history traits, particularly **short generation times** (early age at first reproduction combined with short life span), foster the evolutionary and geographical success of species through their effects on population growth rates. The reproductive success of individual birds in the first generations quickly compounds itself, compared with species that take years to mature and have few young at a time. Short generation time explains why bacteria and insects multiply so fast. In both birds and mobile mammals, such as bats, short generation times also promote the ability to colonize, to speciate, and to diversify.

In general, large-bodied species with low reproductive rates have annual growth potentials ranging from 10 to 30 percent. Small-bodied species with large brood sizes and high reproductive potentials have an annual growth potential ranging from 50 to 100 percent in favorable years (Ricklefs 1973).

A thriving population in a new environment grows in size and then stabilizes in an S-shaped, or sigmoid, growth pattern. The rate of growth increases slowly at first, then accelerates, and later declines because of negative feedbacks that lower reproduction and survival. As the size of a growing population approaches the maximum supportable by the environment, called the environment's **carrying capacity,** the population growth rate slows down as its needs for resources begin to exceed their availability. The growing population also becomes increasingly vulnerable to predation and disease. The population then fluctuates in size about an equilibrium value that an environment can support in a typical, or average, year.

Life Tables

Changing population growth rates derive from the demographic parameters of lifetime reproductive success. Life tables help us to project lifetime reproductive success and population trends from the primary life-history attributes. Like the actuarial tables used in the insurance industry, **life tables** summarize the vital statistics of age-specific survivorship and also age-specific fecundity (Box 18–2). Four major attributes specify the performance of the average bird in a population: (1) the age at which a bird first reproduces, (2) its fecundity (the number of young that it fledges each year), (3) the survival of its young, and (4) its longevity, or life span, as an adult.

Box 18–2

Life Tables

To create a life table for a particular bird population, ornithologists follow the annual progress of a class, technically called a “cohort,” of individual birds from hatching until the last one dies. The proportion of the cohort that survives each year defines the annual survivorship, S_x. The probability of survival to a particular age, L_x, is the product of the preceding annual survival rates. The average number of young produced each year by an adult female in the cohort defines age-specific fecundity, B_x. The product L_xB_x specifies an individual bird’s expected annual fecundity, which is to say fecundity at a certain age discounted by the chance of dying before reaching that age.

The values of L_xB_x for all age categories, x, sum to define R_0, which is the net reproductive rate. R_0 projects an individual bird’s lifetime reproductive success and the expected rate of recruitment of new birds into the population. If one female replaces herself by a daughter during her lifetime, R_0 equals 1. A population composed of many such females should be stable in size. When values of per capita replacement, R_0, are greater than 1, they correspond to a growing population, and values less than 1 correspond to a declining population. Thus, if $R_0 = 1.5$, the population will increase 50 percent in one generation. Conversely, a value of 0.8 indicates a declining population.

The age at which a young bird first reproduces is a vital statistic. Theoretically, an early start has the greatest effect of all the variables on a bird’s potential reproductive contribution to succeeding generations. The age at first breeding controls the interval between generations—or **mean generation time** (when children produce grandchildren)—which, in turn, drives the potential growth rate of a population. Consequently, age at first breeding dictates response time to natural selection or environmental change, and thus the potential for speciation. In addition, slow-maturing species, such as the California Condor and the Whooping Crane, are easily endangered and slow to recover from overhunting, accidental mortality, or outbreaks of disease because they are slow to replace reproductively active adults.

Consider the life tables compiled for Eastern Screech Owls (Table 18–1). Fred Gehlbach (1994) tallied life-table statistics for two study populations in Texas, one in the suburbs and the other in rural woodlands. These small owls commonly nest in cavities in wooded habitats. They live between seven and 13 years and produce one brood of two to three young each year.

Table 18–1 *Time-Specific Life Tables for Female Eastern Screech Owls in Either a Suburban or a Rural Study Area, 1976–1991*

Age Classes[a]	S_x[b]	L_x[c]	**Average Number of Fledglings per Individual**	B_x[d]	LB_x[e]
Suburban					

Fledglings Adults	0.36	1.00	0.0	0.0	0.00
1	0.49	0.49	1.6	0.8	0.39
2	0.58	0.18	2.6	1.3	0.23
3	0.61	0.10	3.1	1.5	0.15
4	0.67	0.06	3.2	1.6	0.10
5	0.75	0.04	2.7	1.3	0.05
6	0.75	0.03	2.7	1.3	0.04
7	0.75	0.02	2.7	1.3	0.03
8	0.75	0.02	2.7	1.3	0.03
9	0.75	0.01	2.7	1.3	0.00
10	0.75	0.01	2.7	1.3	0.00
Rural					
Fledglings Adults	0.30	1.00	0.0	0.0	0.00
1	0.36	0.30	1.6	0.8	0.24
2	0.60	0.11	2.3	1.1	0.12
3	0.67	0.06	3.2	1.6	0.10
4	0.53	0.04	2.0	1.0	0.04
5	0.50	0.02	2.0	1.0	0.02

[a] All age classes present in each study area are included. Numbers in

column represent age (in years) of adult.

[b] S_x, survivorship.

[c] L_x, probability of survival.

[d] B_x, number of female offspring per female subject, based on known 1:1 sex ratio.

[e] Summation of values in this column yields an R_0 (population replacement rate) = 1.01 for the suburban population and R_0 = 0.52 for the rural population.

DATA FROM F. R. GEHLBACH (1994).

In the suburbs, annual survivorship, S_x, of the screech owls increased with age to a maximum of 75 percent per year. Individual owls achieve full breeding potential by the age of two years, by which time each female produces an average of 1.3 female offspring each year, B_x. Actually, reproductive output varies greatly among females, and a minority (less than 25 percent) of long-lived females produced most of the fledglings. Adding the annual products of survivorship and fecundity L_xB_x yields the net reproductive rate, R_0. In this case, R_0 is 1.01, a value indicating simple lifetime replacement of an average female by one daughter and thus a stable population size.

Screech owls, however, do not fare as well in the rural woodlands of central Texas. Both annual survival and fecundity are lower there, yielding a net reproductive rate of 0.5. That study population was declining.

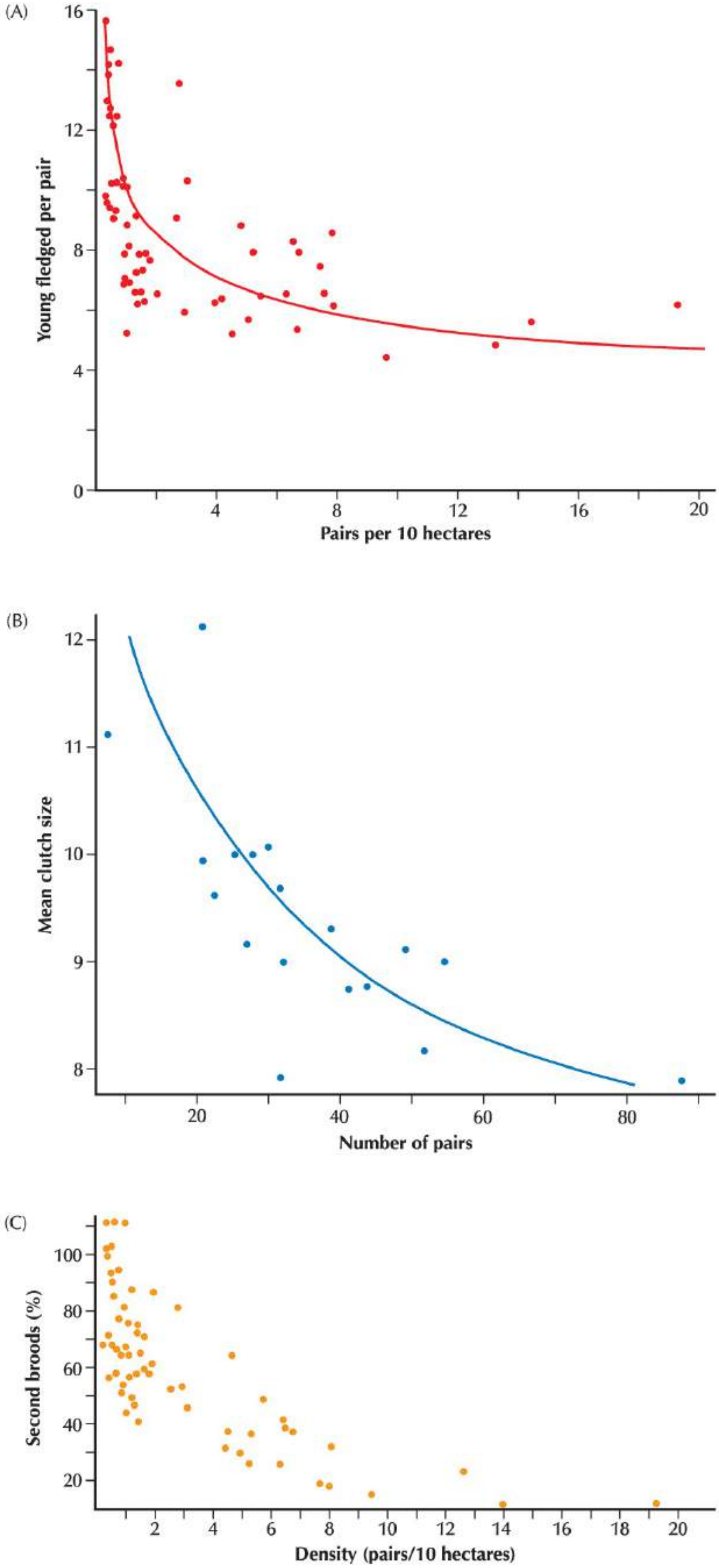
The recruitment of young birds into a local population every year drives the growth of a local population. Local recruitment includes the number of young produced in the breeding season and, particularly, the number that survive their first six months of life. In addition to those produced locally, recruits include young from other places. Immigrants contributed significantly to the 19 percent annual growth of the population of Atlantic Puffins on the Isle of May, off eastern Scotland, from 1973 to 1981 (Harris and Wanless 1991; see also Figure 21–12).

Widespread bird species comprise many smaller local populations that exchange individuals (and their genes) through immigration and emigration. Some local populations, called sources, produce excess young that disperse to find a place in another breeding population. Other local populations (sinks) cannot sustain themselves except through annual immigration. Together, these local populations aggregate into larger metapopulations that integrate landscapes of local population dynamics.

18.2 Limitation and Regulation

Ecologists distinguish between the terms “limitation” and “regulation” of population sizes. **Limitation** refers to any ceiling on population growth. Habitat, food, climate, disease, and predation are the primary forces that limit the sizes of bird populations.

Regulation refers specifically to the effects of population density on population size. Density-dependent changes in birthrates and death rates buffer the short-term fluctuations in populations. Both mean clutch size and number of fledglings of the Great Tit, for example, depend on local population density. Great Tits lay fewer eggs when population density is high than when it is low. Sixty percent of the variation in annual mean clutch size is directly related to population density. Success in rearing nestlings also decreases as population density increases because of increased predation and because fewer females attempt second broods (Figure 18–3).



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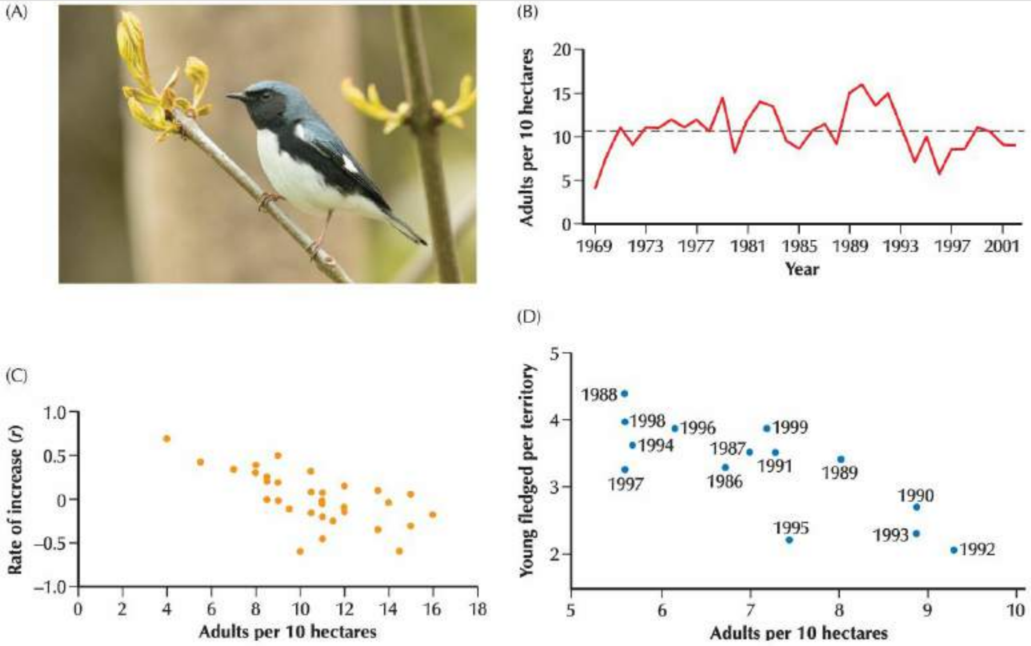
Data from Kluijver 1951, Klomp 1980

Figure 18–3 (A) Reduced fecundity at higher densities in the Great Tit is due to (B) smaller clutches at high population densities and (C) less frequent attempts to raise second broods.

Black-throated Blue Warbler populations exhibit density-dependent stabilization on their breeding grounds in New England—specifically, the number of young that they fledge and the quality of those young (Sillett and Holmes 2004; Figure 18–4; see Chapter 17). As population density of the warblers increased, individual annual fecundity (number of young fledged and average mass of fledglings) declined; so did the annual growth rate of the population. Females in denser populations also attempted fewer second broods. Conversely, the number of young fledged and their quality, as well as the number of second broods, increased at low densities. The experimental removal of neighbors confirmed this dynamic: the number of young fledged on the remaining territories increased (Rodenhouse et al. 2003; Figure 18–5). These density-dependent effects caused low population densities to rebound and high population densities to reduce themselves. Consequently, the population density regulated itself at a long-term stable average of 10 adults per 10 hectares.



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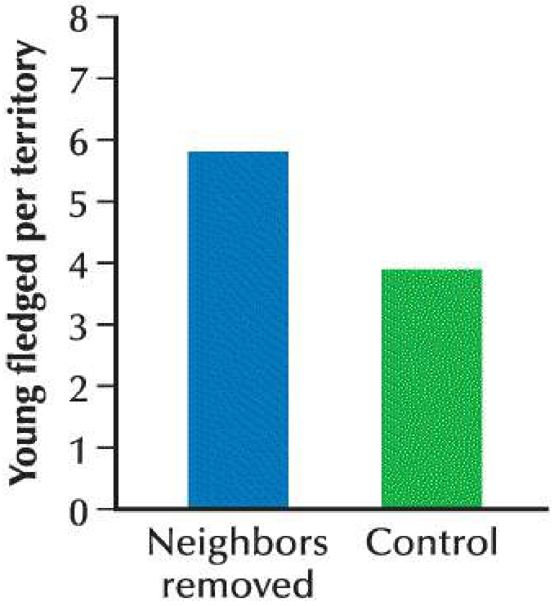
Data from Rodenhouse et al. 2003. Jerry Goldner

Figure 18–4 Density-dependent population regulation in the (A) Black-throated Blue Warbler. Population trends are from plots at Hubbard Brook Experimental Forest in New Hampshire. (B) The number of adults was stable for 30 years with minor fluctuations about an average of 10 per 10 hectares. (C) Population growth rate was negatively correlated with population density each year, causing decreases in abundance after years of high density and increases in abundance after years of low density. (D) Annual fecundity declined as the density of breeding adults increased on a 64-hectare plot. Numbers are years.



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Data from Rodenhouse et al. 2003

Figure 18–5 Black-throated Blue Warblers. Experimental removal of neighbors reduces density and increases fecundity (number of young fledged per territory).

Long-term studies of the demography of the Snow Goose nesting colony at La Pérouse Bay, Manitoba, illustrate other negative consequences of increasing population density (Cooch and Cooke 1991). These studies documented an 8 percent annual growth of the population followed by a decrease in its growth rate due to the damage inflicted by the geese on their own Arctic marsh feeding grounds. The growing population damaged the quality and availability of the nutritious tundra grass required by breeding geese and their goslings. First-year survival declined from 50 to 35 percent. Population growth slowed due to density-dependent processes.

The distinction between “limitation” and “regulation” can be challenging. Food supply, for example, can limit numbers in either a density-dependent way or a density-independent way. The proportion of birds that starve would be independent of population density if mass starvation were due to a major ice storm that eliminated critical food supplies. On the other hand, the proportion of birds that starve may depend on the number of birds that vie for declining winter food supplies that can potentially support, say, 50 birds but not 100 birds.

The life-history parameters of fecundity or survival may be subject to density-dependent influences, but each by itself may not limit population sizes. Density-dependent clutch sizes, for example, might not limit population size if, instead, hurricanes kill most of the juveniles each year, limiting recruitment into the breeding population no matter how many chicks fledge. More importantly, density-dependent effects on the breeding grounds interact with those on the wintering grounds of migratory species to establish the dynamics that control population size (Sherry and Holmes 1995).

Habitat

Habitat availability determines population size more than any other factor. Many endangered species are extreme habitat specialists with limited and local distributions that correspond to their particular needs. The Red-cockaded Woodpecker, for example, is intimately tied to old-growth southern pine forests. Unlike most woodpeckers, Red-cockaded Woodpeckers excavate their nest cavities in living rather than dead pine trees. They require a highly limiting resource—namely, pine trees that are 80 to 100 years old and have been infected by the red heart fungus. The fungus rots the old pine tree’s heartwood just enough to allow the woodpeckers to excavate. This excavation, however, requires a major investment of time and energy. Not surprisingly, clans of this cooperatively breeding woodpecker reuse the same cavities for years.

Major reductions in primary habitats reduce bird populations accordingly and trigger conservation concerns. The losses of California chaparral, riparian forests, grasslands, and wetlands all impact specialist bird species. Like Red-cockaded Woodpeckers, Spotted Owls depend on the remnant old-growth forests in the Pacific Northwest. These forests now cover less than 10 percent of their original extent. The severe loss of chaparral endangers the California Gnatcatcher. Rails, bitterns, and waterfowl populations declined throughout the United States as wetlands were drained for agricultural, industrial, and suburban development. Less than 10 percent of the original wetlands of California remain.

The essential resources provided by a particular habitat range from food to nest sites. For some birds, the availability of nest holes limits population size. Woodpeckers can dig their own nest holes, but other birds must either use abandoned woodpecker holes or dig their own in soft dead wood. Dead trees and branches are routinely removed from the managed forests of Britain and other parts of Europe. The resulting shortage of nest sites there caused the extirpation of the White-backed Woodpecker and clearly limited the population densities of species such as the Great Tit and the Eurasian Pied Flycatcher. In lieu of natural nest holes, these species readily adopt nest boxes, which increase local population densities. In North America, Eastern

Bluebirds rebounded following the installation of bluebird nest-box trails. This recovery is one of the great North American conservation success stories (Chapter 21).

Widespread deforestation favors species that inhabit open country but hurts species tied to large timber, such as Pileated Woodpeckers and Broad-winged Hawks. Once scarce, birds of cleared and second-growth habitats, such as the Chestnut-sided Warbler, the American Robin, and the Indigo Bunting, became widespread and abundant in open fields and shrublands. However, their course has reversed. They are declining with the regrowth of the forests in the eastern United States and the loss of open spaces.

Changes in the forest understory also affect bird populations in forests. The population explosion of the white-tailed deer in eastern North America poses a major threat to the future of deciduous forests in North America (Rooney and Waller 2003). They destroy the normal vegetation structure of a maturing forest by eating and killing young plants that provide the low cover and shrub layers required by many understory forest birds, including Hooded Warblers, Northern Ovenbirds, and Wood Thrushes.

Because of their high densities on tropical wintering grounds, migrant birds are especially vulnerable to the destruction of natural habitats (Terborgh 1980). Clearing one hectare of forest in Mexico eliminates the same number of warblers that clearing from five to eight hectares of breeding habitat does in the United States. Many migrants congregate to winter in the prime agricultural lands of tropical highlands. Conservation of these tropical habitats will be essential to maintain viable populations of Neotropical migrants.

In recognition of the loss of habitat, many conservation efforts have shifted their emphasis in recent years from species protection to the preservation of critical habitats. Birds respond quickly to the availability of good habitat. Restored riparian woodlands and regrowth forest all attract appropriate bird species, which grow robust local populations. Wetland species and grassland species also are highly mobile and opportunistic; they find and use desirable habitat wherever it is available.

Food

Food supplies, which often depend on climate, limit population growth and influence population sizes, most conspicuously in the form of year-to-year changes.

Most of the evidence of starvation among temperate-zone birds comes from density-independent losses of songbirds, waterfowl, and waders during hard winters. In one example, hard winters are the major cause of mortality of adult Carolina Wrens. These wrens have expanded their range northward for decades, with periodic setbacks in winter periods of severe cold, snow, and ice. Maurice Brooks submitted an early report of the severity of these events:

> In central West Virginia, and in most parts of northern West Virginia, Carolina Wrens (*Thryothorus ludovicianus ludovicianus*) have been, as far back as our records go,

> among the commonest permanent resident birds. This spring (1936), however, they have practically disappeared over the entire area, and we are forced to the conclusion that the unusually severe winter of 1935–36 virtually wiped out the species here.
>
> The birds were abundant around Morgantown, Monongalia County, until early January, and were noted in the usual numbers during the week following Christmas at French Creek, Upshur County. During late January, however, this section was subjected to temperatures ranging from sixteen to thirty degrees below zero and after that the species was not again noted until April. One boy in Upshur County found five Carolina Wrens frozen to death, and there were other reports of individuals found dead. [Brooks 1936, p. 449]

Detailed local studies documented the correlation between food abundance and size of island populations of Darwin’s finches (Grant and Grant 2011). Daphne Major, one of the small islands in the Galápagos archipelago, suffered severe drought in 1977, resulting in a critical shortage of the seeds that sustain the resident ground finches. When seed abundance plunged sharply in both number and volume, finch abundance declined by a similar order of magnitude in both number and total biomass (Table 18–2; see also Figure 1–15, which illustrates the effect of this event on average bill sizes in the population).

Table 18–2 *Effects of Seed Availability on Ground Finch Abundance on Daphne Major in the Galápagos*

	Seeds		**Finches**	
Year	**Total Number per Square Meter**	**Total Volume (cm^3/m^2)**	**Total Number**	**Biomass (kg)**
1973 (wet)	4,821	15	1,640	26
1977 (dry)	295	5	300	6
DATA FROM GRANT AND GRANT (1980).				

Seabird populations mirror their food supplies. Millions of Peruvian seabirds starve when their main food—the anchovy, a small fish—disappears over short time periods as a result of changes in surface-water temperatures due to El Niño. The total population of cormorants, pelicans, and other seabirds dropped from 27 million to 6 million birds in 1957 and 1958, increased to 17 million as food supplies returned, and then plummeted again to 4.3 million birds in 1965 (Idyll 1973). In recent years, the maximum number of seabirds in good years has declined due to the overfishing of the anchovy populations. Seabird populations throughout the world face similar challenges.

Widespread food shortages cause **irruptions** of populations, especially of birds from the arctic and subarctic regions. The periodic southward invasions by Snowy Owls are a classic spectacle coinciding

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Figure 18–6 Snowy Owl irruptions can be spectacular to observe.

with the cyclic abundance of lemmings of the tundra (Figure 18–6). More than 14,000 Snowy Owls were counted in southeastern Canada and New England during the great invasion of 1945–1946. Spectacular invasions in recent years have engaged citizen scientists in the study of them. Augmented by the use of geolocation tracking devices of Project SNOWstorm (http://www.projectsnowstorm.org), the study of these irruptions reveals that Snowy Owls undertake more extensive and regular movements than was previously suspected.

Irruptive invasions of the seed-eating birds of northern coniferous forests also create dramatic population events (Bock and Lepthien 1976). Invasion years, which are often the same in the New and Old Worlds, correspond to years of poor boreal forest seed production. During these invasions, flocks of northern finches appear along roadsides and at backyard feeders. Eight North American species—the Pine Siskin, Red-breasted Nuthatch, Red Crossbill, White-winged Crossbill, Purple Finch, Pine Grosbeak, Evening Grosbeak, and Common Redpoll—tend to invade in the same years.

Enemies

Predators, parasites, and diseases are natural enemies that zero in on prosperous species and cause local densities to drop or distributions to contract. If the effect is occasional or short term, the local populations vary in annual size. If the negative forces are chronic or severe, some local populations become extinct, especially if they cannot recruit dispersing birds from other populations.

Natural predators are a major source of annual mortality among birds, especially nestlings, incubating females, and weak, sick young birds in their first year. Relentless predation also is a driving force of natural selection for escape behaviors, camouflage plumage, and social behavior.

Introduced predators threaten endangered island birds. Most of the 129 bird species that have become officially extinct in the past 500 years are island species. Roughly half of these species were exterminated by introduced predators and diseases. The rest were driven to extinction by direct human exploitation and habitat destruction.

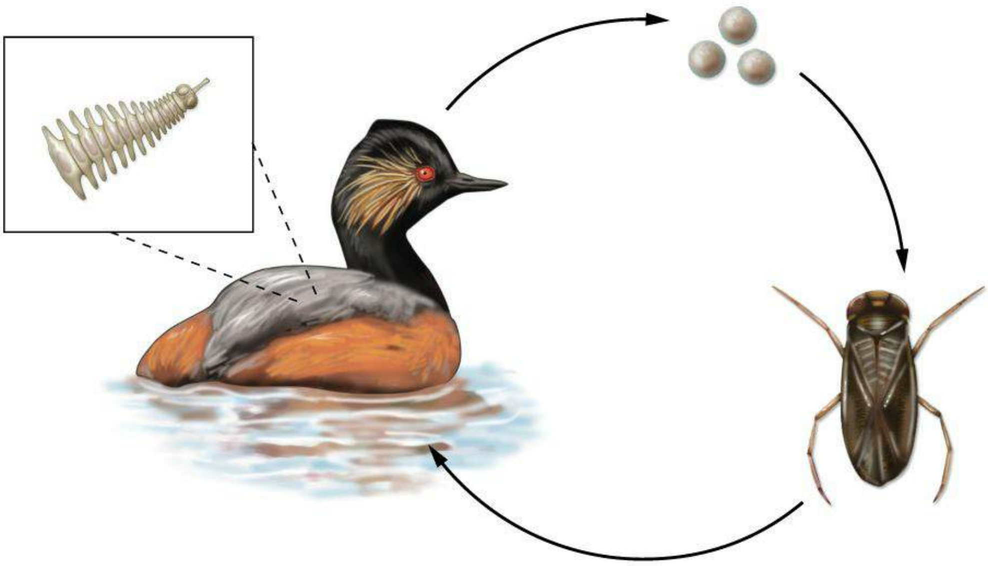
Predators may or may not regulate the bird populations on which they prey. Some populations of grouse, however, go through regular cycles of growth and decline that correspond to the intensity of predation. The populations of the Ruffed Grouse of Alaska, Canada, and the Great Lakes states cycle at intervals of eight to 11 years in concert with population cycles of the snowshoe hare (Rusch et al. 2000). Predators, especially Northern Goshawks and Great Horned Owls, switch to grouse as the hares decline, causing the numbers of grouse to decline also, with a slight lag. The regulation of population cycles, however, usually involves multiple ingredients that are untangled below (section 18.4) for one species, the Red Grouse of the highland moors of Scotland.

Predation on duck nests by mid-sized predators, such as raccoons and red foxes, is a primary source of mortality of hen ducks and other game birds. Ironically, high rates of predation on game-bird nests tend to be our own doing. They are due to the removal of top predators, such as coyotes and wolves. These large animals ate the mid-sized predators but do not severely prey on nests (Crooks and Soulé 1999).

Reduced local persecution of coyotes is now a management strategy to improve nesting success in Canada.

Parasite infections and diseases also can devastate bird populations. They can have severe effects on the ecology, life histories, and evolution of birds. Among the many consequences, increased exposure to parasites spurs birds to invest more into immune defense (Lindström et al. 2004). In that way and others, parasite loads bias mate choice, drain energy required for reproduction, and favor traits, such as plumage quality and display endurance, that signal male health (see section 13.1).

The parasites of birds range from parasitic worms and blood parasites to ticks, mites, bedbugs, and blowflies. Grebes host at least 249 species of parasitic (helminth) worms (Figure 18–7). More than 100 of these worm species are grebe specialists (Storer 2000). Colonial bird species generally host substantial loads and a high diversity of kinds (taxa) of blood parasites, or hematozoa (Tella 2002). Maggots of blowflies and botflies infect a high proportion of the nests of many temperate-zone species as well as tropical songbird species (Figure 18–8). The maggots weaken and kill the nestlings by draining substantial quantities of blood and other fluids.



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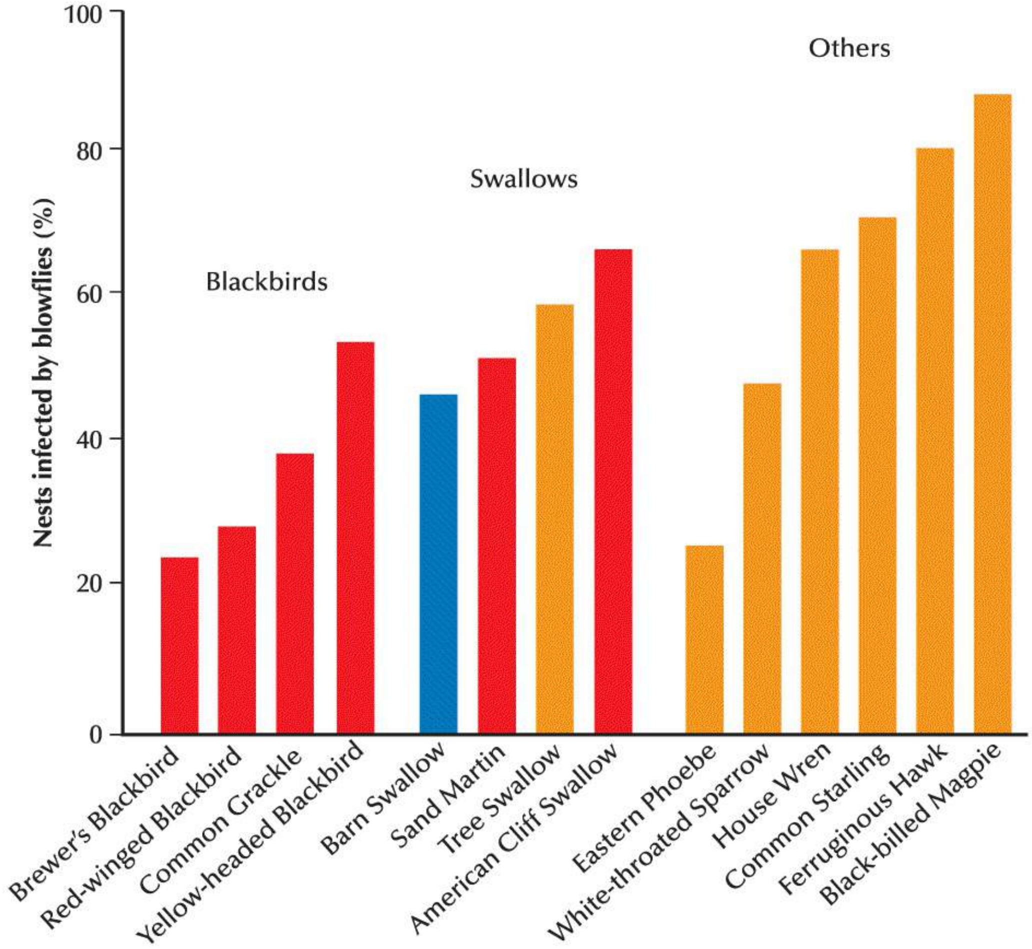
DATA FROM STORER 2000

Figure 18–7 Life cycle of a common cestode parasite (*Tatria biremis*) of grebes of the Northern Hemisphere. All but one of the 29 species in the family Amabiliidae are grebe specialists. Individual Eared Grebes, the definitive host shown here, carry an average of 2,794 worms apiece. Worm eggs passed from the grebe’s intestine are picked up by the intermediate host, a corixid bug, which the grebes later eat and complete the cycle.



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DATA FROM LOYE AND CARROLL 1995

Figure 18–8 Frequencies of nest infection by blowflies. Red bars represent colonial nesting species. Orange bars represent solitary nesting species. The Barn Swallow (blue bar) nests both solitarily and colonially.

Similarly, parasitic blowflies accidentally introduced into the Galápagos Islands in 1997 now infect most of the nests of Darwin's well-known finches, including the endangered Mangrove Finch (Fessl and Tebbich 2002). The larvae feed on the blood of the nestlings at night, and sometimes burrow deep into their bodies, including their brains. On the island of Santa Cruz, the average finch nestling had 23 maggots on it. One-quarter of the nestlings surveyed were dying as a result of the infection. Death rates of finch juveniles also are rising.

Local outbreaks of diseases, both bacterial and viral, occur regularly in bird populations worldwide and make headlines in the news as threats to human health, too (Box 18–3). Island bird populations are particularly vulnerable to disease because they lose their resistance to mainland diseases. For example, diseases destroyed lowland populations of the Hawaiian honeycreepers that survived the early deforestation of the islands. Captain Cook and his successors accidentally introduced mosquitos to the islands in the early 1800s. The mosquitos carried bird pox and malaria, which eliminated native birds at low altitudes (Olsen 1992). The potential spread of other diseases, such as that caused by the West Nile virus (WNV) into small and island populations of endangered species, including the endangered Hawaiian honeycreepers, is a major concern.

Box 18–3

Avian Flu

The global success of modern Euro-Caucasian societies traces to the origins of agriculture and the domestication of animals thousands of years ago. New diseases transferred from domesticated livestock and poultry, however, were one of the costs of the agricultural revolution (Diamond 1999). Smallpox, for example, came originally from swine. Now, animals carry and transmit 863 of the 1,415 microbes that cause diseases in humans. Cats and dogs transmit 43 percent of those human disease–causing microbes, livestock 39 percent, and rodents 23 percent. Birds transmit just 10 percent (Rosenwald 2006).

Outbreaks of viral diseases occur regularly in bird populations. Arboviral and other mosquito-borne diseases, including West Nile, are just one category of them. Their levels of transmission to humans are typically low.

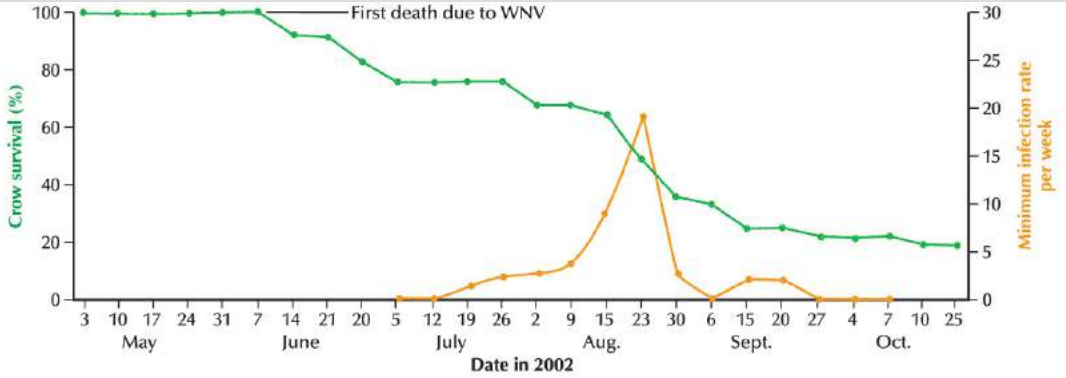
Waterfowl carry many genetically distinct strains of avian influenza viruses, which are occasionally transmitted to domestic poultry and humans, sometimes with deadly results. The “Russian flu” spread from central Asia to Russia, Europe, and North America in 1889–1990 and killed about 1 million people. The “Spanish flu” of 1918–1919 killed at least 40 million people. Subsequent epidemics have been less deadly due in part to the widespread recent use of flu vaccines.

Influenza viruses come in three primary forms. Bird flu is caused by the most virulent of the three forms. A deadly H5N1 strain of avian flu emerged in the chicken farms of Asia, first in China and then in South Korea. It is spreading to wild bird populations as well as throughout the poultry industries of Asia, Europe, and Africa.

The virus causes high levels of mortality in wild birds (BirdLife International 2006). Between 5 and 10 percent of the world population of the Bar-headed Goose perished in the outbreak at Lake Qinghai in China in the spring of 2005. The virus was also isolated from the Red-breasted Goose in Greece. Most of the world population of 88,000 winters in Romania and Bulgaria, both affected countries.

What should be done—or not done? From a human health perspective, H5N1 is not yet a major threat, pending critical mutations of the virus that would enable human-to-human transmission. The mandatory destruction of domestic poultry has major economic and social costs. As to the wild birds themselves, the evidence for the role of wild birds spreading the disease remains weak. Illegal traffic of infected poultry is responsible for the rapid spread of the disease. Further, the World Health Organization, the Food and Agriculture Organization, and the World Organization for Animal Health agree that the control of avian influenza in wild birds by culling is not feasible. They point out that attempts at culling would spread the virus more widely as survivors disperse to new places and healthy birds become stressed and more prone to infection.

The arrival of the West Nile arbovirus on the East Coast of the United States in the summer of 1999 drew both public and professional attention to the potential consequences of diseases in native bird populations. The uncontrolled WNV spread across the country from New York to California in just five years. Heavy summer rainfalls caused local increases in arboviruses transmitted by burgeoning *Culex* mosquito populations. Hard hit were local populations of American Crows, raptors such as Great Horned Owls and Red-tailed Hawks, and a variety of songbirds, including Black-capped Chickadees (Bonter and Hochachka 2003; Caffrey and Peterson 2003; Figure 18–9). Illinois was especially hard hit when the disease arrived in 2002. Widely distributed, abundant species, such as the crows, rebuilt local populations in a few years by recruiting young crows from other populations. Mortality then declines as resistant birds prevail by virtue of natural selection (Reed et al. 2009).



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DATA FROM YAREMYCH ET AL. 2004

Figure 18–9 Effect of West Nile virus (WNV) on a radio-tagged American

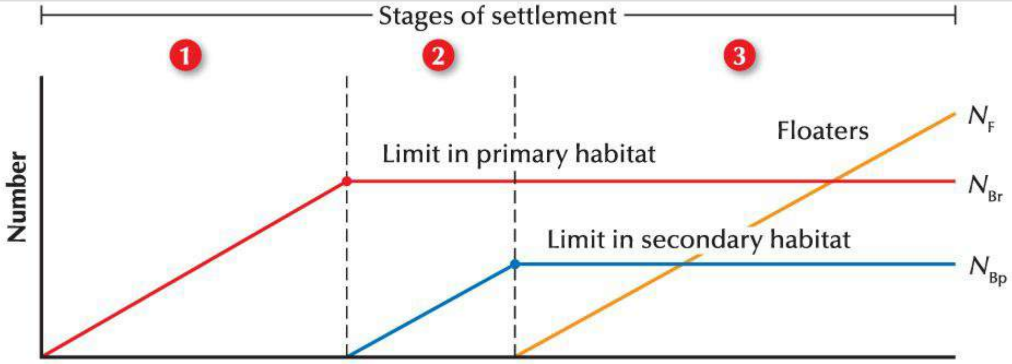
Crow population in Illinois. The survival curve (green) illustrates the short-term loss of 31 of 39 crows relative to WNV minimum infection rates (orange) of mosquitos collected weekly at crow roost sites in east-central Illinois in 2002.

One of the best documented examples of the decline of a bird species caused by bacterial disease is that of the introduced and rapidly expanding population of House Finches in eastern North America, mentioned earlier in this chapter. A new infectious disease reversed their growth into a significant density-dependent decline (Hochachka and Dhondt 2000). The first cases of conjunctivitis, caused by a novel strain of the poultry disease pathogen *Mycoplasma gallisepticum* and manifested as conspicuous swellings of the eye, were reported from Washington, D.C., in the winter of 1993–1994. The pathogen typically kills an infected bird within two to four weeks. Arrival of the disease in different places consistently causes the local House Finch populations to stabilize at a lower level (see Figure 18–2). Also documented by this study for the very first time was the geographical spread, or epizootic, of a novel strain of disease-causing bacteria in wild bird populations.

18.3 Social Forces

Social forces mediate the availability of habitat and, therefore, local population size in density-dependent ways. Territorial behavior, for example, spaces individual birds according to the available resources. Competition for the best territories can be intense and density dependent. The spacing of territorial individual birds in primary habitat excludes some birds from the breeding population or forces them to occupy secondary habitats where nesting is less successful and the risk of mortality is greater.

The occupation of available habitat has three stages (Figure 18–10). First, primary habitat fills up. Then, unable to find vacancies in primary habitat, surplus birds move to suboptimal habitat and wait for vacancies in better habitat. Finally, as suboptimal habitats are filled, remaining birds must wait, usually as floaters, for vacancies in either habitat. Defined as nonterritorial birds whose movements exceed those of territorial birds (Winker 1998), **floaters** live singly on home ranges that overlap the breeding territories of established pairs. They also may form flocks in areas that are not occupied by territorial breeders. In effect, floaters indicate that the size of the breeding population is limited by the (saturated) habitat available.



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DATA FROM BROWN 1969

Figure 18–10 Stages of settlement in a local population of breeding birds. The first breeding birds to arrive in an area occupy primary habitat (stage 1). Birds unable to establish territories in primary habitat settle in secondary—or poorer—habitat (stage 2). Floaters are birds unable to establish territories because they arrive after all the breeding habitat is filled (stage 3). Abbreviations: N_F, number of floaters; N_{Br}, number breeding in primary habitat; N_{Bp}, number breeding in secondary habitat.

Nonterritorial floaters constitute about 50 percent of a population of the Rufous-collared Sparrow (Smith 1978; Figure 18–11). This tropical bunting, which is closely related to the White-crowned Sparrow of North America, defends territories and breeds throughout the year. Floaters, or members of the “underworld,” live in well-defined, small home ranges. Males and females of the underworld with overlapping home ranges have well-defined, intrasexual dominance hierarchies. The dominant birds of the appropriate sex fill new vacancies. Floaters quickly replace established males that disappear or that are experimentally removed. The dynamics of control and attempted takeover of limited territorial spaces are illustrated by Susan Smith’s description of what happened when a territorial male Rufous-collared Sparrow (color-banded RO) disappeared for nine days after capture and banding on August 10:

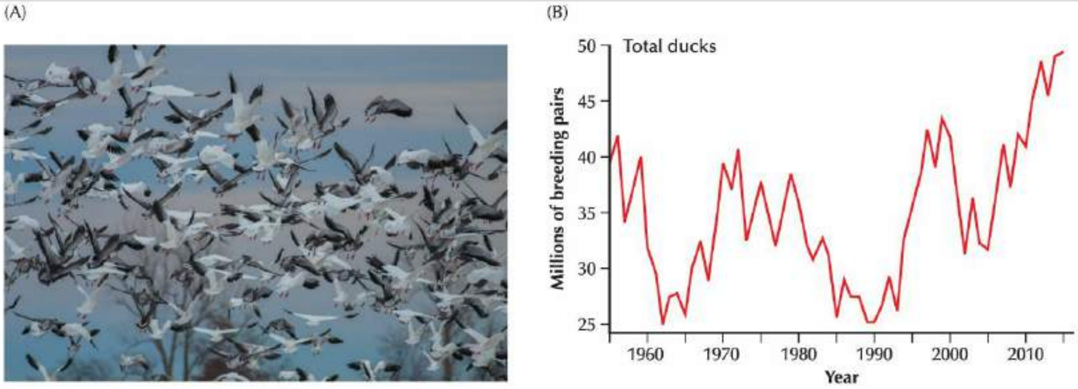
> Less than one hour after his capture, two banded underworld males were courting his mate, GY, but she actively chased both throughout the day. Also, at least four neighbor male owners invaded the territory repeatedly and were driven out by GY. By August 15 one of these, YO, had formed a stable pair with GY, and two other underworld males . . . had established small territories at each end of YO’s former territory. Both actively courted YO’s former mate, RRO, who, unlike GY, readily associated with both. On August 17 I saw RRO copulating with the one that sang more, RBO, and by August 18 they were established as a pair in her territory. Yet less than 24 hours later RO had returned and regained his territory and mate, and YO had reclaimed most of his old territory with RBO, holding a small corner, forming a trio of one female (RRO) and two males (YO and RBO). Five weeks later YO had regained all his territory, and RBO rejoined the underworld. [Smith 1978, p. 577]

MICHAEL TODD

Figure 18–11 Rufous-collared Sparrow, a species with a well-developed “underground” of birds waiting for a breeding opportunity.

18.4 Population Trends

Standardized monitoring of the numbers of game birds guides decisions for managing populations that can sustain annual hunting by sportsmen. The management of waterfowl populations is a major enterprise in this regard. Many species of North American ducks declined severely in the early 1960s to lows of roughly 20 million breeding pairs (Figure 18–12). The number of Northern Pintails alone dropped from historical highs of 10 million pairs to record lows of 1.8 million pairs. Agencies in Canada, the United States, and Mexico then formulated the North American Waterfowl Management Plan (NAWMP), which set population-growth targets for each species, accompanied by close regulation of annual harvests and close monitoring of annual nesting productivity. The stabilization, recovery, and rebuilding of the North American duck populations is well under way.



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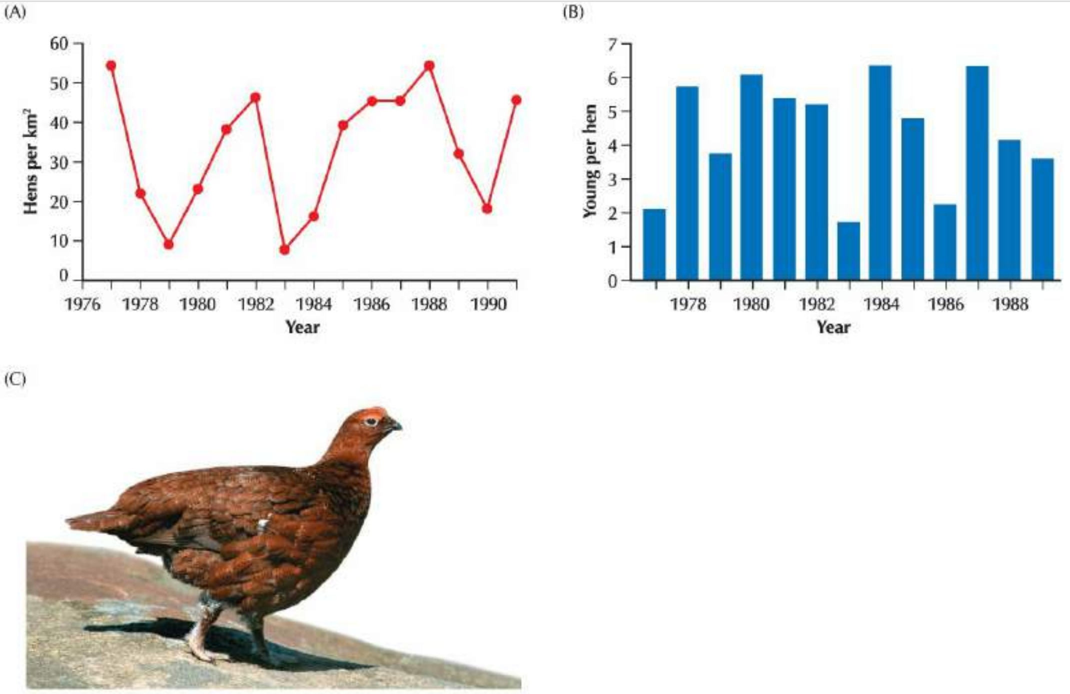
(A) Photo: Michael Todd . (B) Data from U.S. Fish and Wildlife Service 2016

Figure 18–12 (A) Waterfowl populations in North America depend on wetlands, a habitat that is disappearing at the rate of 300 hectares or more per day. (B) Population trends of North American duck populations from 1954 to 2015. Numbers expressed as millions of breeding pairs.

Red Grouse Cycles

Complex mixtures of density-dependent social behavior, parasite loads, and predation regulate the population cycles of the Red Grouse, a popular and strongly managed game species of the moorlands of Scotland. “Red Grouse” is the long-used name for this distinctive subspecies of the Willow Ptarmigan. The populations of the Red Grouse undergo both long-term declines and short-term cycles (Thirgood et al. 2000). Most local populations of Red Grouse in Scotland have four- to eight-year cycles (Figure 18–13). Grouse numbers increase from lows of 30 birds per square kilometer to highs of 120 birds per square kilometer.



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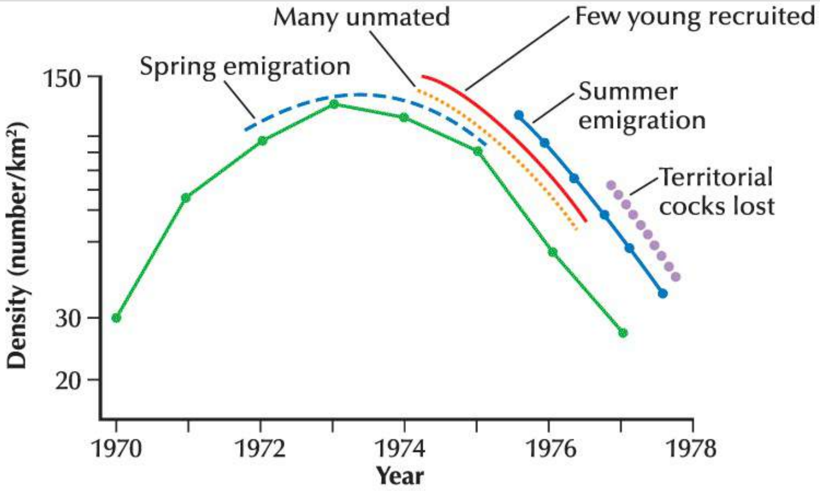
DATA FROM HUDSON ET AL. 1992. PHOTO: NATURE PHOTOGRAPHERS

Figure 18–13 Changes in (A) size of the breeding population (number of hens) and (B) breeding success (young per hen) of (C) Red Grouse in one study area in Scotland.

The population cycles of the Red Grouse partly relate to food availability and predation. Also contributing in a major way to the regulation of these cycles are an intestinal parasite (a nematode worm named *Trichostrongylus tenuis*) and the intensity of aggressive social interactions. We will consider the worm first.

The experimental cleansing of worms from local grouse populations through the application of a specific drug to 20 percent or more of the grouse in the population eliminates or sharply reduces the highs and lows of the population cycle (Hudson et al. 1998). This worm burrows into the soft walls of the intestinal ceca, causing local damage, internal bleeding, decreased absorption, and mortality in the Red Grouse. Infection levels of individual grouse can be severe: this worm was responsible for "grouse disease," which devastated the Red Grouse populations in the nineteenth century. The nematodes reduce the rate of weight gain in females before incubation, as well as clutch size, hatching success, and chick survival. They also affect adult survival. Secondarily, the parasites may increase vulnerability to predation by reducing the ability of the grouse to control scent emission from the intestinal ceca. Both hunting dogs and foxes use these odors to locate grouse. The effects of the parasites on breeding production and survival are density dependent. The effects intensify with population density, ultimately causing short-term population declines.

Social interactions—specifically, density-dependent territorial behavior and spacing—also govern the population cycles of Red Grouse. Early studies showed that the advantage of aggressive males increases with the density of grouse and causes an exodus of less aggressive birds. This aggressiveness leads to low recruitment and thus the downturn of the cycle (Figure 18–14). François Mougeot and his colleagues (2003) caused increasing populations to decline just by adding testosterone implants that increased the aggressiveness of territorial males. Testosterone implants reduced both fall male density and the recruitment of breeding males and females the following spring by 50 percent.



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Data from Watson and Moss 1980

Figure 18–14 Social forces driving the population cycle of the Red Grouse. The density of Red Grouse cocks holding breeding territories cycles from lows of 30 birds per square kilometer to more than 100 birds. The green line shows the density of cocks in the spring. The decline at high population densities is due partly to the control of large territories by increasingly aggressive males, which reduces the recruitment of young and promotes emigration by less aggressive males and the loss of vulnerable territorial males themselves.

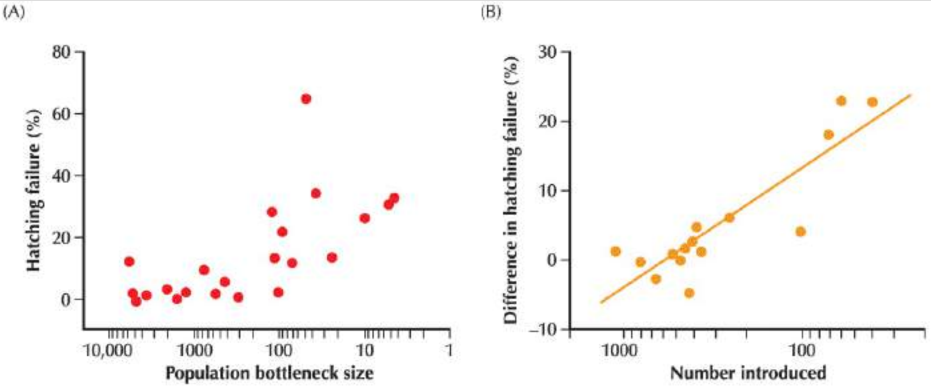
Beyond the short-term cycles of their local populations, numbers of Red Grouse declined by 50 percent in the twentieth century due to the loss of quality moorland habitat. The leaves of heathers are the primary food of this grouse. The grouse select nutritious leaves, and, in the spring, leaf quality affects maternal nutrition, egg quality, brood size, chick survival, and adult summer survival. But increased grazing of sheep favored rough grassland instead of heather moorland, reducing the quality of both food and the cover that the grouse use to hide from predators. The conversion of the moorlands into rough grasslands also favored population increases of pipits and voles. They, in turn, attracted more predators—specifically, Northern Harriers (also known as Hen Harriers). Increased predation by harriers, especially on grouse chicks in the summer and young grouse in the fall, increased mortality rates and suppressed local population cycles of the Red Grouse.

Population Crashes and Bottlenecks

The conservation future of a population depends in part on its size and genetic structure. Small populations tend to have less genetic diversity than do large populations. Severe declines in population size, often called **population crashes,** reduce genetic variability and increase inbreeding among the survivors. Students of population genetics refer to these temporary reductions in population size and reduced genetic diversity as **bottlenecks.**

The survivors that remain after a population crash are subject to increased inbreeding, with negative effects that can limit recovery (Figure 21–17). The failure of eggs to hatch is one of the predictable negative effects of inbreeding due to the effect of deleterious genes on embryological development. Hatching failure of 10 percent is the norm for outbred species. Higher failure rates indicate problems (Briskie and Mackintosh 2004). For example, half of the eggs of the endangered

Kakapo, a flightless parrot, in New Zealand fail to hatch. Many other bird species of New Zealand have undergone severe population bottlenecks, either from historical endangerment or from the small numbers of birds of exotic species introduced onto the islands. A broad comparative survey of these species revealed that hatching failure increased with the severity of the population bottlenecks in both native and introduced species (Figure 18–15). Hatching failure increased in both groups when the bottleneck population sizes fell below 150 birds.



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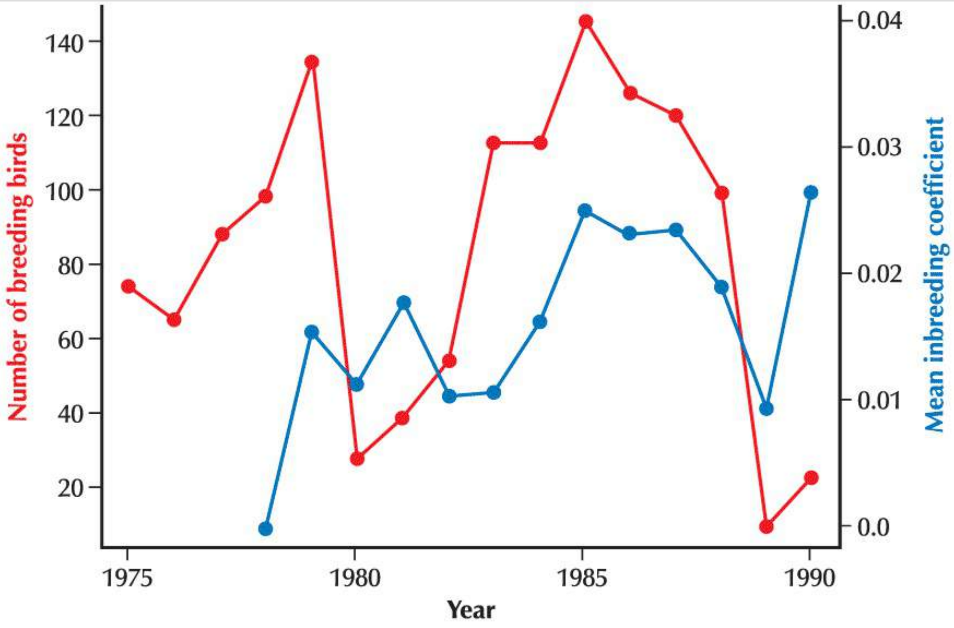
Data from Briskie and Mackintosh 2004

Figure 18–15 Hatching failure rates increase with the severity of bottlenecks in bird populations in New Zealand. (A) Hatching failure in native species, many of which are endangered or recovering from endangerment. The smaller the population bottleneck, the greater the hatching failure. (B) Hatching failure rates of species introduced in small to modest numbers. The hatching failure rates are expressed as the difference between the rate observed in the population after it was introduced to New Zealand and the hatching failure rate observed in the population that was the source of the introduced birds. The smaller the number of introduced birds, the greater is the difference in hatching failure in comparison with the source population.

Population crashes of Song Sparrows studied on Mandarte Island off the coast of British Columbia favored individual birds with little past inbreeding in their pedigrees. This color-marked population crashed severely in 1979–1980 and again in 1988–1989 due to severe winter weather (Keller et al. 1994). Eighteen percent (18 males, nine females) survived the 1979 crash, and 11 percent (seven males, four females) survived the 1988 crash. The survivors had a significantly lower average inbreeding coefficient than did the population before the crash (Figure 18–16). This result is a rare demonstration that inbreeding can depress survival through an environmental challenge.



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DATA FROM KELLER ET AL. 1994

Figure 18–16 Changes in size of the population (red) affect the average level of inbreeding (calculated genetic relationship to its grandparents) that prevails in a population of Song Sparrows on Mandarte Island in British Columbia. Levels of inbreeding (blue) increase during periods of population growth and the retention of multiple generations in the population. Population crashes, as in 1979–1980 and 1988–1989, culled the most highly inbred sparrows from the population, sharply reducing the average inbreeding coefficient.

Island populations in particular tend to be small and to have lower genetic variability than is typical of related species on the mainland. Originally, the Mauritius Kestrel, found only on the same island as that of the fabled Dodo, exhibited about two-thirds of the genetic heterozygosity found in mainland kestrels (Groombridge et al. 2000). Then, from 1940 to 1960, pesticides exterminated most of this island kestrel population, reducing it to fewer than 50 birds and, in the end, to just one breeding pair. The population crash reduced allelic diversity by 55 percent (from 3.1 to 1.4 alleles per locus) and genetic heterozygosity by 57 percent (from 0.23 to 0.10). Conservation efforts rebuilt the population to 200 pairs from just one breeding pair. This replacement population is increasing in genetic variability by accumulating new mutations at a rate predicted for such a small population.

18.5 Birds as Bellwethers

Both biologists and politicians recognize that birds are sensitive indicators of environmental health. Ever since the proverbial use of a canary in a mine shaft, birds have served humanity as bellwethers of the state of the environment. Sensitive to toxic coal-mine gases, canaries would succumb long before such gases reached levels dangerous to miners, forewarning them with ample time to get out of the mine. Outside the mine shaft, not only do birds forage in vast numbers across the hemisphere, but their interactions as predators, prey, pollinators, and seed dispersers make them pivotal players in ecosystem dynamics. As a result, bird populations become respected indicators of biodiversity and barometers of ecosystem health (Box 18–4).

Box 18–4

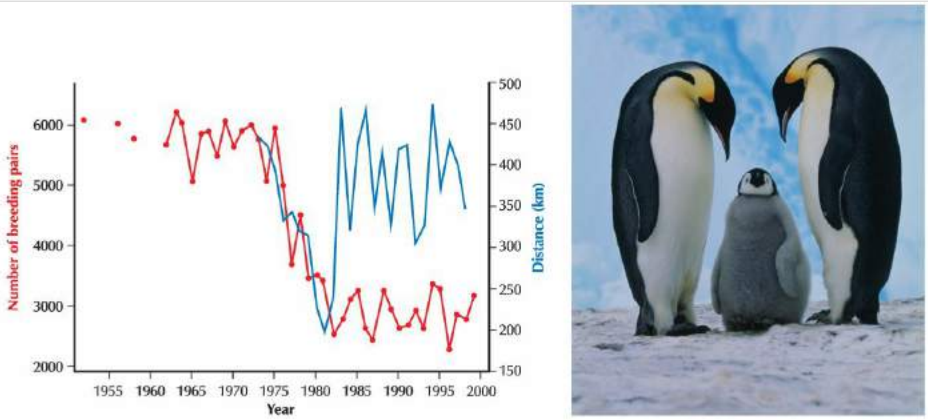
Global Warming and Seabirds

Seabird populations warn us of the effect of global warming on the world oceans as well as the consequences of overfishing. Species that live in the polar regions, both Arctic and Antarctic, are among the first to be challenged by the warming of the oceans. Seabirds of the North Sea had their worst breeding season on record in 2004. The reason? Increases in water temperature due to global warming destroyed plankton populations at the base of the food chain and the small fish populations that depend on plankton. Both seabirds and commercial fisheries at the top of the food chain lost their critical food supplies.

Seabird populations in Antarctica are sensitive to the extent of the sea ice pack there, which is breaking up due to global warming (Croxall et al.

2002). Populations of the Emperor Penguin, for example, declined 50 percent from the mid-1970s to 1982 (see the graph below). Global warming is breaking up the ice too early in the penguins' annual cycle and causing an increase in the mortality of molting adults and juveniles, with a special twist. After breeding, Emperor Penguins must haul themselves onto intact pack ice and stay put there while they molt for three to four weeks. Molting penguins die if they have to swim far in prematurely open water.

Countering this mortality and helping to stabilize their populations is a positive effect of global warming. Open-water feeding areas, called polynyas, are larger and closer to the (winter) breeding colonies. Breeding success and adult survival during this demanding period of the annual cycle are increasing as a result.



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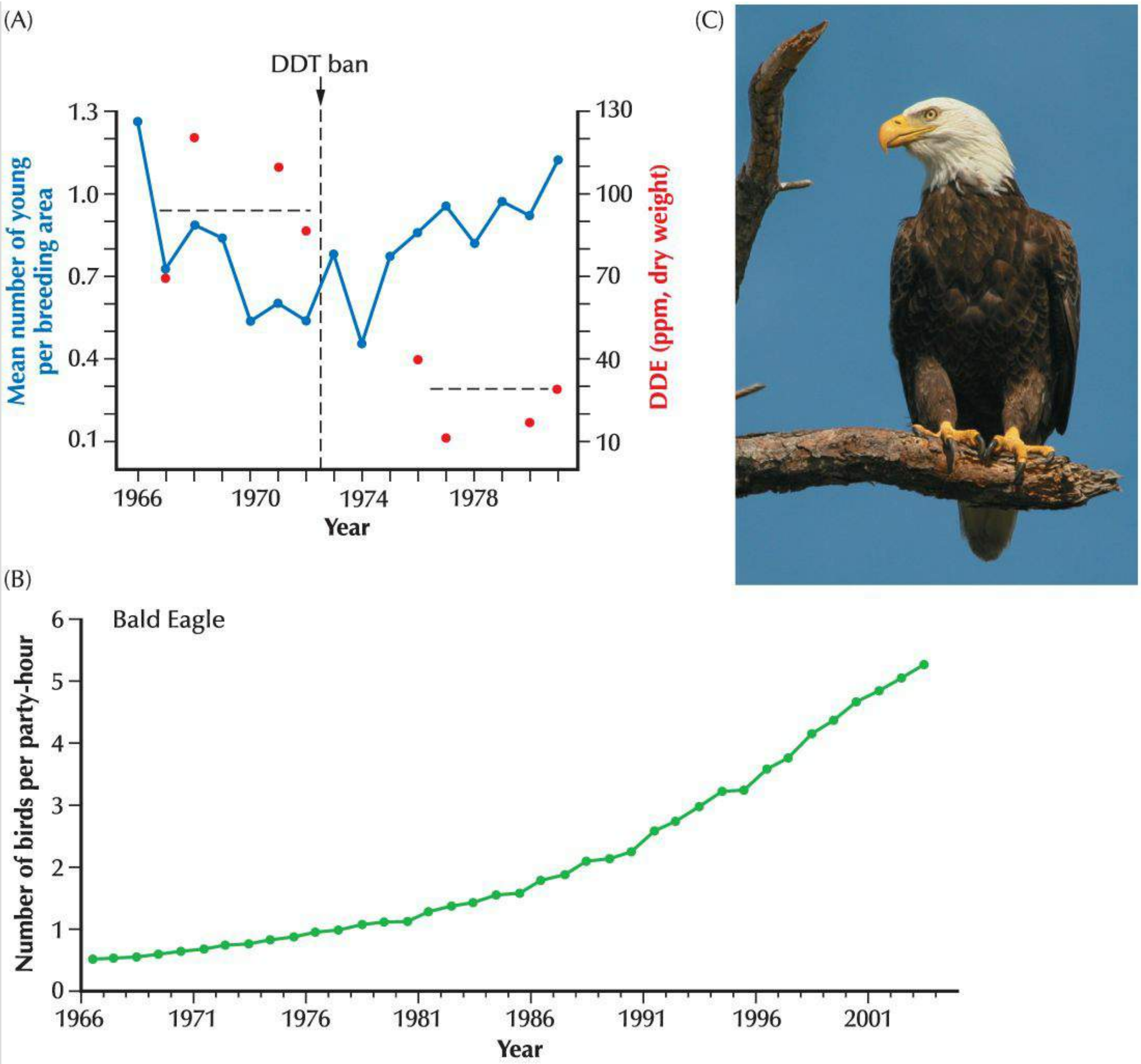
DATA FROM CROXALL ET AL. 2002 . PHOTO: ART WOLFE/GETTY IMAGES

Size trend of the breeding population of Emperor Penguins at Pointe Geologie, Adelie Land, Antarctica, in relation to distance between the colony and the northern limit of the pack ice in winter. More distant colonies are smaller.

The visible deaths and reproductive failures of raptors and songbirds alike in the 1950s sounded the alarm about the overuse of persistent organochloride pesticides, which were quietly taking their toll on human health as well. Accumulated pesticides, particularly DDT, not only kill birds directly but also interfere with eggshell production, and thus cause nesting failure (Risebrough 1986). Pesticide poisoning nearly exterminated Peregrine Falcons and Ospreys in the eastern United States. Together, these raptors served as indicator species because, as predators at the top of the food chain, they concentrate toxins in their bodies.

Similarly, the Bald Eagle, the national bird of the United States, became a national equivalent of the canary. Its population was in steep decline. The reproduction of Bald Eagles in northwestern Ontario, for example, declined from an average of 1.26 young per nest in 1966 to a record low of 0.46 in 1974. Their reproduction increased to an average of 1.12 young per nest after DDT was banned (Grier 1982; Figure 18–17).



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(A) Data from Grier 1982. (B) Data from National Audubon Society 2016.
(C) Barry Spruce Photography

Figure 18–17 Return of the Bald Eagle. (A) Reproduction in Bald Eagles (blue) improved after the use of the pesticide DDT (arrow) was banned. The ban resulted in a drop in chemical residues (DDE) in eggs (red points). Dashed lines represent weighted mean concentrations of DDE before and after the ban. (B) Population recovery of (C) Bald Eagles in Wisconsin based on Christmas Bird Count data.

Paralleling the case of the Bald Eagle is that of the Brown Pelican, one of the most familiar and abundant birds of the Gulf and West

Coasts of North America (Figure 18–18). This species faced extinction in the 1960s because of widespread reproductive failure (Schreiber 1980b). Hydrocarbon pesticides in the marine food webs of coastal California, coastal Louisiana, and nearby Texas interfered with the production of normal eggshells, and the pelicans typically laid eggs with very thin or no shells. The fragile eggs were easily broken under the weight of an incubating parent. The lack of reproduction in Brown Pelicans in California, where eggshell thinning was most severe, and the alarming disappearance of pelicans from Louisiana and Texas placed this bird on the endangered species list in 1973.

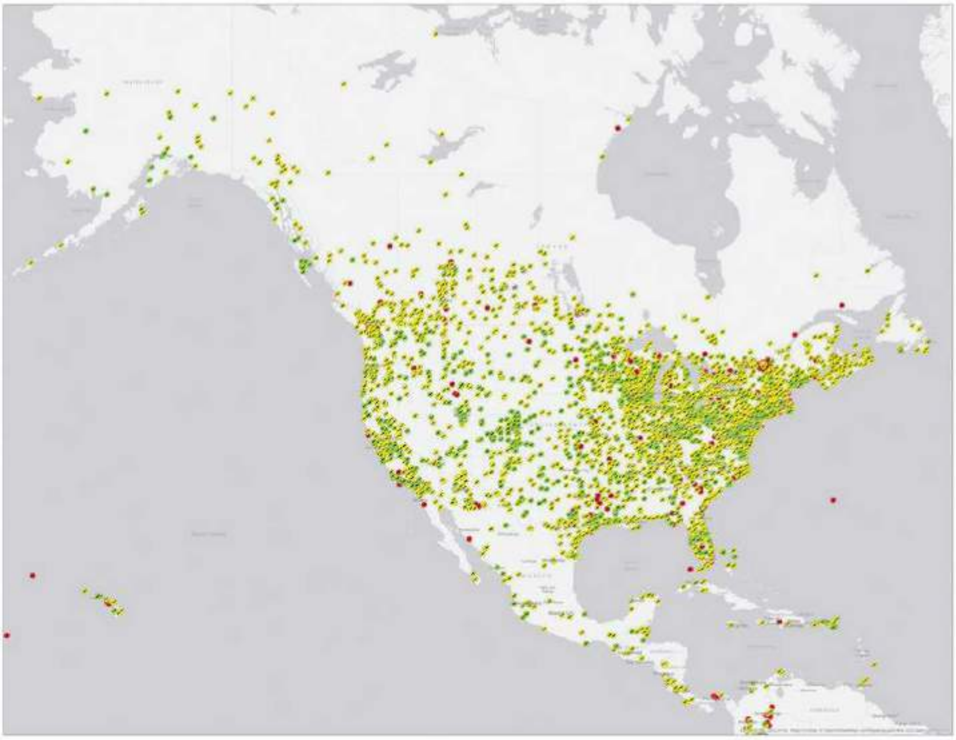
GEOFFREY JONES

Figure 18–18 The Brown Pelican underwent reduced reproduction and severe population declines due to the thinning of eggshells by DDT. The pelican populations are now increasing on both the East Coast and the West Coast of North America.

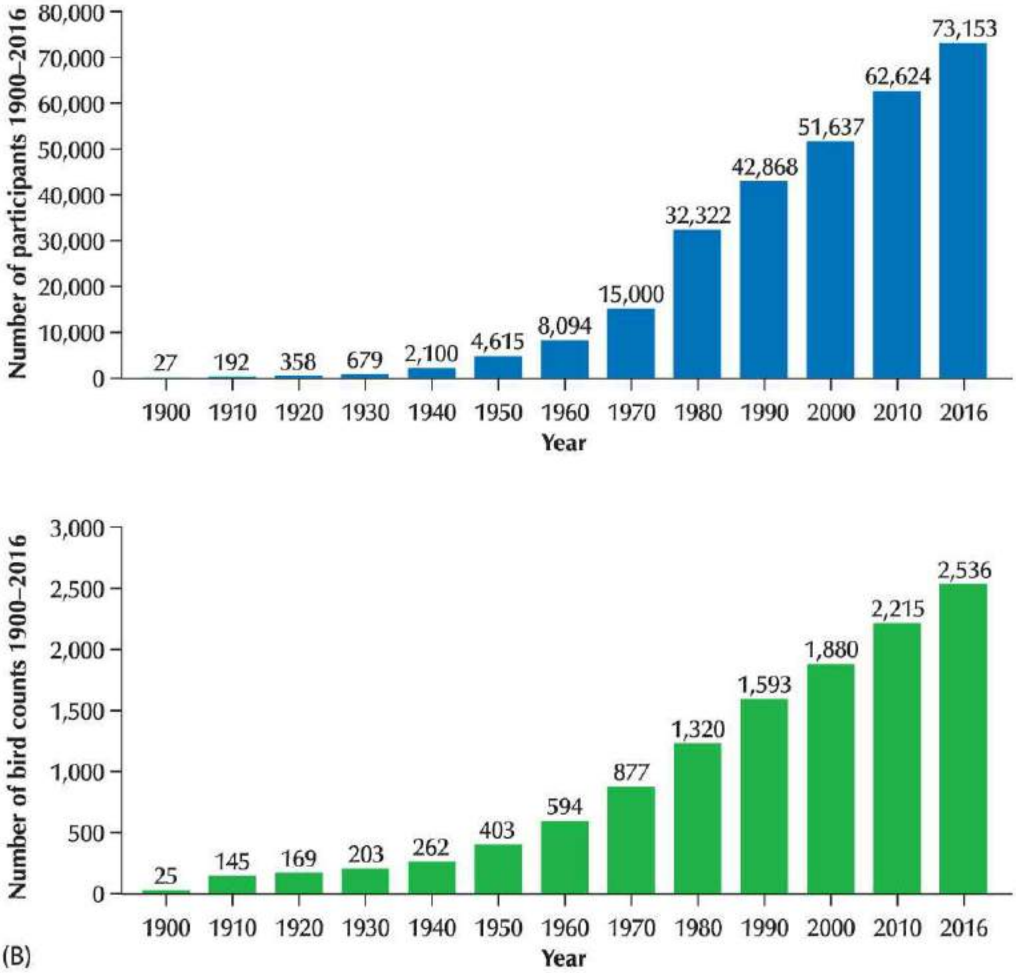
In each case, especially the high-profile plight of the Bald Eagle, conservationists identified the cause of the problems with bird populations. Governments banned the pesticides that were responsible, and users, ranging from home owners to farmers, restricted their applications of the toxins. Under close scrutiny, Bald Eagles, Ospreys, Peregrine Falcons, and Brown Pelicans recovered. No longer endangered, Brown Pelican populations are now expanding rapidly in California and on both the Gulf and the Atlantic coasts. Bald Eagles are now quite common in most of their original range.

18.6 Citizen Science

Nationwide programs monitor the long-term population trends of non–game-bird species in both North America and Europe. Based on the participation and expertise of large numbers of volunteer citizen scientists, the Audubon Christmas Bird Count, for example, documents the changing early-winter distributions of North American birds (Figure 18–19). Twenty-seven pioneers tallied a total of 18,500 individual birds of 90 species across North America on the first (25) Christmas Bird Counts in 1900. In the winter of 2015–2016, 76,669 volunteer birders tallied 58,878,071 birds of 2,607 species on 2,505 count circles throughout North America and the world. The computerized data, available online (http://www.audubon.org/bird/cbc/index.html), document population trends of North American bird species (Figure 18–20).



(A)



(B)

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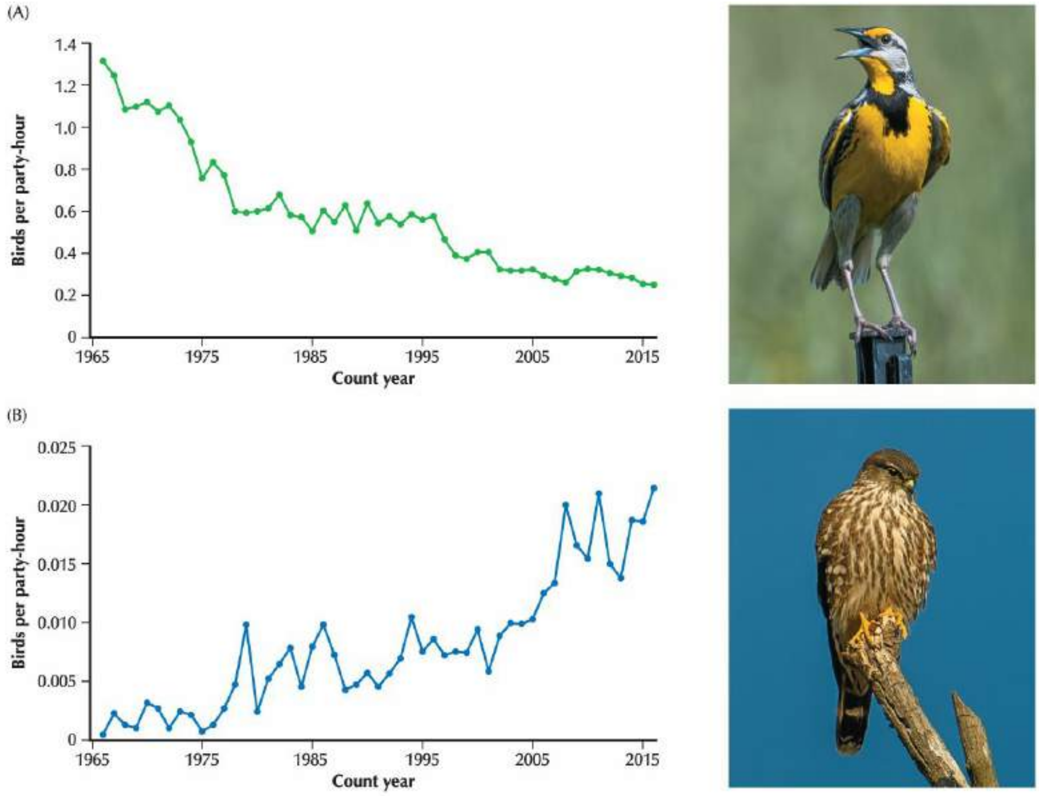
Figure 18–19 Audubon Christmas Bird Count. (A) Map of count circles, 2,536 in all. (B) Growth of citizen scientist participation.



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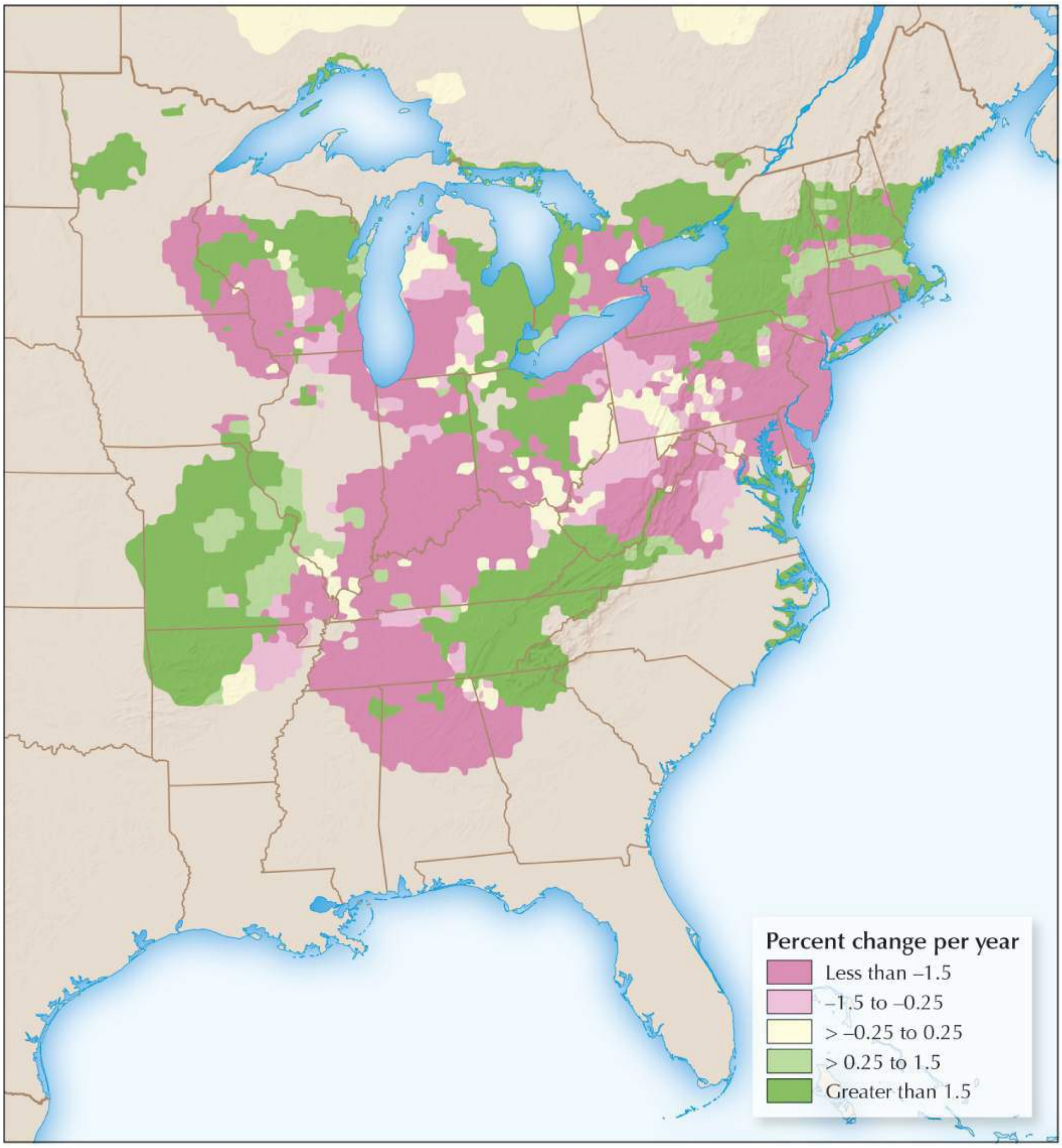
Data on Graphs from National Audubon Society 2016 . Photos: Barry Spruce Photography

Figure 18–20 Christmas Bird Counts document (A) the decline of the Eastern Meadowlark, one of many grassland bird species in trouble, and (B) the growth of Merlin populations.

The Breeding Bird Survey, sponsored by the U.S. government, has been tracking the trends of breeding species since 1960 (Box 18–5). The population dynamics and trends of healthy bird populations are not uniform over such large geographical areas as North America. Instead, some local populations of a particular species increase, while others elsewhere decline over the same time period. Trend data, therefore, are best analyzed in regional and local segments. The resulting maps of the population trends of a species portray a landscape of areas of increase, or sources, and areas of decrease, or sinks (Figure 18–21).



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
DATA FROM SAUER ET AL. 2005

Figure 18–21 Geographical mosaic of population trends of the Blue-winged Warbler throughout its breeding range. Average annual changes in local population density since 1960 correspond to shifts in the population and the loss of suitable old-field habitats.

Box 18–5

The Breeding Bird Survey

Complementing the Christmas Bird Count and based on a more formal protocol of counting birds is the government-sponsored Breeding Bird Survey (BBS). It documents distributions and population trends of breeding bird species in June and July each year. Like the Christmas Bird Count, the BBS relies on the time given by thousands of skilled volunteer birders, or citizen scientists.

Data produced by the BBS survey sounded the alarm on behalf of the Neotropical migrants undergoing broad-scale decline (Robbins et al. 1989). The alarm, based on scientific trend analysis, rallied a conservation coalition of government agencies and nonprofit organizations under the umbrella alliance Partners in Flight. Modern non–game-bird conservation initiatives grew from this platform of broad-scale, coordinated participation, striving to apply the lessons and successes of the North American Waterfowl Management plan to the future vitality of species such as the Cerulean Warbler and Henslow’s Sparrow. Here is a brief summary of its history:

> During the 1960s, Chandler Robbins and his associates at the Migratory Bird Population Station (now the Patuxent Wildlife Research Center) in Laurel, Maryland, developed the concept of a continental monitoring program for all breeding birds. The roadside survey methodology was field tested during 1965, and the North American Breeding Bird Survey (BBS) was formally launched in 1966 when approximately 600 surveys were conducted in the U.S. and Canada east of the Mississippi River. The survey spread to the Great Plains states and prairie provinces in 1967. By 1968, approximately 2,000 routes were established across southern Canada and the contiguous 48 states, with more than 1,000 routes surveyed annually. During the 1980s, the BBS expanded into the Yukon and Northwest

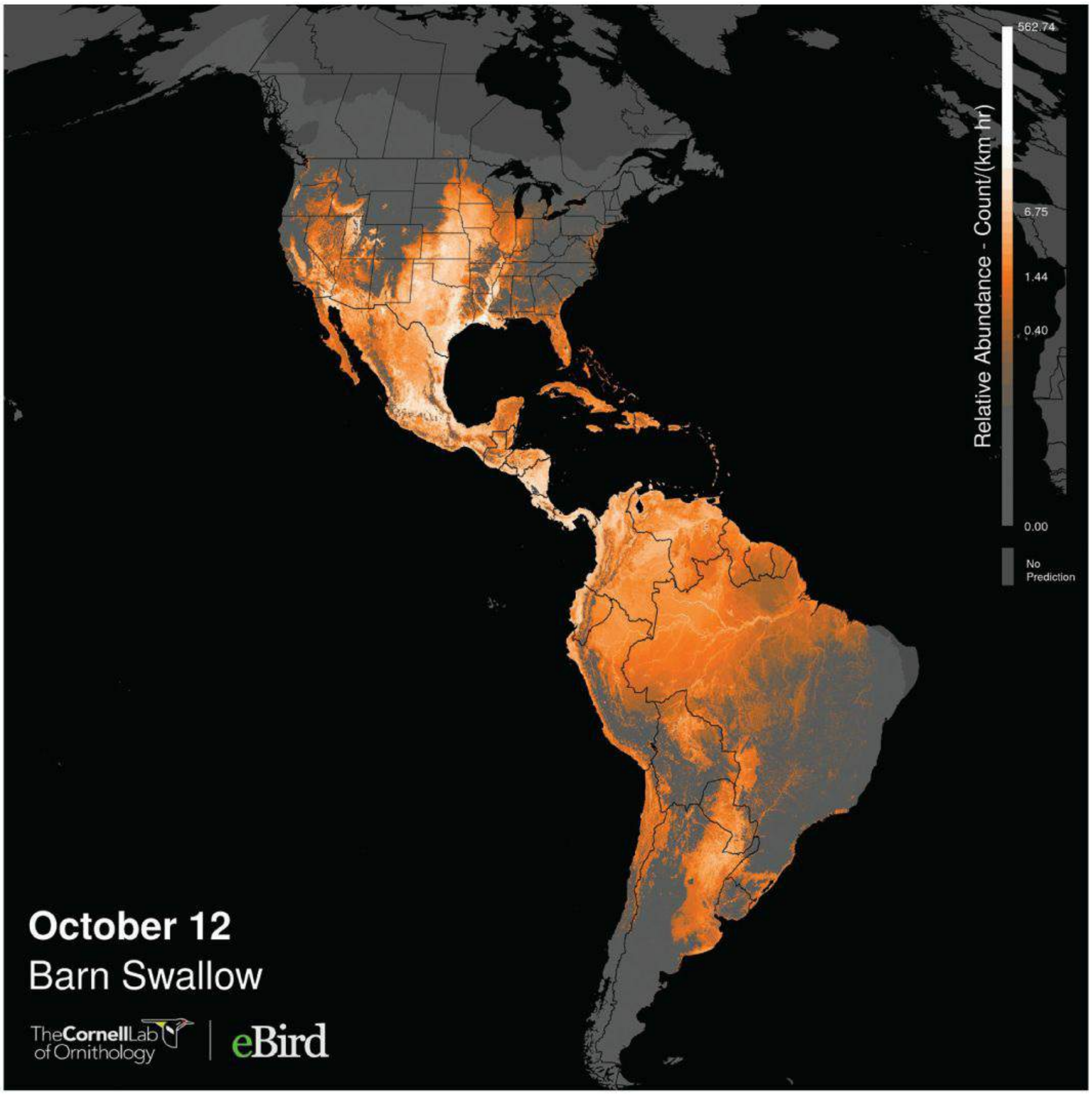
> Territories of Canada, and Alaska.
>
> Today there are approximately 3,700 active BBS routes across the continental U.S. and Canada, of which nearly 2,900 are surveyed annually. BBS data can be used to produce continental-scale relative abundance maps. When viewed at continental or regional scales, these maps provide a reasonably good indication of the relative abundances of species that are well sampled by the BBS. [From Sauer et al. 1997]

THE WASHINGTON POST/GETTY IMAGES

Chandler Robbins (1919–2017) was the founder of the BBS, a participant on Christmas Bird Counts for 80 years, and an early champion of citizen science ornithology.

The eBird project of the Cornell Lab of Ornithology and National Audubon Society engages birders worldwide to monitor the dynamics of bird populations using the growing powers of the Internet (https://ebird.org/ebird/explore). Millions of citizen scientists' records animate the distributions, migrations, expansions, contractions, and local densities of bird species. eBird's real-time tracking powers enable ornithologists to follow winter irruptions of species like the Snowy

Owl (see Figure 18–6) as well as weekly shifts in the local abundance of migratory species (Figure 18–22).



CORNELL LAB OF ORNITHOLOGY, EBIRD.ORG/SCIENCE

Figure 18–22 eBird map of the distribution of Barn Swallows in the Western Hemisphere. Go to http://ebird.org/science/barswa for a year-round animation of the swallow’s seasonal migrations.

Such citizen science projects are increasingly popular and diverse, empowered by social media and online databases. Wikipedia features over 1,100 active projects uniting all disciplines. The websites of the National Audubon Society and Cornell Lab’s Citizen Science Central provide rich menus of bird study projects that welcome volunteer participants. Many of these, such as the Great Backyard Bird Count and FeederWatch, are global in scale yet home based and linked to the conservation initiatives of bird-friendly communities.

REVIEW KEY CONCEPTS

18.1 Growth and Declines

Populations in a new environment usually grow slowly at first, followed by accelerated growth rates, and stabilize or decline in response to reduced reproduction and survival. Major ecological forces—habitat, food, climate, predation, and disease—set upper limits on population growth and the carrying capacity of the environment. Major reductions in primary habitats reduce bird populations and trigger conservation concerns.

Key Terms: short generation times, carrying capacity, life tables, mean generation time

18.2 Limitation and Regulation

Population sizes may be stable and self-regulating or may fluctuate dynamically from year to year as a result of changes in breeding success and mortality. Density-dependent changes in fecundity or survival regulate populations about an average size. Diseases and parasites play a substantial role in limiting bird populations, with implications for people and livestock.

Key Terms: limitation, regulation, irruptions

18.3 Social Forces

Social forces, including territoriality, mediate the availability of habitat and, therefore, local population size in density-dependent ways. Surplus birds wait in the “underground” as floaters waiting for a vacancy.

Key Term: floaters

18.4 Population Trends

Complex mixtures of density-dependent social behavior, parasite loads, and predation regulate the population cycles of birds. Local population bottlenecks reduce genetic variability and provide theaters of evolutionary change and speciation.

Key Terms: population crashes, bottlenecks

18.5 Birds as Bellwethers

Bird populations are respected indicators of biodiversity and barometers of ecosystem health. The recoveries in recent decades of the Bald Eagle, Brown Pelican, and other species followed the removal of DDT pesticides from the environment and successful management practices.

18.6 Citizen Science

Long-standing citizen science programs, such as the Christmas Bird Count and the Breeding Bird Survey, track bird population trends and changes in the environment. Trend data are best analyzed in regional and local segments. The resulting maps of a species portray a landscape of areas of increase, or sources, and areas of decrease, or sinks.

APPLY YOUR KNOWLEDGE

1. Compare and contrast the growth and stability of a population of 100 birds that colonized a small island with a resident population of birds on the same island that had been reduced to 100 birds by a severe storm.
2. Differentiate between “limitation” and “regulation” of population growth.
3. Describe how habitat size can both limit and regulate population growth.
4. Describe the various ways that population density can regulate population growth.
5. Describe the changing moorland habitat of Scotland’s Red Grouse. How did the introduction of sheep change the population dynamics of the Red Grouse?
6. Describe the sigmoid population growth curve of a thriving population in a new habitat by explaining the (a) early, slow growth; (b) the rapid acceleration of growth; and (c) the eventual slowed growth rate as the population reaches carrying capacity.
7. Based on population dynamics, describe the reasons that small songbirds have become more populous and more diverse than larger birds.

CHAPTER 19 *Speciation*

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Golden-winged Warblers hybridize with expanding populations of the Blue-winged Warbler. Just a few genetic loci control their striking plumage differences (see Figure 19–17).

> The origin and nature of species remains utterly mysterious. [BATESON 1922, P. 55]

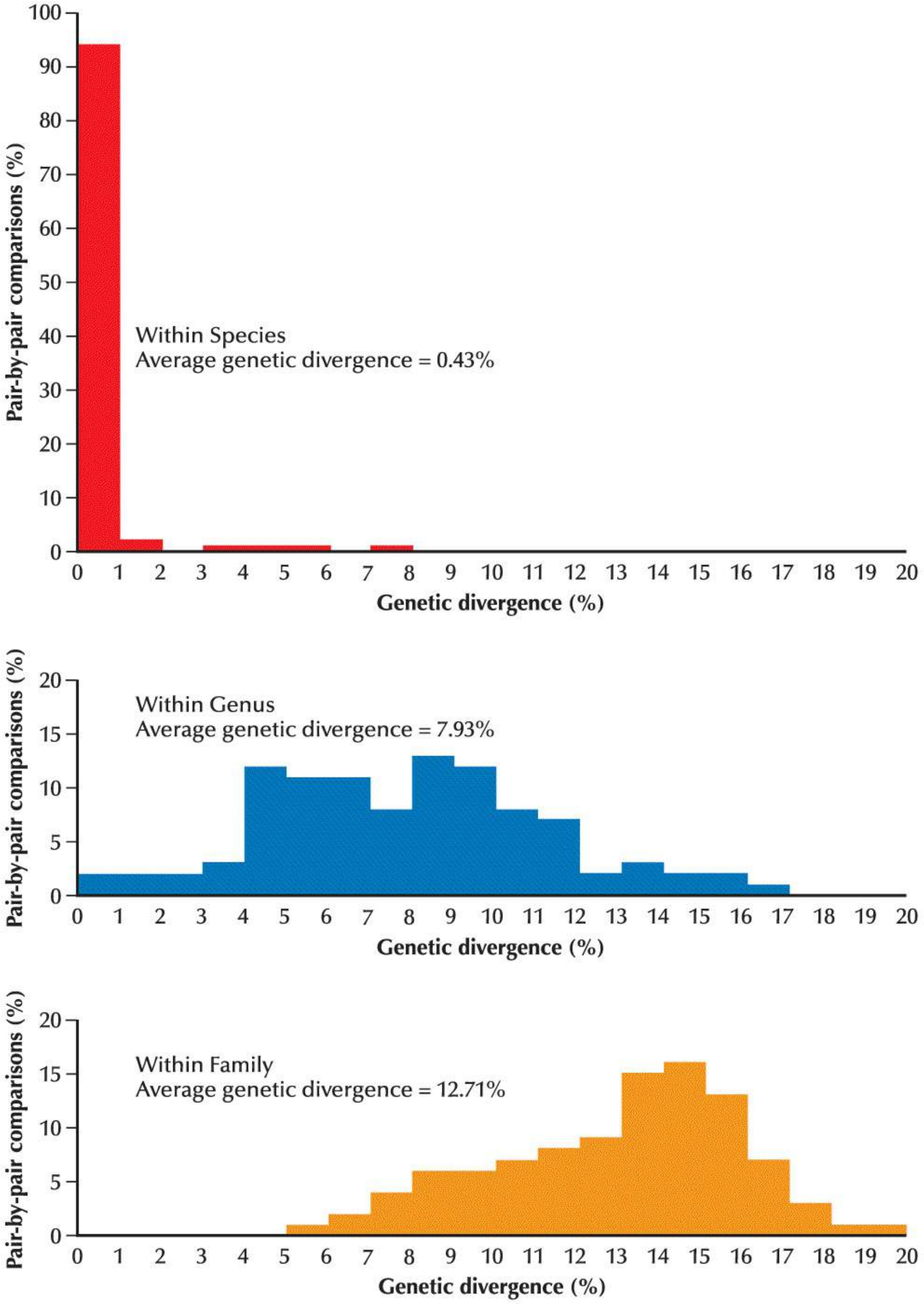
The first bird species of the Mesozoic era 150 million years ago diversified many times. Repeated speciation—the separation of one species into two or more derived species—multiplied their numbers and enriched the biodiversity on Earth. The process of speciation in birds, however, is no longer mysterious.

New species of birds evolve through sexual selection and ecological adaptation in isolated populations. Speciation starts with visual or vocal differences based on minor genetic changes or, sometimes, cultural experience. Continued genetic divergence leads to reproductive incompatibility. Unlike insects, birds retain their reproductive compatibility long after they achieve behavioral isolation.

This chapter begins with an introduction to species concepts and how birds speciate, a topic previewed in Chapter 3. Then follows the patterns of geographical variation and genetic structure of bird populations, including clinal variation—gradients of changing character states, such as darkening feather color—and examples of genetic differences between local populations. Cases of hybridization figure prominently in studies of avian speciation in part because they provide tests of reproductive compatibility. In addition, the details of hybridization help to reveal the social and genetic architectures of species differences. The final section of the chapter summarizes the behavioral aspects of speciation from imprinting to social and sexual selection. Studies of Darwin’s finches on the Galápagos Islands capture some of our best perspectives and insights into the process of speciation in birds.

19.1 What Is a Species?

Species are the primary units for describing and analyzing biological diversity. Each species has a characteristic size, shape, color, behavior, ecological niche, and geographical range. Genetic differences also help us to define species of birds and to track their evolutionary histories. A survey of DNA sequences of the mitochondrial DNA gene encoding cytochrome *c* oxidase I (*CO1*) distinguished 260 species of North American birds (Figure 19–1). Closely related species in the same genus averaged 7.9 percent divergence of these sequences, compared with an average of 0.4 percent for different individual birds of the same species. This pilot survey also revealed surprisingly deep genetic differences within four species: Eastern Meadowlark, Warbling Vireo, Marsh Wren, and Solitary Sandpiper. Each of the first three species is known to comprise two populations that might merit recognition as distinct species. A potentially new species of Solitary Sandpiper, however, was a surprise.



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DATA FROM HEBERT ET AL. 2004

Figure 19–1 The mitochondrial gene *CO1* distinguishes currently recognized bird species from one another. Genetic divergences averaged 0.4 percent within species, compared with 7.9 percent between species within various genera. Species in different families averaged 12.7 percent with much variation. The results are based on pair-by-pair comparisons of the nucleotide-sequence differences found in 437 North American bird species.

The reproductive compatibility of individual organisms—ranging from mate choice to the viability and fertility of offspring—is a fundamental criterion for inclusion in a species. Sexual reproduction links males, females, and their offspring into cohesive populations, sometimes in unexpected ways (Box 19–1). Mating of like individuals with each other, called **assortative mating,** isolates some sets of those populations from other sets of similarly cohesive populations. Thus, White-crowned Sparrows mate with each other, but they do not interbreed with Song Sparrows that nest nearby. American White Ibises mate with each other, but they do not interbreed with the Glossy Ibises that nest in the same colonies.

Box 19–1

Population Cohesion of Cuckoos

Separate populations of Common Cuckoos, a specialized brood parasite (see Figure 14–5A), seem to defy the concept of reproductive cohesion. Recall that females of the brood-parasitic Common Cuckoos sort into sets of individual birds that lay different-color eggs. Their eggs mimic the eggs of their specific hosts. Sets of females that lay similar eggs are called *gentes.* Are the *gentes* different species even though females are not distinct in other ways? What about the males?

The solution to this puzzle is found in the sex chromosomes (Gibbs et al. 2000). Females segregate into genetically distinct sets of birds that carry the same (*gente*) genes for egg color. These genes are located on the W sex chromosome. Recall that females have one W and one Z sex chromosome.

Males have two Z sex chromosomes and are not genetically subdivided into matching *gentes*. They also do not discriminate among females from different *gentes*. Instead, they interbreed nondiscriminately with these host-specific females. Thus, the males provide the genetic cohesion of just one species.

The number of bird species changes with increasing knowledge and criteria (Figure 19–2). In the early stages of avian taxonomy, ornithologists described slightly different populations as distinct species. Knowledge of geographical variation was limited then. Sometimes, our predecessors classified differently plumaged sexes or age classes as different species. As a result, the number of known species climbed to about 19,000 in the early 1900s (Sharpe 1909).

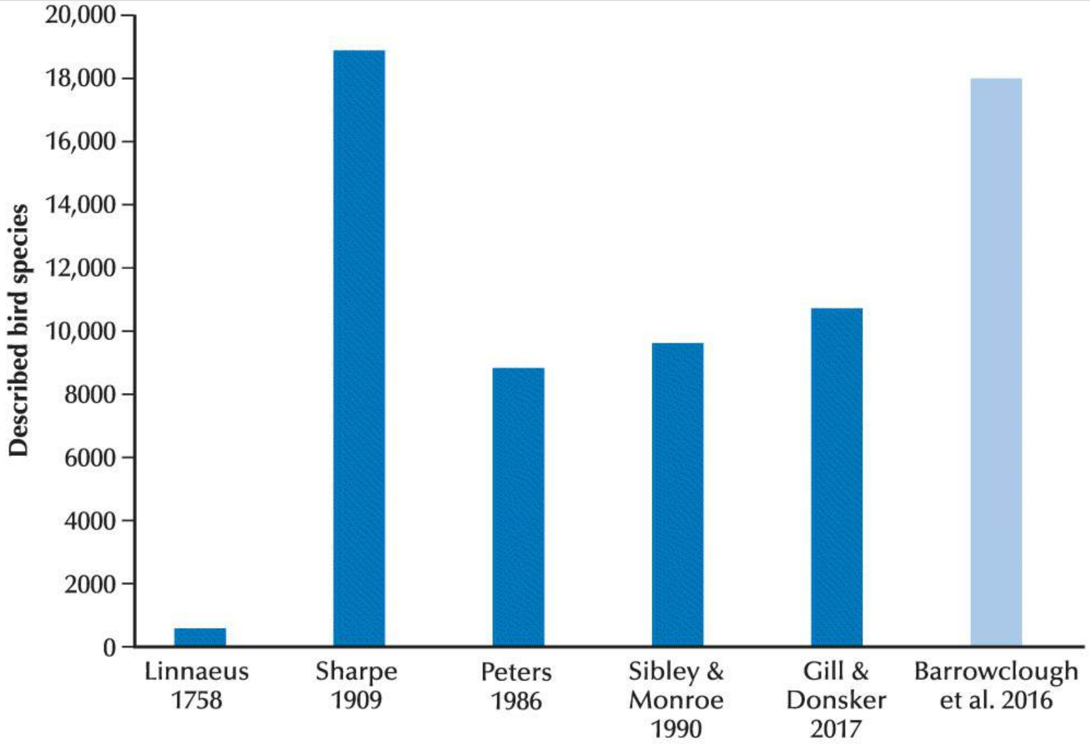

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Figure 19–2 Historical changes in the number of world bird species recognized by ornithologists, including the projection of Barrowclough et al. (2016), based on a statistical sample of museum specimens that qualify as phylogenetic species.

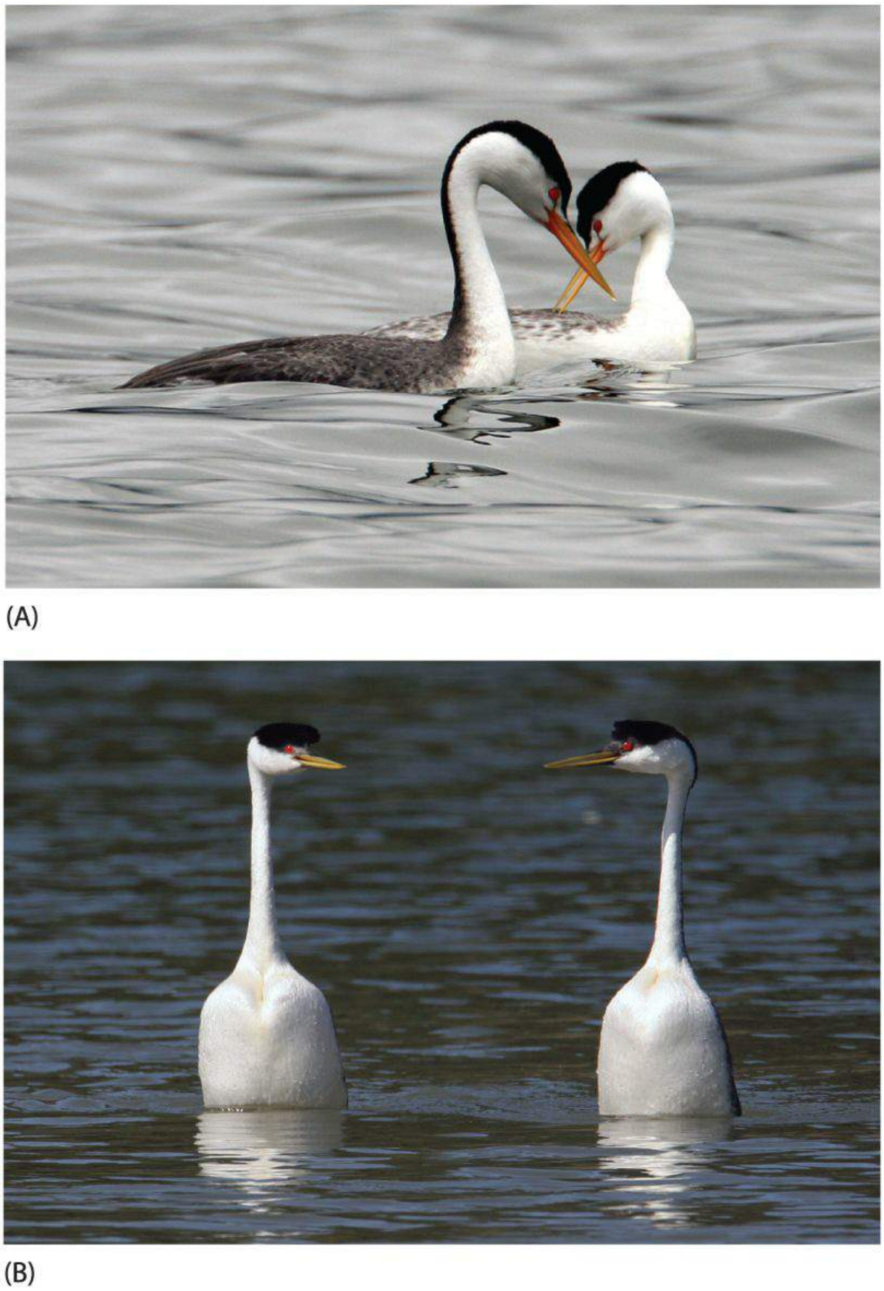
Combining, or “lumping,” species on the initial lists followed as presumed reproductive isolation became a theoretically important criterion for a species in the early twentieth century. Many so-called species were reclassified instead as distinct populations, or “subspecies.” Adding to the mergers of species on the initial lists was the adoption in the 1940s of a broader species concept—the polytypic species concept, which allows a species to contain two or more variant forms. It embraced the potential reproductive compatibility of variable populations. Changing practices in the first half of the twentieth century reduced the number of species that were officially recognized to 8,600 (Mayr and Amadon 1951). More recently, the taxonomic pendulum started to swing back to a middle position with the recognition of more distinct, isolated populations as species. Current lists of the birds of the world recognize over 10,000 species (Gill and Donsker 2017).

How best to define species as the fundamental units of biology has been the topic of a perennial debate that dates to Darwin himself. The Biological Species Concept has long guided taxonomic practice in ornithology (Mayr 1970; Coyne and Orr 2004; Gill 2014). So-called biological species are broad and dynamic entities, or metapopulations, united cohesively by gene flow in geographical space and in evolutionary time, and isolated from other such evolutionary lineages.

Thus, biological species are genetically cohesive groups of populations that are essentially reproductively isolated from other such groups (American Ornithologists' Union 1998, p. xiv).

Documentation of reproductive isolation is not always as straightforward as in sparrow species and ibises. For example, until 1965, ornithologists recognized just one species of large black-and-white grebe (genus *Aechmophorus*) of western North America, called the Western Grebe. This grebe, which is best known for its elaborate "rushing" courtship display, has two color forms. The light-phase bird has a pale back and an orange yellow bill and is white above its ruby red eyes, whereas the dark-phase bird has a yellow green bill, with black extending below the red eyes.

While studying the courtship behavior of these handsome waterbirds, Robert Storer (1965) discovered that light-phase grebes paired preferentially with each other (Figure 19–3). So did dark-phase birds. Mixed pairs of light-phase and dark-phase grebes were rare, constituting less than 3 percent of all pairs. Subsequent study revealed differences in their advertising call, which they use to locate their mates, plus differences in foraging behavior, size, and DNA (Storer and Nuechterlein 1992). The light and dark color phases are species, now called Clark's Grebes and Western Grebes, respectively.



LARRY JON FRIESEN

Figure 19–3 Clark’s Grebes (A) were thought to be a color phase of the Western Grebe (B) until ornithologists discovered that they pair assortatively with each other.

The vast majority of isolated and divergent populations, however, do not come into contact to test their reproductive isolation. Distinctly different, geographically separated, or allopatric, populations therefore force ornithologists to make educated guesses in regard to what might happen should contact be established in the future. Alternative species concepts were developed to avoid the guesses.

The Phylogenetic Species Concept and Evolutionary Species Concept, therefore, focus instead on defining species as distinct evolutionary lineages. They give greater weight to the evolutionary histories of isolated populations than to their potential for interbreeding. In practice, the concept of species as independent evolutionary lineages unifies all three species concepts at a primary level (De Queiroz 2007). Publications in avian taxonomy increasingly accommodate alternative species concepts in the same paragraph and treat different criteria as complementary rather than competitive (alternative species concepts in the same paragraph and treat different criteria as complementary rather than competitive (Sangster 2013). Applications of the Biological Species Concept increasingly incorporate empirical delimitations of lineage independence, the hallmark of the Evolutionary Species Concept. Together, these factors predictably reveal that populations of birds once lumped within polytypic species are independent evolutionary lineages that qualify as species under all three concepts.

19.2 Allopatric Speciation

Most species of birds evolve in geographical isolation, called **allopatry,** under conditions of reduced gene exchange with sister populations (Figure 19–4). The allopatric speciation model explains the origin of most species of birds. Comparisons of the different mockingbirds isolated on different Galápagos Islands, for example, led Darwin to formulate his insights about the origin of species and the importance of geographical isolation. Isolated islands of habitats on continents set a similar stage for speciation of the bird populations that occupy them.

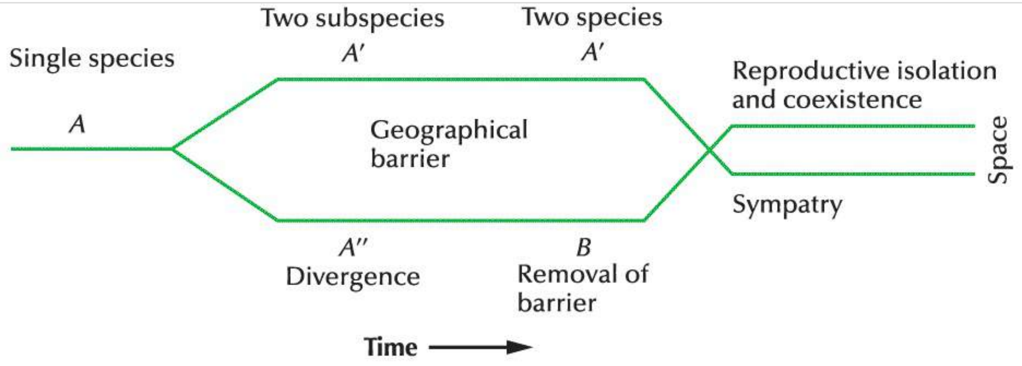


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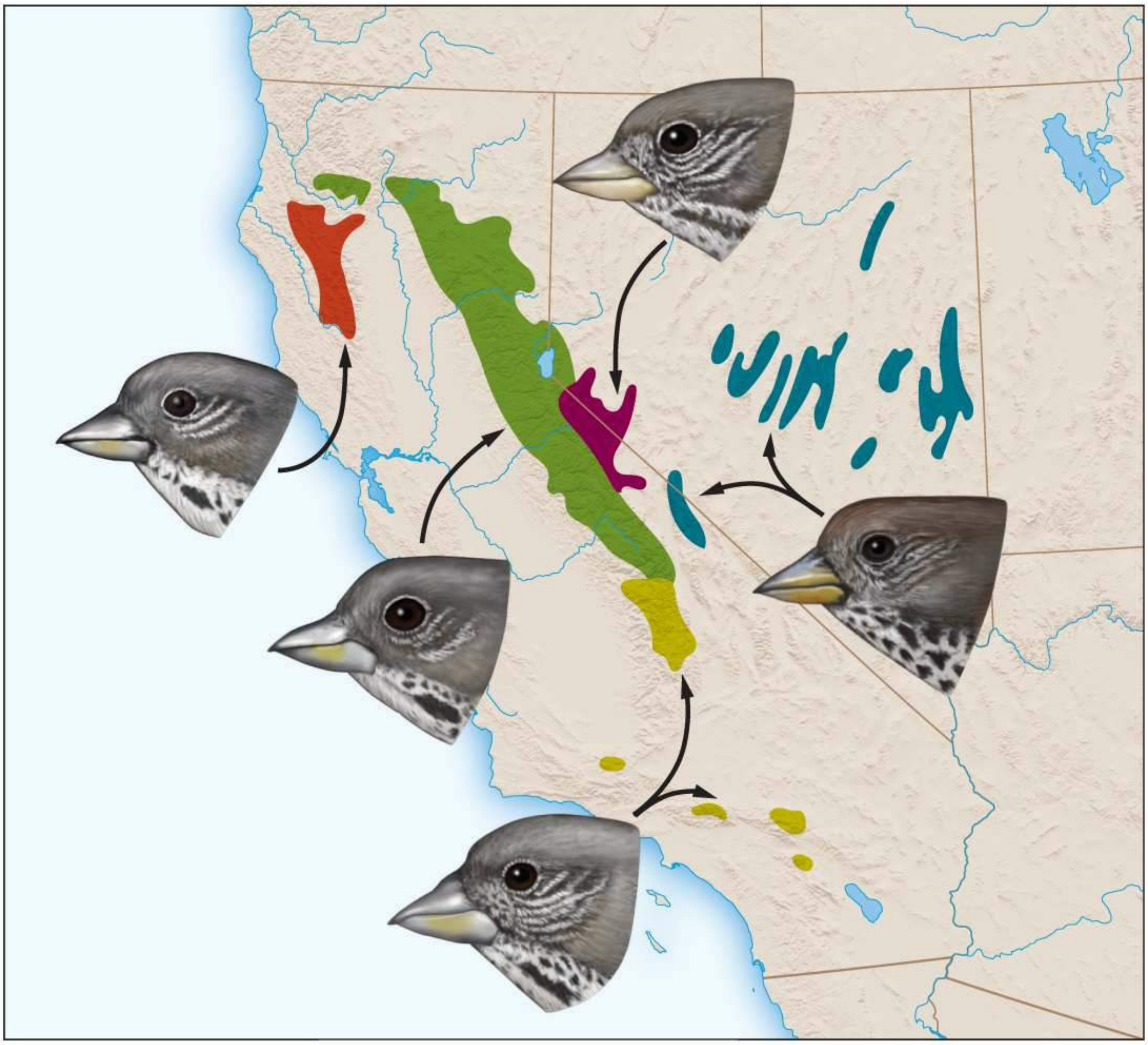
Figure 19–4 Geographical speciation proceeds through the divergence of populations over time. Letters designate genetically discrete populations. The separation of a population facilitates genetic divergence (*A* yields *A*’ and *A*”). The reproductive incompatibility of populations (*A*” and *B*) can result from sustained isolation. A reversal of geographical isolation and range expansions can lead to coexistence as separate species.

The evolution of subspecies is a first step toward speciation (Remsen 2010). Sister populations separated and isolated from each other diverge genetically. Conspicuous patterns of geographical variation among populations, or subspecies, are a result of this divergence.

Geographical variation can evolve, sometimes rapidly, because different environments favor different attributes. One-third of the species of North American birds show conspicuous geographical variation among distinct regional populations. The 51 described subspecies of Song Sparrows, for example, range from sooty in the Pacific Northwest to pale brown in the deserts of California and from medium-sized in Ohio to large, thrush-sized birds in the Aleutian Islands. The western populations of Fox Sparrows vary extensively in bill size and shape (Figure 19–5). Geographical differences in size or color also may be due directly to environmental differences rather than evolved genetic differences among populations (Box 19–2).



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DATA FROM ZINK 1986

Figure 19–5 Geographical variation in Fox Sparrow populations. The bill dimensions of local populations diverge as the sparrows adapt to the food in local environments. These populations, some of which are candidates for species status, also differ in body coloration.

Box 19–2

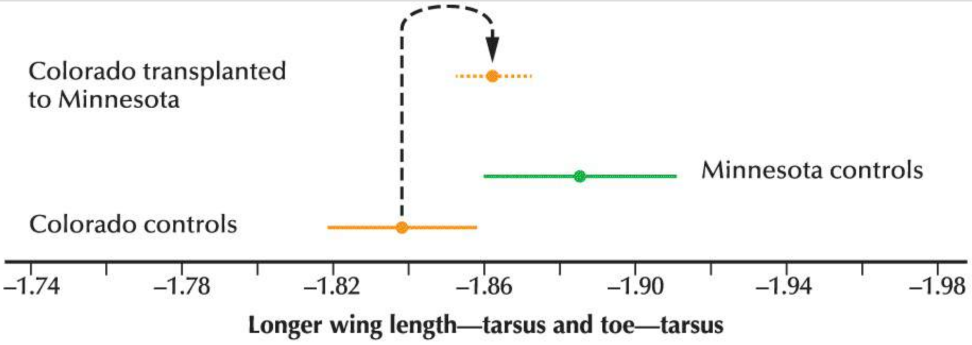
Character Heritability

We tend to assume that size and color variation are genetically controlled and that they are not directly affected by the environment. This assumption is reasonable, but it is not certain.

In her pioneering study, Frances James (1983) demonstrated the effects of local environments on size features of Red-winged Blackbirds. Both their bill shapes and their wing lengths vary geographically. Some of this variation can be attributed directly to the environment.

When James transplanted eggs from the nests of one population to nests of another morphologically distinct population, the dimensions of fostered chicks grew to resemble those of their foster parents. Red-winged Blackbirds transplanted from the Everglades to Tallahassee, Florida, grew shorter, thicker bills, similar to those of the Red-wings in Tallahassee. Red-wings from Colorado transplanted to Minnesota developed longer wings and toes (see graph). Thus, these young acquired some of the attributes of the host population. The incompleteness of morphological shifts by transplanted birds, however, revealed a significant degree of genetic control or heritability.

The heritability, *H*, of a character is the proportion of total observed variability that is controlled by the genes rather than by the environment. From one-half to most of the size variation observed in bird species has a genetic basis. Body masses of chickens are moderately heritable (H = 0.53). In contrast, feathering traits, breast angle, body depth, keel length, and shank pigmentation have lower heritabilities: H = 0.25 to 0.40 (Kinney 1969). Studies of character heritability in wild birds, often difficult exercises in quantitative genetics, indicate moderate to high heritabilities: H = 0.43 to 0.95 (Boag and van Noordwijk 1987). Such heritabilities expose characters to long-term genetic change by natural selection and to short-term environmental modifications (because H is less than 1.0).



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DATA FROM JAMES 1983

Environmental influence on the dimensions of nestling Red-winged Blackbirds. When transplanted to nests in Minnesota, eggs from nests in Colorado yielded nestlings that were shaped more like Red-wings in Minnesota than were the controls in Colorado. Nestling shape is here defined in terms of a discriminant function that relates wing length to size of the legs and feet.

Divergence of subspecies may follow adaptation to different habitats, or it may result from sexual selection. Prezygotic incompatibilities, including those in social signals and ecology, are the primary ingredients of essential reproductive isolation in birds (Edwards et al. 2005; Price 2008; Nosil and Schluter 2011). The enhancement of plumage ornamentation, size, and song traits through sexual selection is especially important to the early divergences of sister populations. The crests of Steller’s Jays in the western United States, for example, vary in length in relation to the openness of the vegetation in their habitats and to their effectiveness as social signals (see Figure 11–9). The divergence of ornaments or song then leads to reproductive isolation through assortative mating. Accordingly, advances in speciation genomics focus on the roles of genes that control traits such as plumage and vocalizations.

The interactions of divergent sister taxa—if and when they come back into contact, called **secondary contact**—test their reproductive, ecological, and behavioral compatibility. Species in secondary contact encounter new opportunities to mate with dissimilar birds. Of particular relevance to the speciation process, hybridization may be limited at first in its frequency of occurrence, or the species may practice strict assortative mating that leads to reproductive isolation and, thus, conformity to the definition of biological species. Alternatively, divergent taxa in secondary contact might hybridize and blend with each other.

Ornithologists have long predicted that divergence among populations linked in a series or chain over a large continental area could lead to the reproductive isolation of the populations at the distant ends of the chain. The discovery of such so-called **ring species**—two reproductively isolated forms connected through a chain of interbreeding populations—would support this prediction, but few such discoveries have materialized. The Greenish Warblers of central Siberia provide a good but controversial example of an avian ring species (Box 19–3).

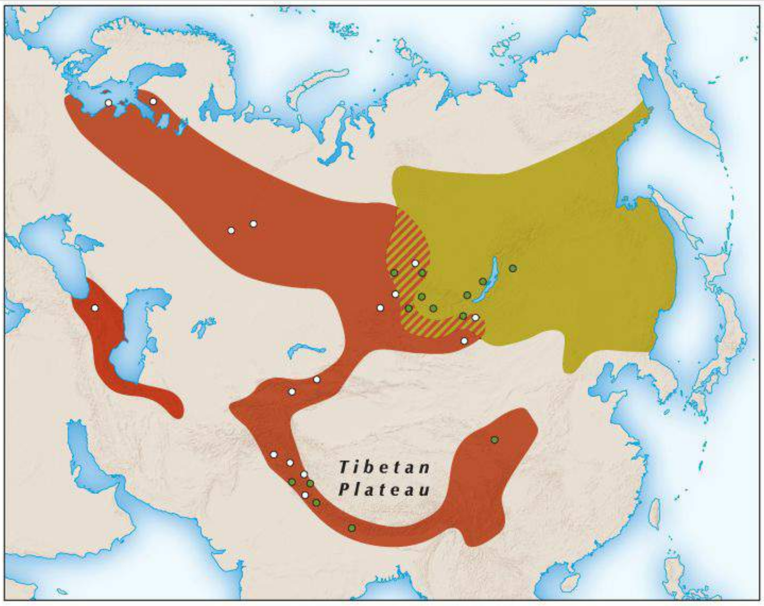
Box 19–3

A Ring Species in Siberia

The Greenish Warbler ranks high on the list of truly nondescript birds of the world. Nevertheless, it invites our attention as the best example of an avian ring species in which intergrading populations connect two reproductively isolated populations (Irwin et al. 2005; Alcaide et al. 2014).

The Greenish Warbler breeds in a narrow band of tree-line habitat in Siberia and the Himalaya. The band of that tree-line habitat encircles the high-altitude deserts of the Tibetan Plateau, forming a geographical ring of connected populations (see map). The one large gap in the ring in northern China is probably due to recent habitat destruction. Classical studies of size and plumage coloration, what there is of it, defined a series of intergrading subspecies (or closely related species) throughout this ring. New genetic data are refining how locally isolated versus truly continuous with gene flow were the member populations of this complex. The two northernmost ones coexist without interbreeding in central Siberia. They are reproductively isolated, terminal populations of increasingly divergent, interbreeding populations.

Historically, Greenish Warblers expanded on two fronts into Siberia as the climate warmed. Rapid adaptation to the northern forests and the migration distances required to reach them, which favor longer wings, caused the populations to diverge on the two fronts and to be reproductively isolated as biological species when the two northernmost populations came into secondary contact.



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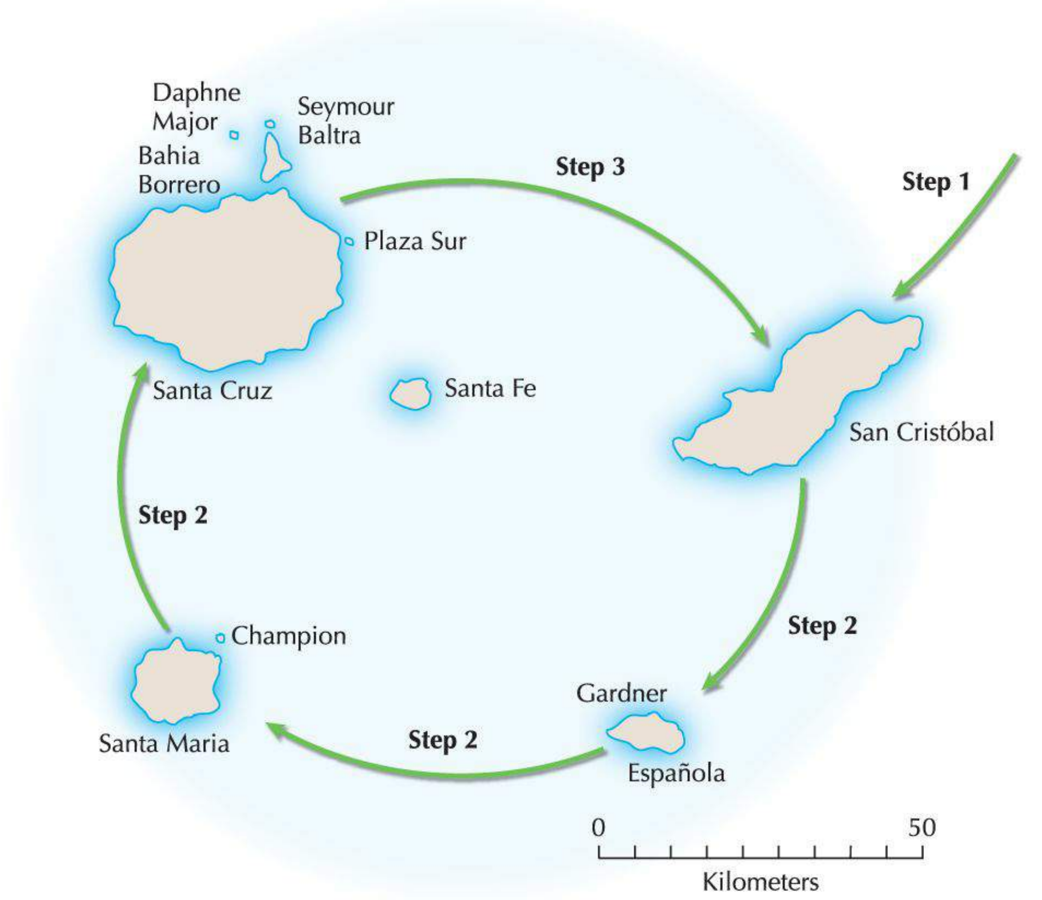
DATA FROM IRWIN ET AL. 2005

Ring populations of the Greenish Warbler in Siberia. Different shades represent different morphological subspecies that intergrade with each other. The two widespread northern subspecies *Phylloscopus trochiloides nitidus* (west) and *Phylloscopus trochiloides plumbeitarus* (east) coexist without hybridization (hatched area) in central Siberia. Habitat destruction in northern China has recently interrupted the continuity of the ring of populations. Symbols for localities sampled indicate major clades (groups related by evolutionary descent from a common ancestor) based on mitochondrial DNA. White circles represent western clades; green circles represent eastern clades. The genetic distance between individual birds within and between clades increases with geographical distance around the southern chain of populations.

Darwin’s Finches

Peter and Rosemary Grant (2008) and their colleagues studied the details of the process of speciation by Darwin’s finches on the Galápagos Islands for more than 30 years. Their findings helped to define the rules of the speciation process (Box 19–4). The multiplication of species of Darwin’s finches followed three basic steps, repeated over and over again (Figure 19–6). First was the original colonization of the Galápagos Islands by the ancestor from mainland South America, probably a grassquit of the genus *Tiaris* (Sato et al. 2001). Second was the colonization of other islands by dispersal from the first island. Speciation of these finches took place when small colonizing founder populations underwent rapid but simple genetic changes followed by population growth and adaptive divergence. Third, derived and divergent populations recolonized the original, or "first," islands. Secondary contact and coexistence with their sister populations or species completed the speciation process. Some of Darwin's finches now have moderately large populations on several islands united by gene flow.



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DATA FROM GRANT AND GRANT 1997

Figure 19–6 A model of allopatric speciation by Darwin's finches in the

Galápagos Islands. First, their mainland ancestor, a grassquit, colonized one of the islands (step 1). Its descendants dispersed and colonized additional islands (step 2), starting new isolated populations that diverged from one another. In the final step (3), members of a divergent population established themselves on the original island and coexisted there—in sympatry—without interbreeding with the descendants of a parent population.

Box 19–4

Seven Rules of Speciation in Birds

Seven primary rules summarize the essential features of the speciation process in birds (Grant and Grant 1997):

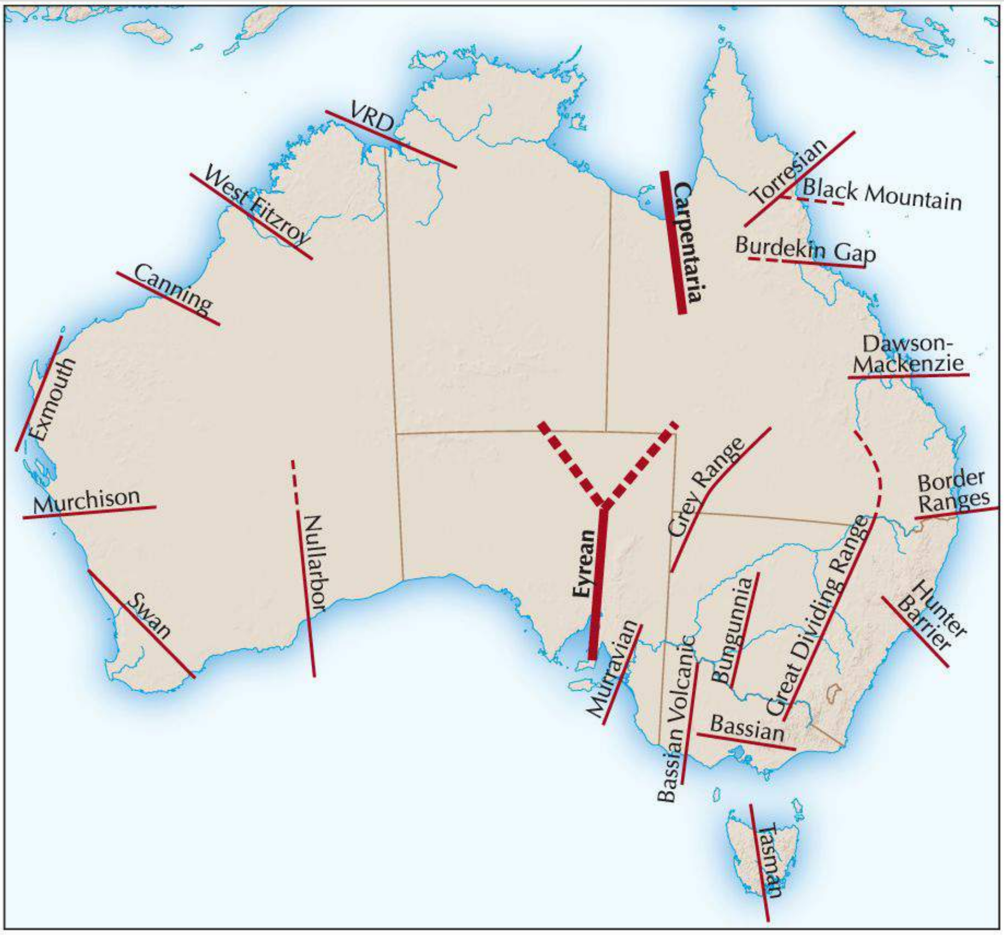
1. Speciation starts with divergence in geographical isolation, or allopatry.
2. Divergence in allopatry through ecological adaptation or sexual selection precedes sympatry (coexistence in overlapping geographical areas without interbreeding).
3. Premating isolating mechanisms evolve in allopatry before postmating isolating mechanisms evolve in either allopatry or sympatry.
4. Premating mechanisms include the effects of learning and cultural processes, such as sexual imprinting.
5. Postzygotic incompatibilities arise first in females (the sex with two different sex chromosomes), in accord with Haldane’s rule. (Haldane’s rule says that both male and female hybrids may be sterile, but the heterogametic sex with two different sex chromosomes—male fruit flies and mammals and female birds—tends to be sterile more often than the homogametic sex with two of the same sex chromosomes.)

6. Genetic mechanisms differ for the control of premating mechanisms (additive polygenes) and for the control of postmating mechanisms (nonadditive effects of dominance and epistasis, which is an interaction between nonallelic genes, especially one in which one gene suppresses the expression of another).
7. Divergent bird species retain genetic compatibility and the potential for viable F_1 (first generation) hybrids longer than do mammals and for millions of years after speciation.

Hybridization occurs between some pairings of all six species of ground finches as well as with other Darwin finches—namely, the tree finches and cactus finches. First-generation (F_1) hybrids are viable and fertile, as are later backcross hybrids. The current species retain substantial genetic compatibility with little sign of postmating isolating mechanisms. These mechanisms will develop slowly as a result of continued divergence of species that are essentially isolated by their species-recognition behavior.

Geographical Isolation on Continents

The isolation of bird populations on remote oceanic islands, such as the Galápagos Islands, is easy to envision. Isolation on the mainland is less so. In overview, changing climates and their effects on habitats isolate bird populations on continental landscapes. Wet–dry cycles fragmented the habitats and isolated bird populations from one another within Australia, Africa, and South America (see Figure 3–12). Fractured sets of sister populations, or vicariants, then evolved into different species. The history of modern Australian birds, for example, broadly reflects the continent’s division into a vast central arid zone: monsoonal tropics and subtropics in the north and temperate zones in the south (Figure 19–7).



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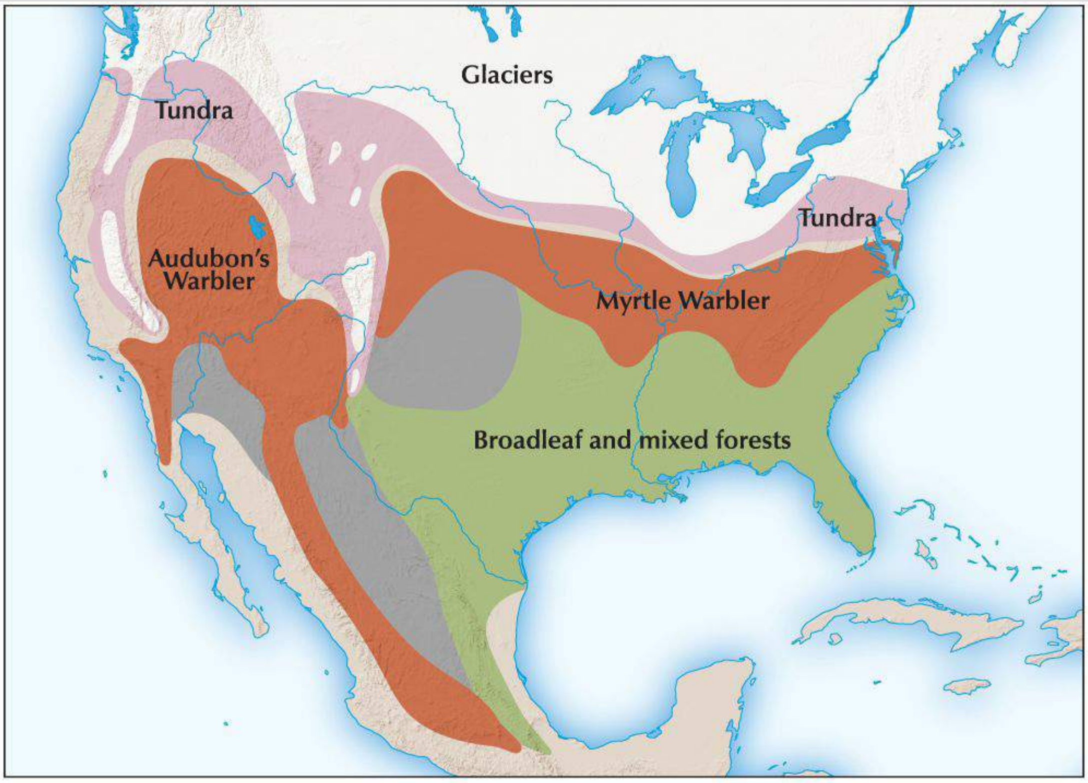
DATA FROM SCHODDE AND MASON 1999

Figure 19–7 Fragmentation of Australian habitats promoted geographical speciation of perching birds on that continent. Within the continent, 22 major or minor biogeographic barriers are thought to have emerged in response to cycles of climatic deterioration and improvement during the Pleistocene epoch. Sister taxa diverged with these geographic separations, producing current assemblages of species and subspecies. The Carpentarian Barrier separated many northern tropical species into east–west pairs, whereas the Eyrean Barrier did likewise within the vast central arid zone. The vast central arid zone separated the birds of the temperate biomes in Australia’s southeast and southwest.

DNA comparisons help us to investigate how long ago bird populations speciated. Sister species of birds exhibit nucleotide divergences in 2 to 8 percent of their mitochondrial DNA (mtDNA). Assuming that mtDNA diverges at a rate of roughly 2 percent every million years, many species originated in the late Pliocene (1.5 to 3.5 million years ago), but some are older still (Klicka and Zink 1997). Histories of species divergence also include predictable declines of genes retained from a common ancestor. Estimates of the time back to a common genetic ancestor, or coalescence, reveal the history of fragmentation in relation to past changes in global ecology and climate. Winter Wrens, for example, underwent repeated fragmentation, or vicariant events, of their populations throughout the Northern Hemisphere dating to the Miocene (Drovetski et al. 2004; see the geologic time scale in Table 2–1). From their original populations in North America, they spread widely throughout the Northern Hemisphere roughly 13 million years ago. Much later, the glaciations of the early to mid-Pleistocene split the wren populations sequentially into six evolutionarily significant units with species-level genetic divergences (3–8.8 percent).

Pleistocene climate changes played a major role in defining modern birds of the northern continents. Through numerous extinctions, the glaciers pruned the species assemblages that had prospered in the gentler preceding climates of the Tertiary. Losses accrued with the habitat fragmentation that was a regular consequence of the repeated advances and retreats of the glaciers. Those bird populations that survived the effects of changing climates on major habitats shrank in size and became fragmented in their distribution. When the glaciers retreated, the bird populations followed and engaged in new confrontations with one another.

Myrtle Warblers and Audubon’s Warblers are one example of this (Figure 19–8). Breeding generally in boreal forests to the east and west of the Rockies, they came into contact in the narrow mountain passes of the Canadian Rockies about 7,500 years ago, when the glaciers retreated and the northern forests reunited. Reduced survivorship of their hybrids suggests that these two warblers exhibit essential reproductive isolation, one criterion for species status (Mila et al. 2005).



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DATA FROM HUBBARD 1969

Figure 19–8 Model of the distributions of the Myrtle Warbler and Audubon’s Warbler. They became separated during the Pleistocene epoch (Wisconsin glaciation), when they diverged from a common ancestor. Gray areas indicate regions for which the habitat type at that time is unknown.

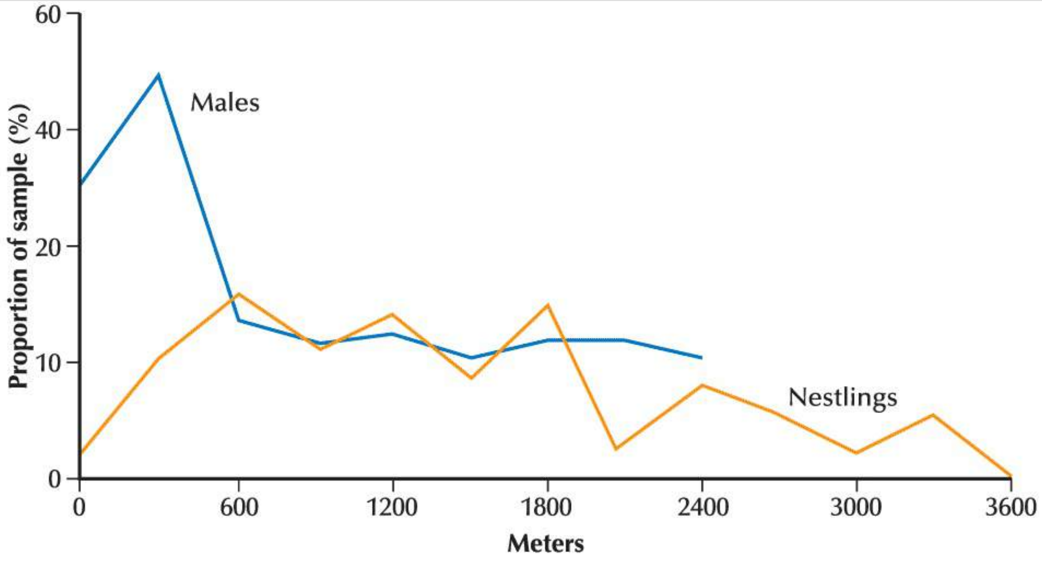
In other cases, coalescence analyses reveal that expansions of populations throughout the northern United States and Canada have been too recent to allow substantial genetic divergence. For example, widespread North American bird species, such as Mourning Doves (Figure 19–9) and Black-capped Chickadees, each have species-specific mtDNA genotypes from one side of the continent to another.

ALL CANADA PHOTOS/ALAMY

Figure 19–9 Mourning Doves are a common sight (and sound, with their mournful coo) throughout much of the United States. Their populations have expanded too recently to allow substantial genetic divergence in mtDNA.

19.3 Gene Flow, Clines, and Local Evolution

In previous chapters, we explored the forces governing the sizes of bird populations, their trends, and their connectivity (see Chapters 10 and 18). Population sizes and structures also guide the evolution of geographical variation and eventually species. In particular, the movement of young birds from the sites where they hatched to the sites where they breed, called **natal dispersal,** connects local populations by gene flow. Large natal dispersal distances unite geographically diverse populations. Small natal dispersal distances enhance genetic isolation of local populations and favor their evolutionary divergence. Songbirds such as the House Wren and the Song Sparrow stay within a few kilometers of their natal territories (Figure 19–10). Only a few individual birds of such species disperse widely.



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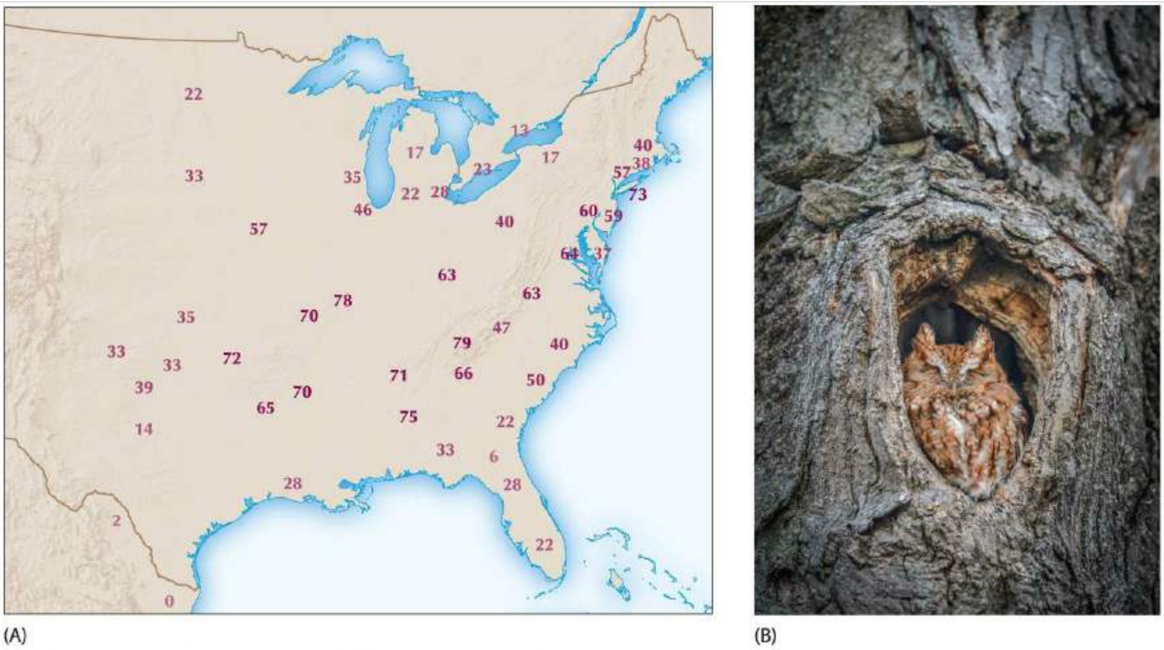
Data from Barrowclough 1978

Figure 19–10 Dispersal of adult male and nestling House Wrens. Most adult males disperse over a small area, whereas young wrens disperse more widely.

The evolution of geographical differences among bird populations depends on the relative strength of two opposing forces: natural selection and gene flow. **Natural selection**—the differential propagation of genotypes—promotes divergence by favoring one genetic attribute over another. **Gene flow**—the movement and incorporation of alleles among local populations due to dispersal—opposes divergence by blending the differences among adjacent populations. How much the local compositions of genes change from site to site, or **cline,** depends on the relative intensities of divergent selection and gene flow due to natal dispersal.

Clines are especially conspicuous in birds that have simple (Mendelian) genetic color morphs. The proportions of red (actually bright rufous) versus gray Eastern Screech Owls, for example, change systematically with locality. Local populations change from mostly red owls in Tennessee to mostly gray owls in Maine and Florida (Figure 19–11). The advantages of color alternatives derive from protective coloration and exposure to predators such as the Great Horned Owl. As the type of forests changes from rich brown hardwoods in the center of their range to grayish conifers in the north and to pinelands in the far south, the concealing coloration changes from reddish to gray.



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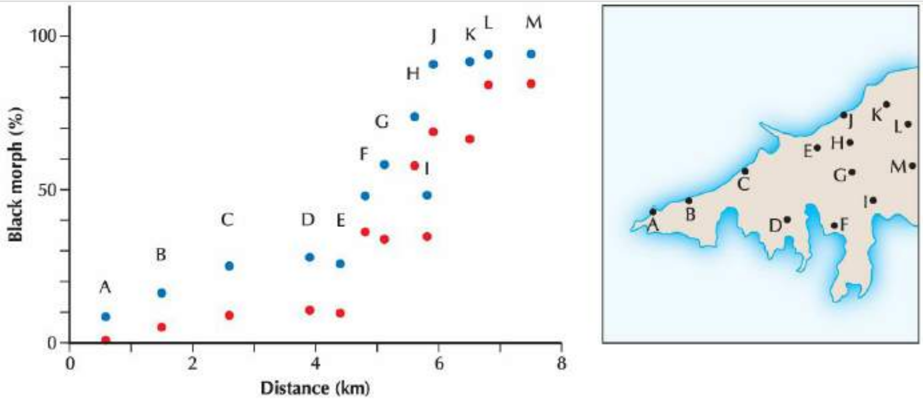
(A) Data from Owen 1963 .(B) Barry Spruce Photography

Figure 19–11 The proportions of red-phase Eastern Screech Owls found in local populations (A) decline from high values of 70 to 80 percent in the center of the range of this species to 30 percent or less at the edges of the range. (B) Eastern Screech Owl.

Clines may be either static or dynamic. In static clines, the equilibrium between selection and gene flow is stable: the composition of the populations will stay the same. Dynamic clines change with time as a result of an ongoing diffusion of neutral traits due to gene flow or as a result of an advantage of one trait over its alternatives.

Bananaquits provide one example of a dynamic cline (Figure 19–12). These small, tropical, warblerlike, nectar- and fruit-eating birds are abundant on islands of the Caribbean. The yellow-and-black color form of Bananaquits prevails throughout most of the Caribbean. An all-black form of this species, determined by a single dominant mutant *MC1R* allele, inhabits the island of Grenada (Theron et al. 2001; see Figure 4–

22).



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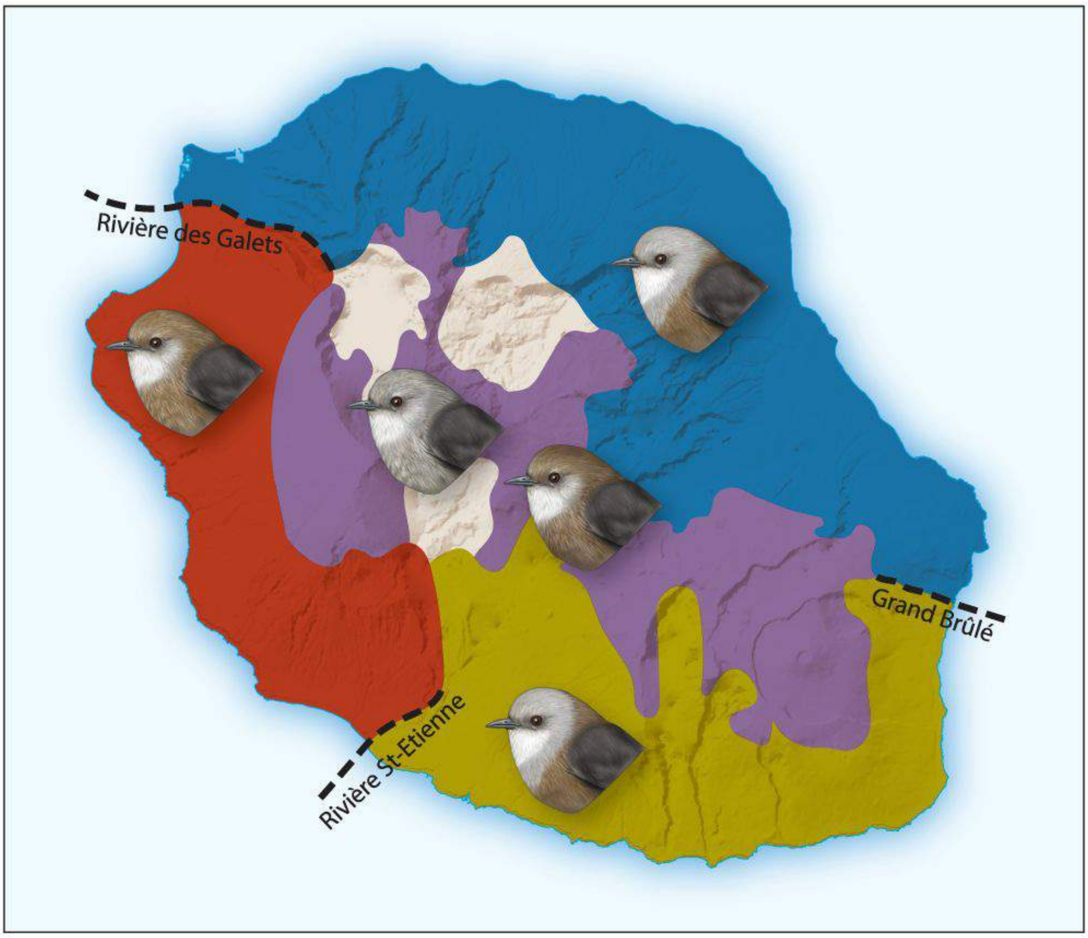
Data from Wunderle 1983

Figure 19–12 Yellow-and-black Bananaquits are common only in southwestern Grenada, the region of their recent colonization of this island. All-black birds (black morphs) occupy the rest of the island. Shown here are the proportions of the black morph (blue circles) at sampling sites (A through M) for the interval 1974–1978, graphed with regard to distance from the westernmost point of the island. Red circles indicate the results of resampling the localities in 1981 and show how proportions of the black morph have declined.

Yellow-and-black Bananaquits from adjacent islands colonized the arid southwestern corner of Grenada in the early 1900s. They replaced the black form in their initial foothold on the island, and then expanded progressively to the north and east. Exhibiting a 17 percent selective advantage, yellow-and-black Bananaquits advanced eastward at a rate of roughly 400 meters per year, mixing with and then replacing black forms. As a result, the proportions of the remaining black form increased clinally to the north and east. The replacement continued dynamically for 21 years and then stopped when droughts limited continued population growth and expansion of yellow-and-black Bananaquits (MacColl and Stevenson 2003). The dynamic cline stopped and stabilized as a static cline.

Sometimes, bird populations evolve differences on an extremely local scale. Two examples illustrate this phenomenon. First is an unusual, striking geographical divergence among populations of a species of white-eye (*Zosterops*) within the confines of a small island in the Indian Ocean. Second are detailed studies of genetic population structure of the Great Tit on the small island of Vlieland off the coast of Holland. These studies refocus our attention on the power of microevolution (evolutionary change between local populations) in birds.

White-eyes are Old World island specialists and ecological equivalents of the Bananaquit. On a small, rugged island in the western Indian Ocean, the Reunion Gray White-eye exhibits extraordinary patterns of local geographic variation due to social and ecological selection favored by low dispersal (Bertrand et al. 2014; Cornuault et al. 2015; Bourgeois et al. 2017; Figure 19–13). Five genetic and morphologically distinct forms occupy different parts of the lowlands: four that are brown in color and a fifth that is all gray. Three of the brown ones are separated by modest river and lava flow barriers in the lowlands. Highland populations include the fourth brown morph together with a gray morph. Genomic analyses of these white-eyes reveal that they are highly sedentary with restricted dispersal among local populations less than 10 kilometers apart. Reduced gene flow allows local microgeographic patterns of genetic population structure to evolve. Coalescence analysis of their recent genetic history suggest that a novel, dominant mutation in the highland brown form produced the gray morph, which then swept through that population but not to fixation. Mixtures of brown and gray morphs persist by virtue of unknown advantages of heterozygote white-eyes, that is, the individuals that carry both of the alternative alleles responsible for these plumage colors.



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DATA FROM BERTRAND ET AL. 2014

Figure 19–13 Microgeographic variation in the Reunion Gray White-eye on the island of La Réunion in the Indian Ocean. Narrow hybrid zones separate the distinct populations.

Much smaller than La Réunion is the tiny 4,022-hectare island of Vlieland on the coast of the Netherlands. Vlieland is home to two genetically distinct populations of Great Tits. A remarkable 30-year study documented the movements and genetics of the Great Tits and quantified the microevolutionary interaction between selection and gene flow (Postma and van Noordwijk 2005). Different levels of immigration and gene flow from the mainland sustain a genetic difference between the two populations.

Specifically, female Great Tits on the western part of the island consistently lay on average 1.15 more eggs in a clutch than do female Great Tits on the eastern part of the island only a few kilometers away. This difference in clutch size has a strong genetic component: females that move eastward or westward within the island continue to lay the clutch sizes that are consistent with their place of origin. The root cause of the difference between sites lies curiously in the rates of immigration and settlement by tits from the mainland.

Selection on Vlieland as a whole favors females that live twice as long as the mainland tits and produce smaller clutch sizes. But each year, females from the mainland, which are genetically predisposed to lay larger clutches, migrate to Vlieland. They migrate mostly to the west side of the island. Immigrants account for 43 percent of the annual recruitment to the west side compared with only 13 percent to the east side. The local selection for small-clutch females can override the 13 percent influx in the east but not the 43 percent influx in the west.

19.4 Hybrids

More than 10 percent of bird species are known to pair with at least one other species, or hybridize (Grant and Grant 1992). The word "hybrid" itself grabs our attention. It evokes the powerful concepts of novelty, strength, sterility, inferiority, and superiority (Gill 1998). Hybrid birds both challenge and fascinate ornithologists. Each year, ornithologists report new novelties due to hybridization. Deciphering their parentage can be a wonderful puzzle.

Descriptions of the first "Brewster's" and "Lawrence's" Warblers collected in Massachusetts in 1874, for example, provoked much debate. They finally proved to be hybrids between Blue-winged Warblers and Golden-winged Warblers (see Figure 19–17). In another case, at the beginning of North American ornithology, Audubon himself described the enigmatic "Cincinnati Warbler." A century and half later, Gary Graves (1988) determined it to be a hybrid between a Kentucky Warbler (*Oporornis*) and a Blue-winged Warbler (*Vermivora*).

Hybrid Inferiority

Much early thinking about speciation in birds emphasized hybrids as indicators of reproductive compatibility or isolation. This emphasis was based on applications of fruit fly (*Drosophila*) genetics to birds (Grant and Grant 1996; Gill 2014). Small genetic changes tend to cause male sterility in fruit flies but not in birds. Instead, with some exceptions, birds retain the potential for successful hybridization through surprisingly high levels of genetic divergence. Consequently, successful hybridization among birds is not limited to closely related or sister species. Even parents in different genera hybridize successfully because of their retained genomic compatibility. Hybrids between species of wood warblers, ducks, and pheasants, among the many examples, testify to this potential compatibility.

Some bird hybrids, however, exhibit sterility or substantial inferiority. For example, almost all the hybrids of the closely related Eastern Meadowlark and Western Meadowlark are sterile (Lanyon 1979). The hybrids appear normal and healthy, but they produce infertile eggs when paired in captivity with an Eastern Meadowlark or a Western Meadowlark. Because there is no gene flow between them, the two meadowlarks remain distinct biological species.

Both male and female hybrids may be sterile, but the sex with two different sex chromosomes tends to be sterile more often than the sex with two of the same sex chromosomes (see Box 19–4). Data from vertebrates and invertebrates broadly support this expectation—known as **Haldane's rule** because it was stated first by J. B. S. Haldane (1922). Unlike mammals, female birds are the heterogametic sex with the ZW pair of sex chromosomes; males are ZZ. Female hybrids, therefore, are more likely to be sterile than are male hybrids.

Hybrids may produce viable sperm or fertile eggs but have fertility problems later in the development. Incompatible gene combinations can disrupt the delicate process of embryo development in the second-generation (F_2) offspring. This phenomenon is called F_2 breakdown. For example, female F_1 hybrids between different species of junglefowl (wild chickens) lay fertilized eggs, but few of them hatch (Morejohn 1968).

Hybrid Zones

Ornithologists have long used the extent of hybridization between different populations to decide whether two populations belong to the same species. Separate biological species status is warranted if no hybrids are present and complete reproductive isolation is manifest. Conversely, two populations belong to the same biological species when hybrids are abundant and blend freely with parental types in zones of overlap. Species status also is warranted with evidence of essential reproductive isolation, that is, if hybrids appear in low frequencies, if interspecific pairings are infrequent, if hybrids are less viable than the parental forms, or if a zone of contact and hybridization is narrow and stable.

The eastern and western populations of the Northern Flicker—the Yellow-shafted Flicker and the Red-shafted Flicker—hybridize extensively in the Great Plains of North America (Moore and Buchanan 1985). To assess the extent, dynamics, and consequences of hybridization, ornithologists obtained samples of individual birds from a series of localities throughout the zone of overlap. In the procession from east to west through the zones of contact between these taxa, the first samples include only the eastern representative of the pair. West of the hybrid zone, the composition switches to include only the western representatives. The samples from the hybrid zone consist of intermediate and variable phenotypes. Most birds at localities in the hybrid zone are intermediate in appearance, a finding that indicates that they freely interbreed. In accord with the Biological Species Concept, the eastern and western counterpart populations of the flickers are currently lumped into one species.

The pendulum of species taxonomy has swung back and forth in regard to another pair of species that hybridize in the Great Plains: the eastern Baltimore Oriole and the western Bullock’s Oriole (Figure 19–14). Initial studies of their hybrid zone suggested extensive interbreeding. Consequently, in 1983, the Committee on Classification and Nomenclature of the American Ornithologists’ Union lumped the two species into a single species, the “Northern Oriole” (American Ornithologists’ Union 1983).

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DATA FROM RISING 1983. (A) ROBERT L KOTHENBEUTEL/SHUTTERSTOCK.COM. (B) © GEOFF JONES 2008/BARRAIMAGING.COM.AU

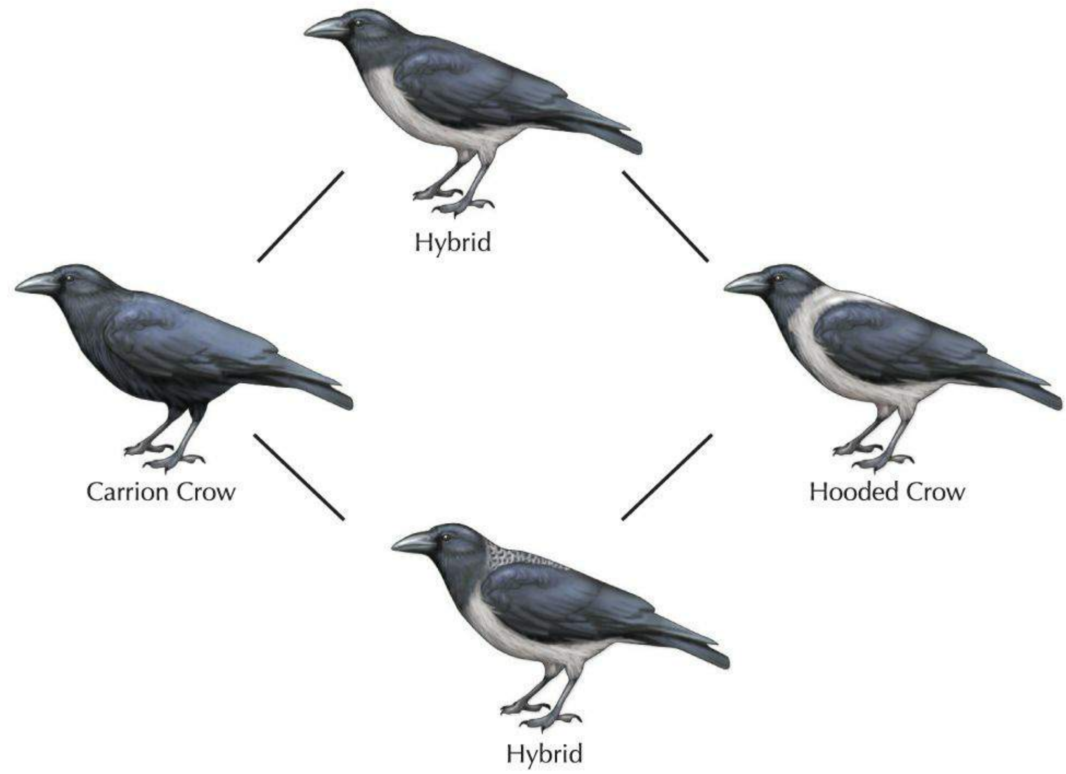
Figure 19–14 The western Bullock's Oriole (A) and the eastern Baltimore Oriole (B) interbreed in a narrow zone of overlap in the Great Plains. The hatched area indicates the extent of infiltration of Bullock's characters eastward and of Baltimore characters westward. These two oriole species were once lumped together as the Northern Oriole, but later study revealed that they are not sister species.

Additional studies of the hybrid zone revealed that it was narrow and stable in some areas and that hybridization decreased with continued contact in other areas. In addition, phylogenetic studies revealed that Baltimore and Bullock's Orioles were not closely related sister species after all. Consequently, the American Ornithologists' Union Checklist committee reversed its original decision and, in 1995, restored the two orioles to full species status, to the delight of the residents of Maryland (American Ornithologists' Union 1995).

Hybrid Zone Dynamics

In addition to informing taxonomic decisions, hybrid zones offer ways to study the genetic and social architectures of speciation (Harrison 1993). Some are old, narrow, and continuing sinks of hybrid inferiority. Others are stable zones of hybrid superiority. Still others are new contacts in the early test phases of genetic and social confrontation that may be resolved through natural selection.

Hybridization in zones of secondary contact often persists and continues unabated for centuries. The narrow hybrid zone between the Hooded Crow and the Carrion Crow of Europe has not changed in width for at least 500 years. Hybrids between the all-black Carrion Crow and the black-and-gray Hooded Crow are easily recognized by their variable color patterns (Figure 19–15). At least some of the hybrid zones in the Great Plains region of North America, including that of the Northern Flicker, date back to the expansion of isolated populations after the retreat of the glaciers 10,000 years ago. The hybrid zone between the western and the eastern populations of the Northern Flicker has not changed in width or location for at least 100 years and probably much longer (Moore and Buchanan 1985). The continued free interbreeding between the flickers suggests no disadvantages and perhaps some advantages of hybrids in the zone of their contact.



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DATA FROM SAINO AND VILLA 1992

Figure 19–15 Color patterns of Carrion Crows, Hooded Crows and their hybrids. Hybrid phenotypes combine the gray underparts of a Hooded Crow with variable amounts of Carrion Crow black pigment on their backs and necks.

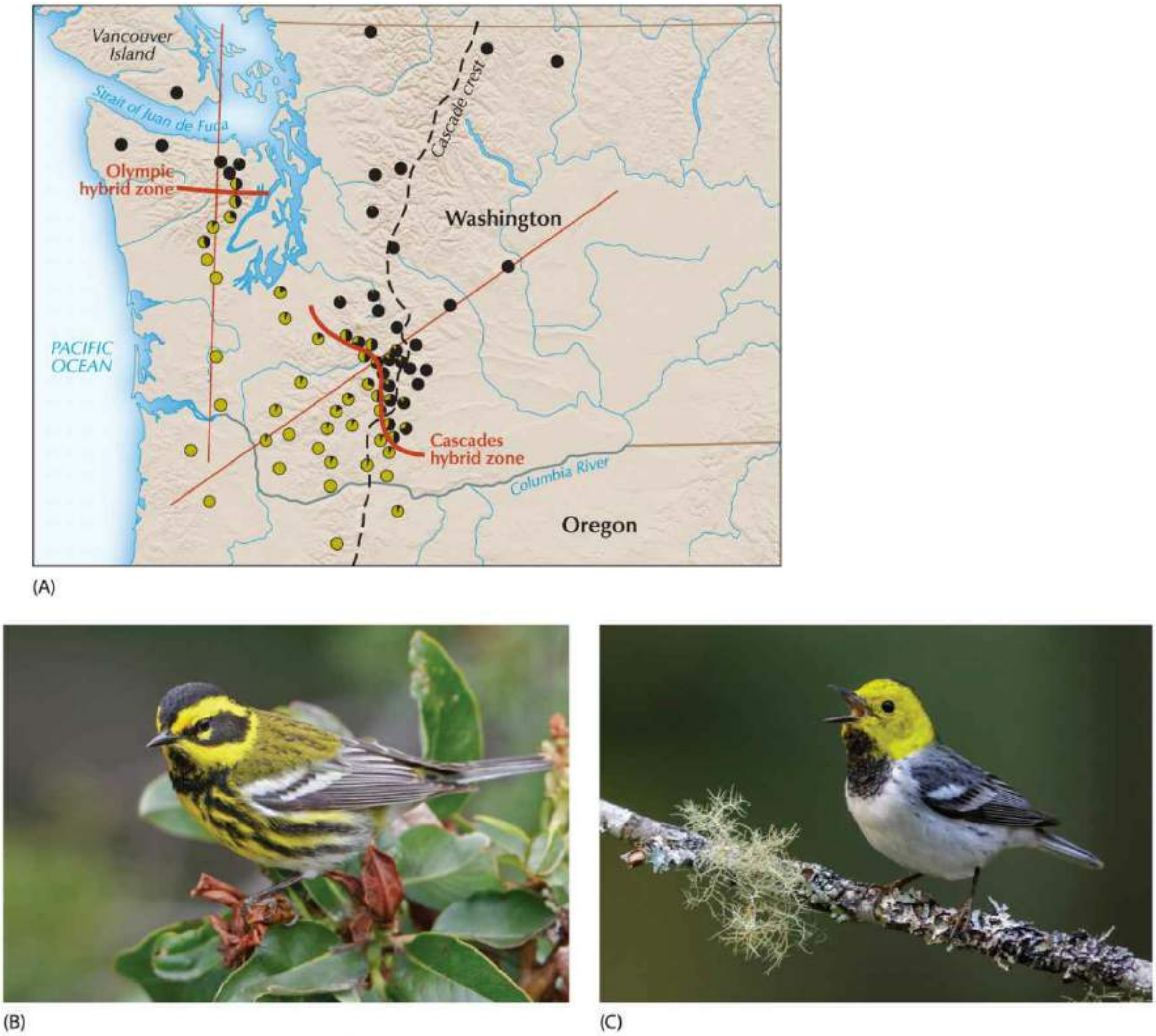
Two theoretical models explain the stability of such hybrid zones. The bounded superiority model of Moore (1977) proposes that hybrid zones coincide with intermediate ecological or climatic conditions where hybrids are equally or better adapted than their parents. The model best explains the stable hybrid zones of the flickers in North America and the crows in Europe (Saino and Villa 1992).

The alternative, dynamic equilibrium model of Nicholas Barton and Godfrey Hewitt (1985) proposes that a stable hybrid zone is a population sink of inferior hybrids produced relentlessly by immigrants from the adjacent, large, pure populations. Sharp boundaries between the hybridizing species are a result. This model applies with a twist to the Townsend's Warblers and Hermit Warblers in the Pacific Northwest, described in the next section.

Transient Hybridization

Hybridization sometimes occurs just on the initial contact of two species and then stops as reinforcement of correct species recognition sets in. For example, the Silvereye of Australia colonized Norfolk Island in the South Pacific east of Australia at least three times, most recently in 1904 (Gill 1970). Shortly after the third invasion, some of the Silvereyes hybridized with the descendants of the preceding invasion, which in the interim had evolved into the larger Slender-billed White-eye. But hybridization did not continue, and the two white-eyes now coexist as distinct species on Norfolk Island without interbreeding.

Sometimes, new competitive interactions cause the local extinction or replacement of one species by another (Rhymer and Simberloff 1996). The Townsend's Warblers and Hermit Warblers of the great forests of the Pacific Northwest of North America provide a prime example of replacement following transient hybridization (Figure 19–16). Of the two, Townsend's Warbler is the competitively superior, aggressively dominant species. By virtue of their behavioral advantages, Townsend's Warblers are steadily replacing Hermit Warblers. Townsend's Warblers have been winning for thousands of years. The hybrid zone between the Townsend's Warblers and the Hermit Warblers stays narrow due to selection against the hybrids, which don't compete successfully for quality territories. The location of the hybrid zone, however, is moving steadily southward into the remaining Hermit Warbler populations. As the hybrid zone moves forward, a genetic footprint of Hermit Warbler mtDNA remains behind in the replacement Townsend’s Warbler populations. The markers persist as a “ghost” image of the original Hermit Warbler range that once extended into southern Alaska.



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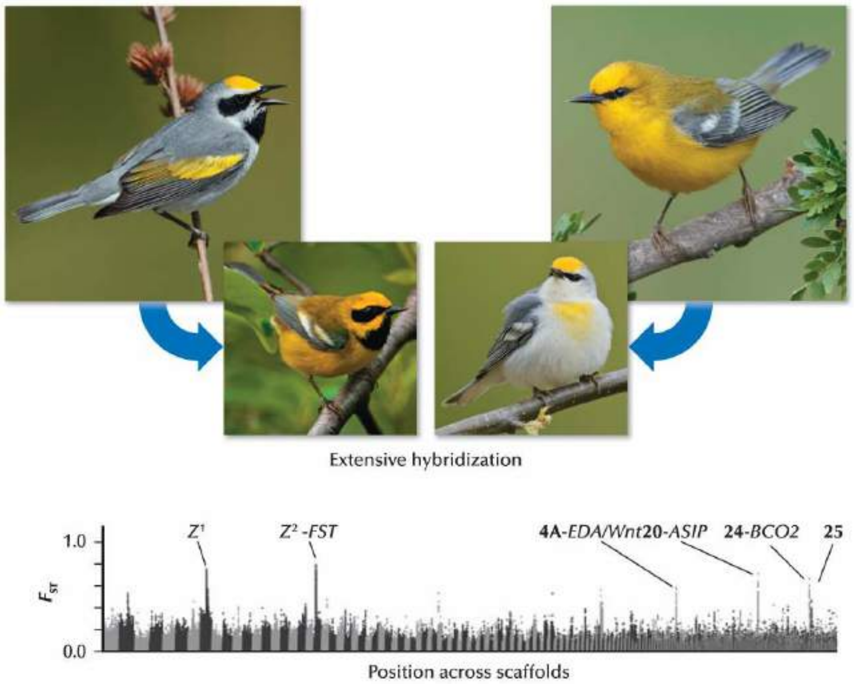
(A) Data from Rohwer et al. 2001. (B) Glenn Bartley/AGE Fotostock. (C) All Canada Photos/Alamy Stock Photo

Figure 19–16 (A) Location of two hybrid zones (Olympic and Cascades) of Townsend’s Warblers and Hermit Warblers in Washington State. Black circles indicate pure Townsend’s Warbler (B) populations, and yellow circles indicate pure Hermit Warbler (C) populations. Samples from mixed populations show proportions of the two phenotypes. Heavy red lines indicate midpoints of phenotype transitions. Thin straight lines indicate transects sampled through zone used to analyze changes in characters.

Blue-winged Warblers and Golden-winged Warblers further illustrate the dynamics at work in transient hybridization (Vallender et al. 2007; Toews et al. 2016; Figure 19–17). Populations of Blue-winged Warblers have been expanding their range northward with the availability of their preferred habitat, early stage forest regrowth. They hybridize with and replace Golden-wings within 50 years of local contact. Consequently, the Golden-winged Warbler is increasingly endangered and of conservation concern throughout most of its original range. First-generation hybrids, called “Brewster’s Warblers,” are slightly disadvantaged with respect to obtaining mates but are fertile. So, a long history of sharing genes through hybridization has nearly blended their genomes, perhaps beneficially. Genomic analysis reveals that despite divergent mtDNA genes, the warblers differ by only a few nuclear genes that control their striking plumage color differences, including face patterns.



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(Photos (left to right): Jim Zipp/Science Source, Jay Ondreicka/Shutterstock, Science Source/Jim Zipp, Nature Photographers Ltd/Alamy. Map: Republished with permission of Elsevier, from Toews DP, Taylor SA, et al., "Plumage Genes and Little Else Distinguish the Genomes of Hybridizing Warblers," Current Biology, 2016, September 12; 26(17): 2313-8, Figure 2a. Permission conveyed through Copyright Clearance Center, Inc.

Figure 19–17 Whole genome comparison identified six genes that distinguish the Golden-winged Warbler (left) and Blue-winged Warbler (right). The different face color patterns of these two hybridizing species are controlled by a single pair of alleles with dominance (20-ASIP). The blending of plumage colors coupled to the alternative facial color patterns produces a variety of hybrid types, including the Lawrence's Warbler (middle left) and the Brewster's Warbler (middle right).

19.5 Behavior and Speciation

The behavior of birds, particularly their capacity for new behavior and its cultural transmission, can drive their speciation (West-Eberhard 1983; Wyles et al. 1983). Behavioral innovations and new habits can spread rapidly through a population by cultural transmission, followed by the evolution of anatomical traits that enhance the effectiveness of individuals practicing the new habit. Speciation in birds can itself be a cultural process based on sexual imprinting of parental characters and behaviors. The brood parasitic indigobirds are the classic though specialized example of this process in the wild (see Chapter 14). Cross-fostering of young birds with other species also illustrates the power of sexual imprinting (see Chapter 16).

Cultural learning of paternal songs can drive mate choice. Early imprinting starts a process of social preference that segregates coexisting birds into distinct clusters. Assortative pairing follows, with rare mistakes. Recall that early imprinting by Snow Goose goslings on the color of their parents determines later mate preferences and leads to assortative mating (see Chapter 16).

How, then, do young precocial birds and young of other species without parental care develop a sense of social identity? Recall the megapodes, or mound builders, that leave the compost nest independently on hatching, running off on their exceptionally strong young legs (see Chapters 15 and 16). They provide valuable insights into early social recognition. Experiments using robotic chicks of the Australian Brushturkey revealed that the young megapodes gather naturally with other young of their own species. They do so by responding innately to a series of visual cues, both behavioral and morphological (Göth and Evans 2004). In particular, the strong ultraviolet and other short-wavelength reflectance of the legs of their kin evokes a strong innate social response. The chicks approach robots with the right ultraviolet leg color. So the color of their powerful little legs, which are not readily seen by hawks from above, serves as a natural club membership card. However, no one knows how these initial social responses lead to their choice of mates when they grow up.

Social Selection

This chapter and preceding chapters emphasized the power of social recognition in birds. Social selection favors new signals or communication of identity that can drive the speciation process (West-Eberhard 1983). Songs, in particular, are subject to elaboration through vocal contests and cultural change. Through social ritualization, these same attributes enable pair formation, species recognition, and initial reproductive isolation.

Recall that western Marsh Wrens have innate brain capacities for larger song repertoires than do eastern Marsh Wrens (see Chapter 8). Specifically, sexual selection and the behavior of countersinging have led to the elaboration of the brain nuclei that control singing behavior, associated differences in song-learning abilities, and mating preferences. Male Marsh Wrens duel vocally with one another to control prime territories and to attract evaluation by potential mates. The larger repertoires and brain capacities of the western Marsh Wrens reflect more intense competition in restricted pothole cattail marshes.

Generally separated by a 100-kilometer gap, eastern and western Marsh Wrens coexist and pair assortatively in some marshes in the northern Great Plains (Kroodsma and Verner 1997). Divergence has proceeded far past the initial stages of premating isolation through song divergence. The two Marsh Wrens also exhibit substantial divergence in the base pair sequence of the cytochrome oxidase I gene of their mitochondrial DNA (Hebert et al. 2004).

Species Recognition in Darwin’s Finches

Early in this chapter, we examined the basic steps and seven rules of speciation in Darwin’s finches. The field studies of these birds by Peter and Rosemary Grant have revealed the importance of behavior in the speciation process. Periodic and stringent sorting of individuals with new behaviors and new anatomical features promote the evolution of new species of finches.

Darwin’s finches are prime examples of adaptive radiation of bill sizes, feeding habits, and behavioral innovations (see Chapter 1). The evolutionary history of Darwin’s finches has been marked by episodes of strong selection for changes in bill morphology. The drought of 1976, for example, resulted in a shift of bill sizes to those that enabled the finches to feed efficiently on the seeds that were available (see Chapter 1).

Changes in bill size and feeding behavior then lead to premating isolation because Darwin’s finches use bill morphology to choose their mates. Experiments with finches in their natural habitat demonstrated that bill size, shape, and color are primary visual cues that determine mate choice. Laurie Ratcliffe and Peter Grant (1983) tested the responses of several pairs of sympatric species of ground finches (*Geospiza*) to taxidermy mounts of different species. Both males and females discriminate between their own species and other species based on visual cues of bill morphology.

The use of visual cues starts when young finches imprint on the appearance of their parents. Later, they use those visual cues and also song to choose their mates. In this way, bill size and shape serve as a premating isolating mechanism. Visual differences in bill size also channel early social interactions to other individuals of the same species.

In addition to bill morphology, song differences acquired through vocal imprinting play a significant role in species recognition and mate choice by Darwin’s finches (Grant and Grant 1997). The songs of Darwin’s finches diverge between populations due to errors of chance or copying as well as extinction of local songs. Territorial males discriminate between songs of their own and other species in carefully controlled playback experiments. Song also tends to be a primary cue for mate choice. With rare exceptions, females avoid mating with males that sing another species’ song. They also avoid mating with males with songs that closely match the songs of their father, which reduces the risk of inbreeding.

The process of imprinting on the father’s song, however, is not perfect. On the island of Daphne Major, occasionally a young male

Cactus Finch learns the song of the Medium Ground Finch. Such a mistake leads further to mistakes in mate choice and thus to hybridization. In one case, a female Medium Ground Finch mistakenly mated with the male Cactus Finch that wrongly sang her species’ song. Their hybrid offspring then backcrossed without serious penalty to other Medium Ground Finches (which sing like their father).

Ecology

This chapter stressed the process of divergence and speciation of birds, particularly the genetic and behavioral features of that process. Ecological changes feature strongly in the completion of the speciation process. Coexistence of reproductively isolated species in sympatry requires resolution of competitive interactions for food, for nest cavities, or for other limiting resources. Ultimately, these interactions define the community of species that coexist in a particular habitat or locale. The next chapter examines the formation and richness of ecological communities of birds.

REVIEW KEY CONCEPTS

19.1 What Is a Species?

Species are the primary units of systematic biology that serve as the basis for describing and analyzing biological diversity. The Biological Species Concept frames species as cohesive sets of interbreeding populations that are essentially isolated reproductively from other such sets of populations. The Phylogenetic Species Concept and Evolution Species Concept stress instead historical patterns of lineage divergence and recognize more distinct local populations than does the Biological Species Concept. These concepts emphasize complementary criteria for diagnosis.

Key Term: assortative mating

19.2 Allopatric Speciation

Most species of birds evolve in geographical isolation, called allopatry. Isolation on oceanic islands or disjunct habitats reduces gene flow between sister populations. Evolutionary divergence then leads to speciation. Birds on continents speciate through vicariant events, such as division of large populations by glaciations or wet–dry climate cycles. Secondary contact—the reuniting of previously isolated populations—tests the ability of populations to interbreed.

Key Terms: allopatry, secondary contact, ring species

19.3 Gene Flow, Clines, and Local Evolution

The evolution of geographical differences among bird populations depends on the relative strengths of two opposing forces: the intensity of natural selection favoring advantageous genetic attributes and the rate of genetic blending as a result of interbreeding of individuals from different locations, or gene flow. Clinal variation of simple genetic differences or color phases can track the dynamics of these two forces. Bird populations can evolve differences on an extremely local scale due to limited dispersal and the prevailing influence of natural selection.

Key Terms: natal dispersal, natural selection, gene flow, cline

19.4 Hybrids

Birds retain the potential for successful hybridization through surprisingly high levels of genetic divergence. Consequently, hybridization among birds is not limited to closely related or sister species and can be a new source of advantageous genes.

The genetic architectures of hybrid zones provide opportunities to study the dynamics of speciation. Narrow zones usually indicate some features of essential reproductive isolation. Alternatively, hybrid zones may be adaptive transitions between sister taxa with hybrid superiority or transient events in which one species replaces another.

Key Term: Haldane’s rule

19.5 Behavior and Speciation

New species of birds evolve via behavioral isolating mechanisms, such as visual or vocal differences, that arise through sexual selection or ecological adaptation. Darwin’s finches on the Galápagos Islands provide examples and insights into this process. The capacities of birds to develop new, learned behaviors contributes to the process of speciation. Behavior, rather than the environment, can be the driving force of evolutionary change if a new behavior is followed by the evolution of new traits that support the behavior. Sexual imprinting contributes to a process of cultural speciation in some but not all birds.

APPLY YOUR KNOWLEDGE

1. How has the interpretation of “species” changed since the time of Darwin? What factors and observations have led to increases and decreases in the estimated number of bird species?
2. Discuss the nature and importance of climate change over the past several million years to bird speciation in the Northern Hemisphere.
3. How does hybridization of birds of different species inform ornithologists about factors leading to speciation?
4. Describe the effects of natural selection and gene flow on polytypic species, such as the Song Sparrow.
5. Describe competition between species that hybridize as one of the sister species gains dominance. What are the most important factors that lead to the success of one or the other species? Explain what is meant by “the ghost image” of hybridization.
6. How has the advance of molecular techniques increased our understanding of historical divergences and speciation?
7. Explain how reproductive isolation can occur within local populations.

8. Describe clinal species and the factors that result in either static or dynamic clines.
9. Explain why hybrids can be either inferior or superior to either species and why male and female hybrids can differ in vigor.

CHAPTER 20 *Communities*

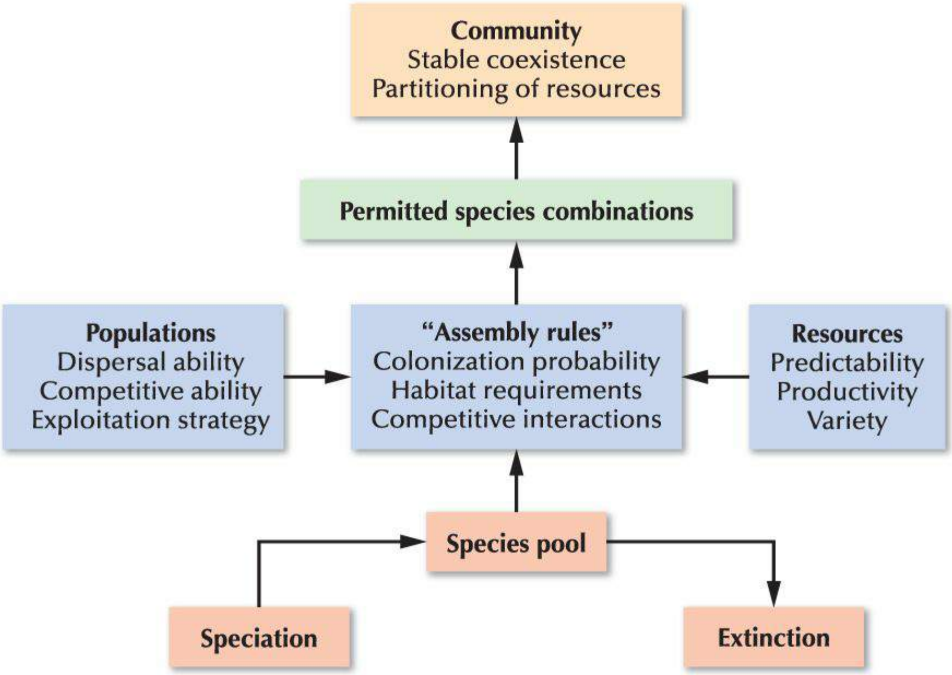
STEVENRUSSELLSMITHPHOTOS/SHUTTERSTOCK.COM

Chickadees are keystone members of local bird communities. Different-sized species may coexist, but same-sized species tend to segregate geographically or by habitat.

> The wet tropical lowlands are rich in diversity of species, in diversity of structure, and in their general aspect of luxuriance.

> [MacArthur 1972, p. 199]

Understanding which species coexist in a community is one of the most challenging issues in ecology with far-reaching consequences for the conservation of biodiversity. Community compositions are complex because they integrate historical factors, resource availability, and interspecific interactions, such as competition and predation, vegetation structure, and climate (Figure 20–1). Birds, however, are prime subjects of research on community structures because we know so much about them. We have accurate range maps showing the distributions of essentially all of the world’s birds, and because most of them are diurnal and sing, birds are relatively easy to census. Imagine trying to do this with insects, reptiles, and amphibians or with silent, nocturnal mammals. On the other hand, birds are large and mobile and tend to be relatively wide ranging, making them logistically difficult subjects for the kinds of manipulative, whole-community experiments that are possible with smaller, less mobile organisms. For these reasons, experimental studies of community composition in birds tend to involve just a few species and genera that have convenient life histories, such as nesting in nest boxes.



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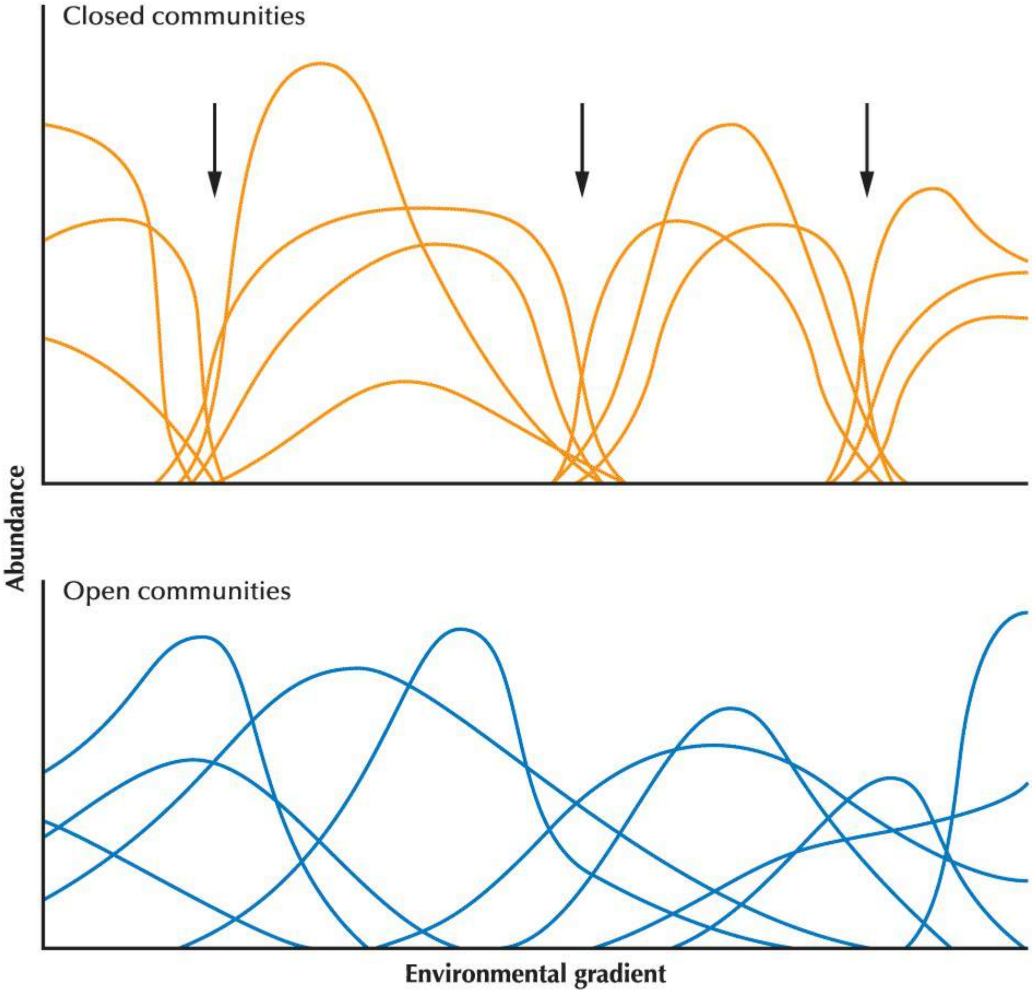
Data from Wiens 1983

Figure 20–1 According to some ecologists, stable communities of coexisting bird species derive from a larger pool of species filtered by local climates, enhanced through the dynamics of population dispersal and through colonization in relation to habitat or other resources, and sometimes modified by competitive resolution of unstable species combinations.

In this chapter, we explore five big topics: (1) global patterns of species avian diversity; (2) the role of resources and vegetation structure; (3) the extent to which abiotic/climatic factors, such as temperature and precipitation, act as filters that determine which species can live in a community; (4) the role of biotic interactions, such as predation, parasitism, interspecific competition, and mutualisms; and (5) geographical and historical factors that can limit or enhance the total number of species available to join a community through their effects on colonization and extinction.

20.1 Patterns of Species Diversity

Two polar views derived from early botanical thought embrace the continuum of community formation and dynamics (Figure 20–2). One view is that so-called **open (Gleasonian) communities** are fortuitous, dynamic assemblages of essentially noninteracting species. The species in these communities each align themselves independently along environmental gradients according to their own ecological requirements (Gleason 1926; Wiens 1990). The other view is that so-called **closed (Clementsian) communities** are stable combinations of species drawn from a larger pool of possible colonists. Complementary sets of species in Clementsian communities tend to replace each other at the same point along environmental gradients (Clements and Shelford 1939). Competition for limited resources can structure these local compositions of species. So can mutualistic interdependencies of species, such as those that consort in mixed-species flocks (see Chapter 11).



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DATA FROM RICKLEFS 1976

Figure 20–2 Open and closed communities are extremes on the continuum of possible community structures along environmental gradients, such as dry forest to wet forest. In open, or Gleasonian, communities (bottom), species are arrayed independently according to their particular ecological needs. In closed, or Clementsian, communities (top), distinct sets of species occupy particular habitats with breaks at the interfaces between habitats, called ecotones (arrows).

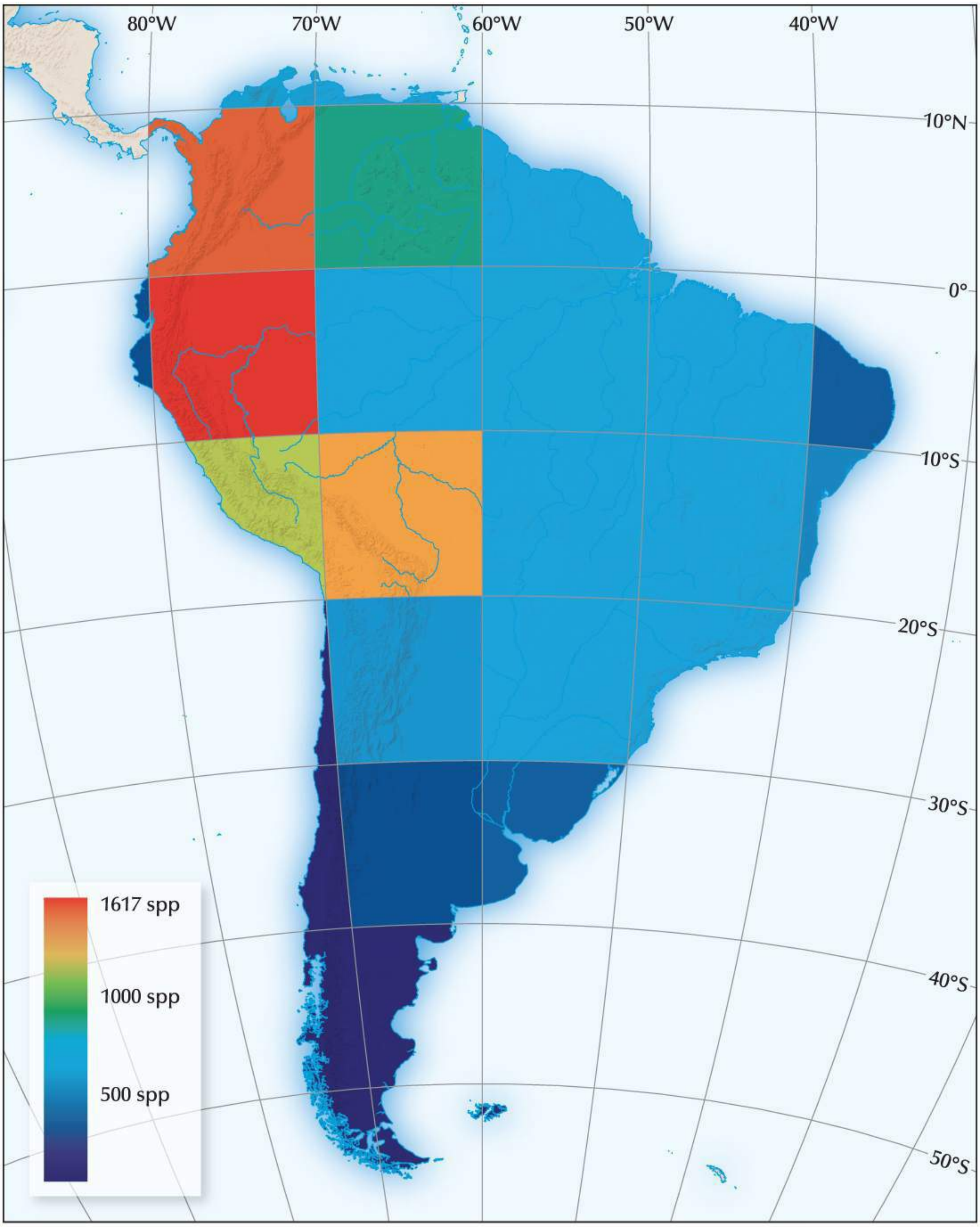
How birds array themselves along environmental gradients reveals some of the processes that structure communities. Bird communities change along gradients of latitude, elevation, rainfall, isolation, patch size, and succession. For example, bird community richness changes along natural rainfall gradients that control for elevation (McCain

2009). Adaptations to specific temperature regimes along elevation gradients also restrict which species can live in a community (termed **environmental filtering**; Graham and Fine 2008). Studying gradients, therefore, offers an opportunity to learn how communities will change under different scenarios of future climates.

Latitudinal gradients in diversity are among the best-documented patterns in avian community ecology. It is axiomatic that tropical habitats have more diverse communities than those in the temperate zone in terms of both **species richness** (the number of coexisting species in a community) and **community diversity** (the extent to which communities are dominated by just a few or by many different species). Although there are exceptions to this pattern (see section 20.4), community diversity reaches its maximum in the tropics of Asia, Australasia, Africa, and, especially, South and Central America. This is true of **alpha diversity** (the number of species coexisting over a single point or site); **beta diversity** (the extent to which species composition changes in different habitats, such as forests, at different stages of succession or along elevation gradients); and **gamma diversity** (the total number of species occurring in a region).

Alpha diversity tends to reach its maximum in lowland tropical forests, especially in Amazonia. For example, 100-hectare plots in western Amazonia can harbor as many as 330 species with over 170 species overlapping on a single point within these plots (Terborgh et al. 1990). Temperate forests typically contain just 30 to 50 breeding species in comparable areas.

Beta diversity also reaches its global maximum in the tropics—but in the mountains rather than the lowlands. The northern and central Andes, for example, have the world’s highest beta and gamma diversity (Figure 20–3), at least in part due to the huge number of endemic species that have small (50,000-square-kilometer) ranges, usually restricted to narrow elevation bands (Terborgh 1985).



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DATA FROM RAHBEK 2005

Figure 20–3 South America’s generally high bird species diversity peaks in the northern and central Andes with over 1,600 species found in 10-degree quadrants.

20.2 Resources and Climates

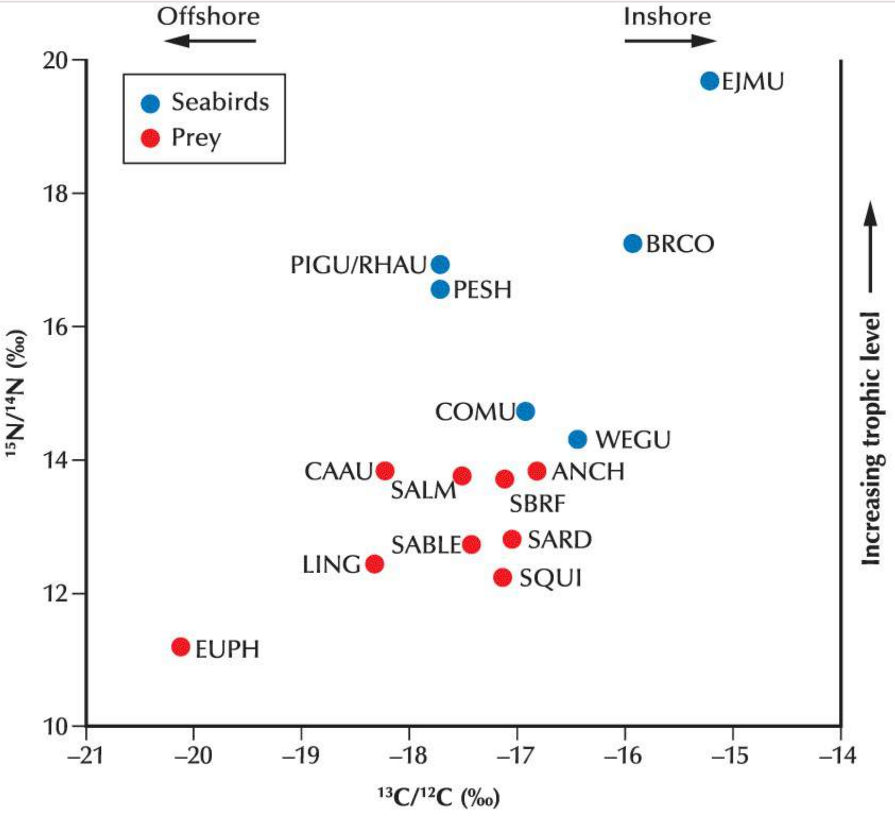
The species in a community can occupy different **trophic levels,** or feeding levels, and range from insect-eating warblers to the hawks that eat them and from plankton feeders to fish eaters (Box 20–1). Each species has specific requirements, called its **fundamental ecological niche** (Grinnell 1917). For example, we expect to find Pileated Woodpeckers in forests with large trees full of carpenter ants. Pileated Woodpeckers occupy a wide variety of forests with big, ant-ridden trees, but the Red-cockaded Woodpecker of the southeastern United States has a different and highly specialized niche. It requires old pine forests with trees from 80 to 100 years old that have been infected by the red heart fungus.

Box 20–1

Stable Isotopes Clarify Seabird Food Webs

Stable isotope analysis (SIA) helps ornithologists decipher food webs, especially marine systems that are hard to study directly. The ratio of two isotopes of nitrogen ($^{15}N/^{14}N$) in animal tissues, for example, increases from zooplankton (krill) to krill-eating fish or birds to fish-eating birds (cormorants) and sea lions at the top of the food chain (Sydeman et al. 1997; see graph). This ratio increases with each step in the food chain because the metabolic synthesis of new protein from food consumes more of the lighter isotope ^{14}N, leaving more (3 percent) ^{15}N in the predators' tissues. The marine-system food web off the coast of California, for example, includes five levels, with seabirds occupying the upper levels, from three to five.

The ratio of stable isotopes of carbon ($^{13}C/^{12}C$) in tissues reveals where seabirds feed on the basis of the kinds of prey that they eat and whether they change feeding habits at different stages of the breeding cycle. Feeding on fish near the coast leaves a different signature of carbon isotopes in the tissues from that left by feeding on krill in the open ocean. Stable isotope analysis of the egg albumen of California seabirds, for example, revealed that Cassin’s Auklets and Common Murres use krill to produce their eggs. Common Murres then shift to fish to feed their young, as do most of the other seabirds. Rhinoceros Auklets and Pigeon Guillemots rely on fish throughout the breeding cycle, including egg production.



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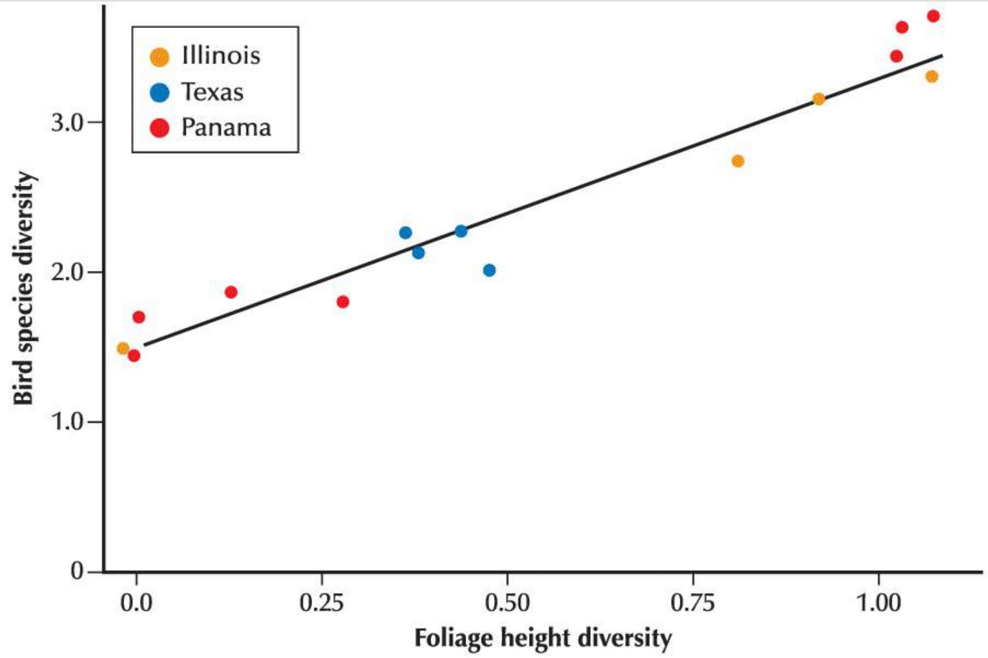
DATA FROM SYDEMAN ET AL. 1997

Trophic structure of a community of seabirds and their prey on the coast of California based on analyses of stable nitrogen and carbon isotopes, expressed in parts per thousand (‰). (The formula for calculating these values in standard delta notation produces a negative number for carbon.) Nitrogen isotopes change with trophic level in the community. Birds and sea lions occupy higher trophic positions than fish, squid, and krill. Carbon isotopes vary with inshore versus offshore feeding habits. Abbreviations:

EUPH, krill (or euphausids); LING, lingcod; SQUI, squid; SABLE, sablefish; SARD, sardine; SALM, salmon; SBRF, short-bellied rockfish; CAAU, Cassin's Auklet; ANCH, anchovy; WEGU, Western Gull; COMU, Common Murre; PIGU, Pigeon Guillemot; RHAU, Rhinoceros Auklet; PESH, Pelagic Shag; BRCO, Brandt's Cormorant; EJMU, northern sea lion.

Alpha diversity increases with the structural complexity of a forest. The physical structure of habitats provides courtship and display stations, nest sites, protection from predators, shelter from climatic stress, and food. The vertical distribution of vegetation roughly defines the variety of foraging opportunities and, hence, the variety of species that can occupy a habitat (Figure 20–4). As a result, alpha diversity increases with succession as forests regain their structural complexity following logging or other disturbances. For example, after about 80 years of plant succession (recovery) since logging, the Hubbard Brook Forest of New Hampshire contains about 25 breeding bird species, each of which has a distinct foraging niche. There are ground feeders, such as thrushes, Ovenbirds, and Dark-eyed Juncos; shrub-layer feeders, such as the Black-throated Blue Warbler; tree-trunk feeders, such as woodpeckers and nuthatches; general canopy feeders, such as Scarlet Tanagers, some vireos, and one species of flycatcher, which search widely in both deciduous and coniferous trees; and specialized canopy feeders, such as Blackburnian Warblers and Black-capped Chickadees, which tend to restrict their searches for food to the outer twigs of conifers (Holmes et al. 1979). A closer look reveals that variation in foraging behavior among insectivorous birds is directly related to variation in foliage height and, to a lesser extent, the tree species composition of the forest (Holmes and Robinson 1981).



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DATA FROM KARR AND ROTH 1971

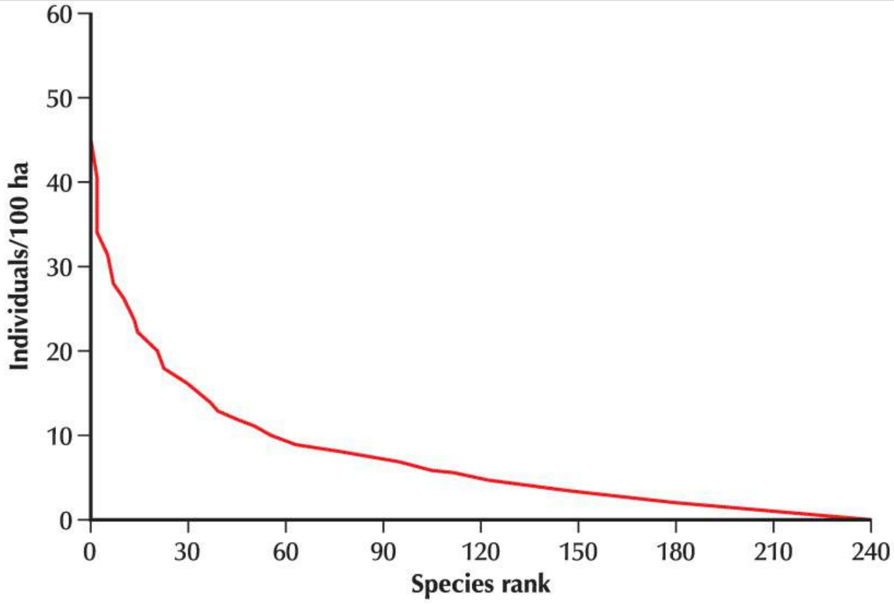
Figure 20–4 The local diversity and relative abundance of bird species are correlated with the relative height and diversity of the foliage, illustrated here for sites in Illinois Texas and Panama.

Species diversity is also affected by the availability of different kinds of food. The highly productive alkaline lakes in Africa, for example, contain just a few resources—principally blue-green algae and a few kinds of zooplankton that feed on them. Not surprisingly, these communities have very few breeding bird species—two species of flamingos, one of which eats algae and another of which eats the zooplankton, and a huge stork that feeds on the flamingos themselves. Yet these resources are also phenomenally abundant and can sustain millions of the flamingos that feed on them (Figure 20–5).

ANNA OM/SHUTTERSTOCK

Figure 20–5 Lakes such as Nakuru in Kenya can contain more than a million flamingos at a time, which makes the entire lake look pink from a distance. Even though they are extremely productive, as evidenced by the huge numbers of flamingos, the breeding bird communities of these lakes may be among the least diverse in the world with one species accounting for more than 99 percent of the individuals.

At the other extreme of the diversity gradient are tropical forest bird communities. In these habitats, alpha diversity is extremely high, but the vast majority of species are rare (Figure 20–6). In one western Amazonian community, more than two-thirds of the bird species had population densities of less than three breeding pairs per square kilometer.



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DATA FROM TERBORGH ET AL. 1990

Figure 20–6 The rain forests of Amazonia are home to high local diversities of over 245 bird species in a 100-hectare census plot. Lost species are represented by fewer than 10 individuals on such plots in Cocha Cashu, Peru. Only a couple of species occur in higher densities.

The greater diversity of species in the Tropics compared with diversity in the temperate zone is due in part to different and more varied food resources (Ricklefs and Travis 1980). For example, groups of fruit eaters—toucans, hornbills, barbets, trogons, cotingas, manakins, broadbills, and turacos—expand the dimensions of tropical bird communities. Parrots large and small consume a wide variety of seeds, fruits, and nectars that are not available in northern forests. Hummingbirds and tanagers abound in New World tropical forests, but only a few species live in the north.

The diversity of insect sizes also is greater in the Tropics than in temperate-zone habitats, and the diversity of bill sizes of tropical birds increases accordingly. Some families of strictly tropical birds—

puffbirds, motmots, antbirds, wood hoopoes, and jacamars—specialize on large insects and small reptiles that are not present in temperate ecosystems. Foraging specialists, such as ant followers and epiphyte probers, also add to the diversity of bird communities in tropical regions.

For decades, ornithologists thought that greater structural habitat complexity was responsible for the high diversity of species in tropical forests, but this proposal may not be so (Marra and Remsen 1997). Despite their obvious differences, tropical and temperate forests do not differ in overall heterogeneity or complexity. Direct comparison of the use of the forest structure by foliage-gleaning insectivorous birds of the understory, however, exposes more specialized forest-floor foraging behaviors in the tropical species. Compared with temperate species, each tropical species is more selective of particular horizontal and vertical habitats and has narrower niche breadth in foraging substrates and foraging heights. In addition, the tropical species overlap less in foraging stations than do comparable temperate-zone species.

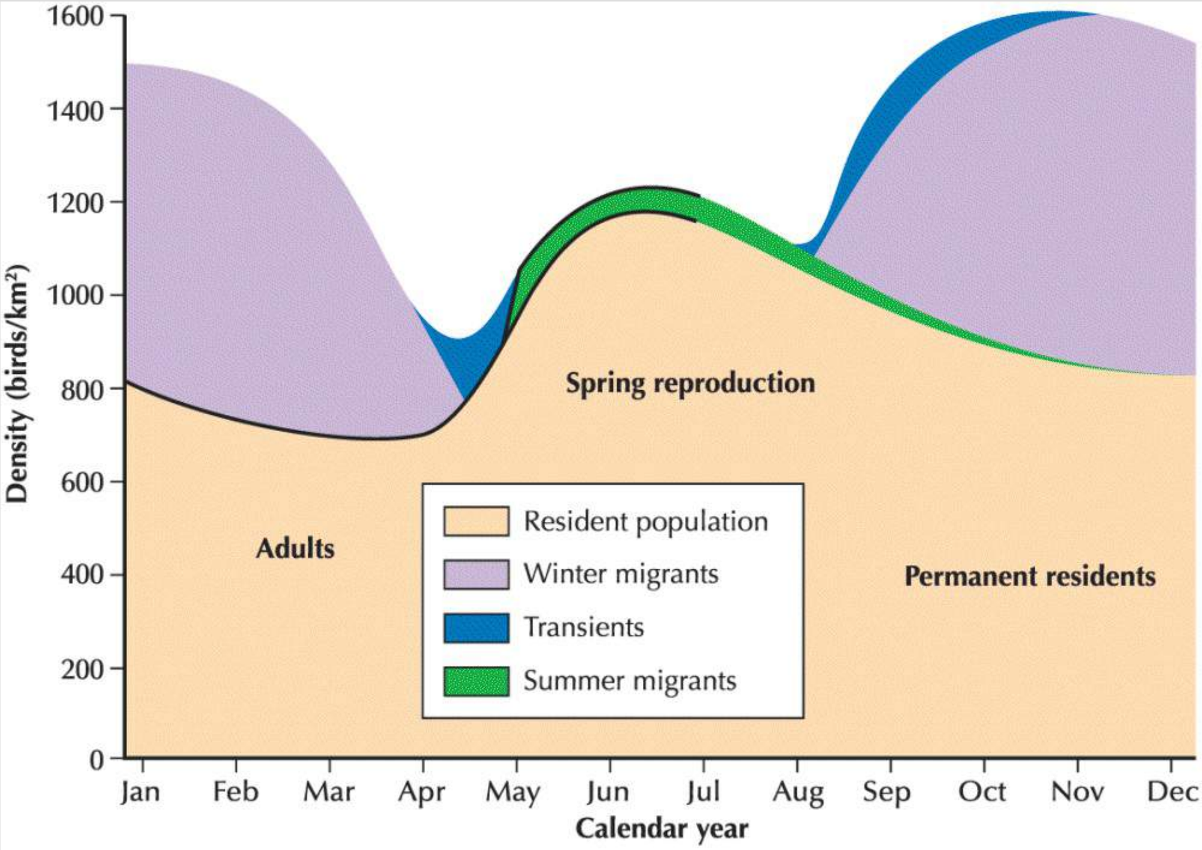
Tropical species tend to use a narrower range of habitats. They may be more specialized in their foraging behavior and less tolerant of climatic variation than their temperate counterparts. Greater ecological specialization leads to tighter packing of species in local communities, smaller geographical distributions, greater species richness, and reduced abundance of most species.

Temporal Patterns

Resource availability is almost always seasonal, which can lead to profound temporal changes in bird communities. Virtually all bird communities comprise both resident and nonresident species. Residents stay put and accommodate monthly changes in climate and food availability. Nonresidents are seasonal specialists that take advantage of predictable periods of local regional food abundance, such as in the temperate summer. The mobility of birds and the evolution of the migratory habit have made possible nonresidency and the opportunistic exploitation of variable environments (see Chapter 10).

Ephemeral resources attract opportunistic species. Temporary assemblages of highly mobile birds may last hours, weeks, or years. Flocks of seabirds over a shoal of fish, for example, are brief in duration (minutes or hours) and highly variable in species composition. Assemblages of hummingbirds and sunbirds at flowers feature high turnover of both individual birds and species during the brief blooming periods of days or weeks.

Seasonal residents form a major part of most bird communities. For much of the year, migrant shorebirds can dominate the bird life of coastal wetlands. The influx of wintering migrants from the north triples the number of species found in the open pine forests of Grand Bahama Island and increases the density of birds from 900 to 1,600 per square kilometer (Figure 20–7). In some north temperate forests, more than 90 percent of the breeding birds are nonresidents that winter farther south.



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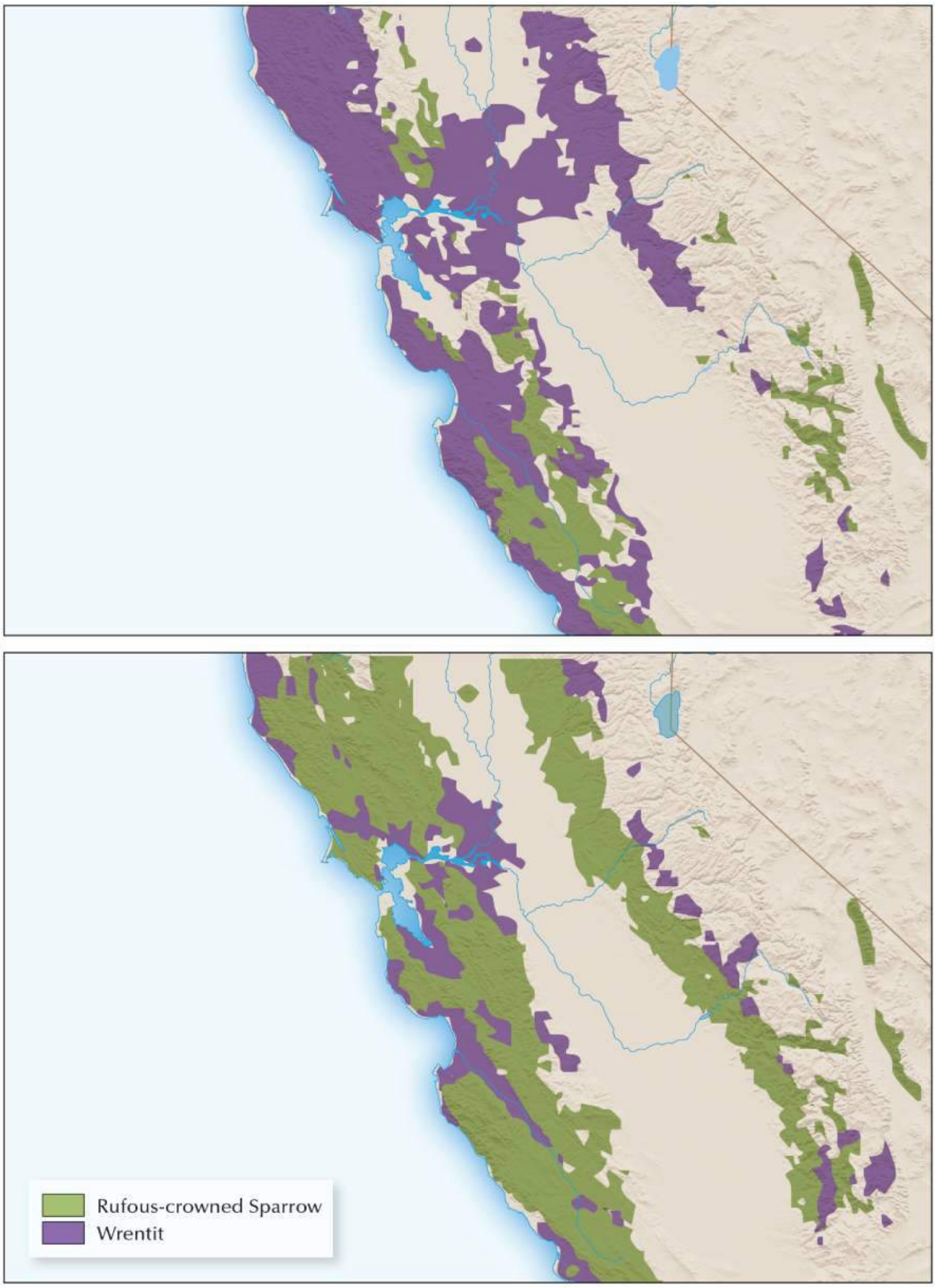
Data from Emlen 1980

Figure 20–7 Model of seasonal composition of the pine-forest bird community of Grand Bahama Island. Local numbers increase with the addition of young birds in the summer and again with the arrival of wintering migrants, which leave in April.

Climate

To what extent do abiotic factors, such as climate, limit community composition? Climatically extreme environments, such as deserts, clearly require physiological adaptations that limit which species can occupy them (see Chapter 6). But the filtering effects of less extreme climates on species compositions remain an area of active research. In particular, ecological niche modeling predicts species ranges from climatic variables (principally temperature and precipitation). Niche modeling has become a powerful tool for predicting how community composition will change under different scenarios of climate change (Wiens et al. 2009; Figure 20–8).



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DATA FROM WIENS ET AL. 2009

Figure 20–8 Distributions of the Wrentit and Rufous-crowned Sparrow in central California. (A) Current distributions. (B) Projected future distributions.

As a rule, strong environmental filtering constrains bird communities in climatically extreme environments. Species from just a few lineages tend to have the physiological adaptations required for living in particularly extreme conditions. Communities in more benign environments, on the other hand, are colonized by species from diverse lineages without physiological specializations. These models are fundamental to the newly emerging study of phylogenetic community structure (Graham and Fine 2008). Such communities would be structured more by biotic interactions, such as competition (see below).

One of the leading hypotheses for the increased beta diversity of tropical organisms was developed by ecologist Dan Janzen (1967), who asked the question, “Are mountain passes higher in the tropics?” He hypothesized that the increased climatic stability and reduced seasonality of temperatures in the tropics favor species that are physiologically more specialized than temperate species. As a result, tropical species should occupy narrower elevation ranges compared with temperate species. There is some evidence for this hypothesis (McCain 2009). Namely, temperate species tend to be far more tolerant of extreme temperatures and occur over wider elevation ranges than those in the tropics. Whether metabolic differences constrain species to narrower elevation ranges, however, remains unclear because biotic interactions, such as competition, predation, and mutualisms, also play crucial roles in community composition (Jankowski et al. 2013; Londoño et al. 2016). We will explore the role of biotic interactions in determining which species can occur in a community in the next section.

20.3 Biotic Interactions

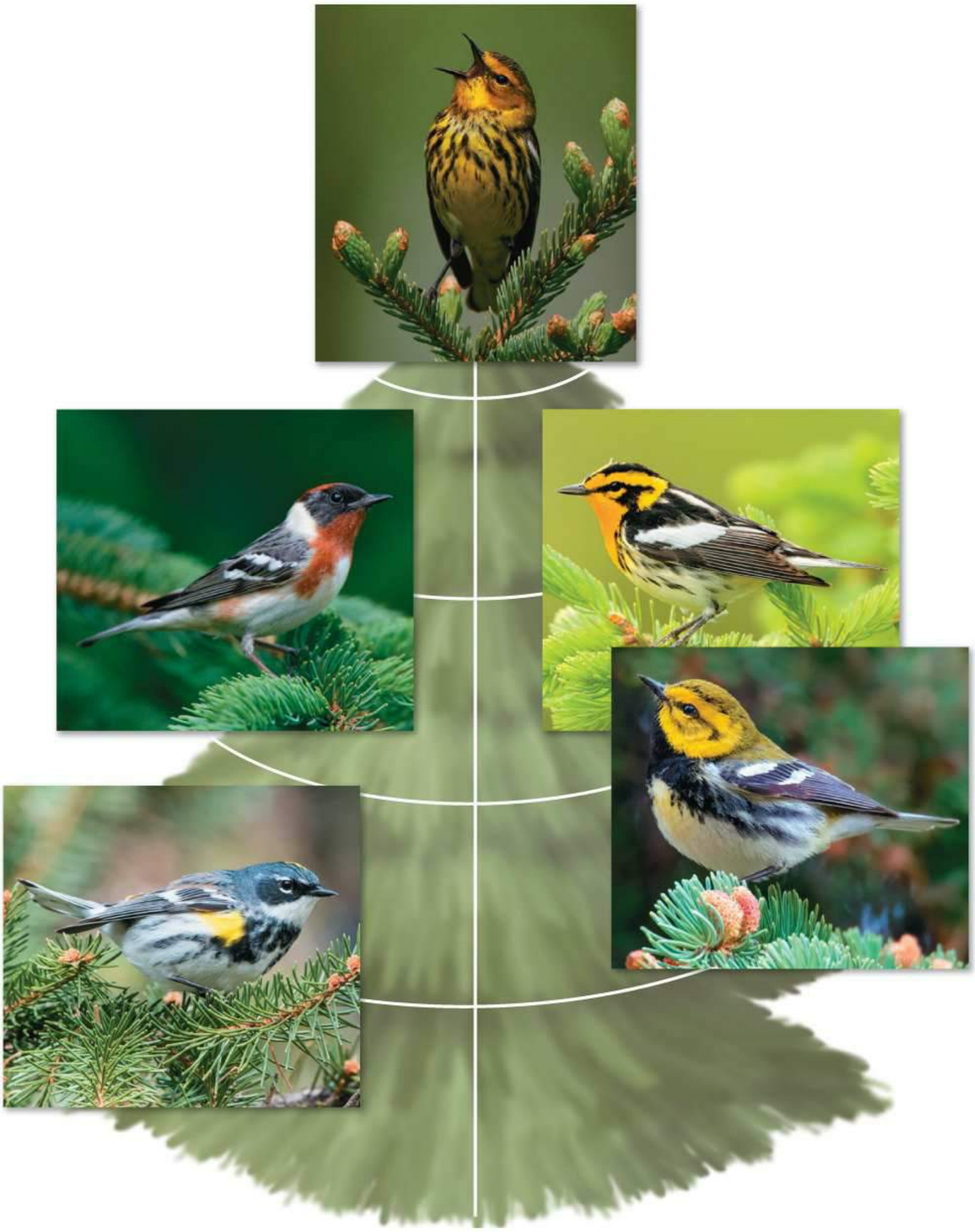
Biotic interactions, such as interspecific competition, predation, parasitism, and mutualisms, limit which species can occur in a community. By far the best-studied of these interactions is interspecific competition, but we now know that predation and parasitism profoundly affect community composition. Such “top-down” forces in which interactions between trophic levels (predators and their prey) regulate entire communities and ecosystems have become a central topic in ecology. In this section, we begin with interactions within trophic levels (competition), then proceed to the ways in which predation can alter community composition. We conclude with an exploration of the role of mutualistic interactions, a new frontier of avian community ecology.

Interspecific Competition

Competition arises when one bird’s use or defense of a resource makes that resource less available to other birds. Interspecific competition arises when birds of coexisting species vie for the same limited resources. The use or defense of those resources by members of one species reduces the availability of resources to members of another species. Recall that competition among members of one species reduces the rate of population growth in that species by limiting survival or reproduction. Competition among members of different species also can affect population growth.

Resource Partitioning

One of the foundations of community ecology is that most species have distinct foraging niches. Consider the classic study of niche partitioning by warblers in northern spruce forests of Maine (MacArthur 1958; Figure 20–9). There, the Myrtle Warbler feeds mostly in the understory below three meters, the Black-throated Green Warbler in the middle story, and the Cape May Warbler at the tops of the same spruce trees. The species sharing the midsection of the tree feed in different ways. The Blackburnian Warbler feeds on the outer twigs and sallies out after aerial insects. The Bay-breasted Warbler searches for insects close to the trunk. In Europe, different species of tits show parallel choices of their feeding stations.



CLOCKWISE FROM LOWER LEFT: FOTOREQUEST/SHUTTERSTOCK; NATURE PHOTOGRAPHERS LTD/ALAMY; ALL CANADA PHOTOS/ALAMY; ALL CANADA PHOTOS/ALAMY; ALL CANADA PHOTOS/ALAMY

Figure 20–9 North American wood warblers feed in different parts of a spruce tree. Clockwise from lower left to right: Myrtle Warbler, Bay-breasted Warbler, Cape May Warbler, Blackburnian Warbler, and Black-throated Green Warbler.

This niche partitioning has been observed in virtually every system

MIKELANE45/GETTY IMAGES

Figure 20–10 The Ringed Kingfisher is the largest of different-sized kingfishers that coexist on the waterways of South America.

that has been studied—coexisting species from the same **foraging guild** (a group of species that eat the same resources in the same times and places) almost always differ in some aspect of their foraging ecology or body size (Root 1967). This pattern suggests but does not prove that species can coexist only if they differ in their resource use and that there might be a limiting similarity that determines whether two species can coexist. Some coexisting species, such as kingfishers, follow what have been termed **Hutchinsonian ratios,** in which each coexisting species is about twice the body mass of the next smallest (Remsen 1991; Figure 20–10). Presumably, these species can coexist because they feed on different sizes of fish. Finches with different-sized bills can also coexist mainly because they feed on different sizes of seeds, which has formed one of the classic cases of how interspecific competition can also lead to speciation (Grant and Grant 2008; see Chapter 19).

Hotly debated is the idea that resource partitioning might reflect competition that limits which species can occur in a community (**Gause's competitive exclusion principle**). Factors such as disturbance, predation, and extreme weather events can depress populations of coexisting species far below the levels at which resource availability can be limiting (Wiens 1990). Nevertheless, there is mounting evidence that resources are at least occasionally limiting even in the most variable environments and that species can coexist over the long term only if they differ in some critical aspect of their ecological niches (Schluter 2000; Price 2008).

Interference Competition

Competition can be expressed as the overt aggressive displacement of individual birds, called **interference competition,** or as the reduction of the fecundity and survival of one species by another, called **exploitative competition.** In an unambiguous example of interference competition, large, dominant species of hummingbirds aggressively exclude other species from the densest concentrations of flowers. Forced by dominant species to use other feeding grounds with fewer flowers, subordinate species quickly shift back to the best available feeding grounds whenever it is possible to do so. Interspecific dominance can also be easily observed at bird feeders where larger species are generally able to chase subordinate species away from food. Coexisting antbirds that gather at swarms of army ants in tropical forests exhibit similar behavior with smaller species occupying perches that are farther from the leading edge of the swarms where insects are being flushed (see Figure 11–10).

Larger, dominant species can also exclude subordinate species from the best habitats by defending interspecific territories (Robinson and Terborgh 1997; Jankowski et al. 2010). The larger of these species responds aggressively to playbacks of the song of the subordinate, but the reverse is often not true. As a result, the dominant species is able to occupy the most productive habitats, which are also those that provide the resources needed to support their larger body. In these situations, habitat segregation is enforced by interference competition, with the result that beta diversity is increased.

Smaller species, however, are not always excluded from resources. Some smaller hummingbirds are simply more aggressive than larger ones. Smaller species can also overwhelm competitive dominants by visiting food sources in large flocks. The Eastern Kingbird, for example, is able to overcome resource defense by resident dominant species at tropical wintering sites by visiting trees in flocks of up to 200 individuals (Fitzpatrick 1980). The resident kingbirds are simply unable to chase away so many competitors.

Exploitative Competition

Interspecific competition can also subtly depress a species' survival or breeding success by reducing critical resources. Such competition is exploitative competition. Some of the best evidence of the effects of one species on the fecundity, survival, and population recruitment of another comes from research on Great Tits and Blue Tits. This research is an extension of the work on population regulation of the Great Tit (see Chapter 18).

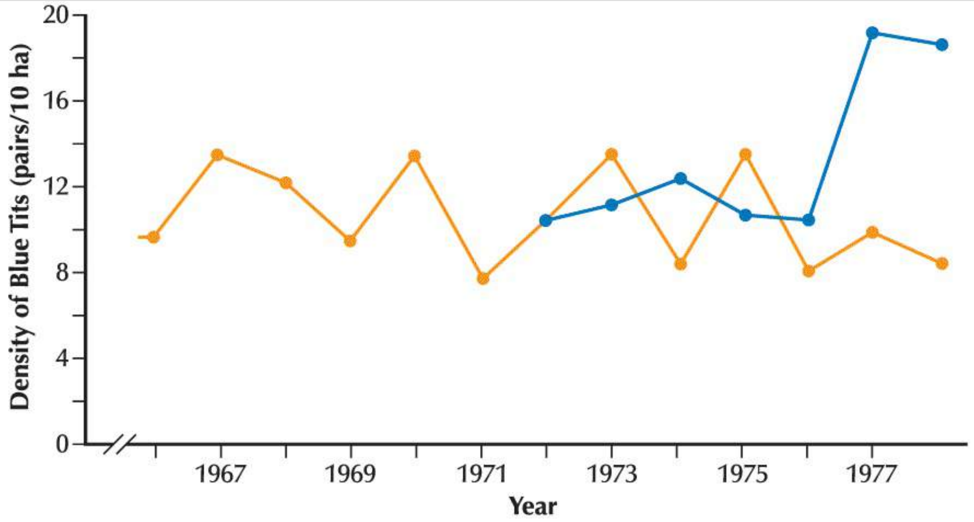
The local assemblages, or guilds, of titmice have been the focus of intense, often experimental research on the role of interspecific competition in bird communities (Dhondt 2012). The reduction of the food supplies by tits can affect the reproductive success of species outside their guild, such as Collared Flycatchers in Sweden (Gustafsson 1987). However, the details of competitive interactions between Great Tits and Blue Tits are of particular interest. These two species negatively affect each other in a variety of ways; the balance of their interactions leads to coexistence rather than the exclusion of one species by the other.

Recall that reproductive success, or fecundity, in Great Tits decreases as population density increases. In addition to being sensitive to the local densities of members of their own species, the fecundity of

Great Tits is sensitive to the numbers of coexisting Blue Tits. Even though they tend to use different foraging stations, there is overlap. High densities of Blue Tits during the breeding season reduce food availability. Reduced food availability increases nestling mortality and causes fewer Great Tits to attempt second broods. In this way, high densities of Blue Tits reduce the reproductive output of Great Tits. The effects of Blue Tits on the reproductive output of Great Tits during the breeding season, however, are only temporary ones and have little final effect on the population density of Great Tits. Instead, their density is controlled primarily by winter survival and the recruitment of juveniles (see Chapter 18).

The reproduction of Blue Tits is neither density dependent nor greatly affected during the breeding season by the local numbers of Great Tits, with one caveat: Great Tits control nest boxes if they are in short supply. They may even kill Blue Tits in the process (Löhrl 1977). This form of interference competition is extreme.

Of greater consequence is the reversal of competition between these two species outside the breeding season. Then Great Tits truly limit the number of Blue Tits in a woodlot by controlling the availability of roost holes. When the number of Great Tits in a population that depended on man-made boxes for roosting (as well as for nesting) was halved (by narrowing the nest entrances from 32 to 26 millimeters and thereby excluding the larger Great Tits), many more male juvenile Blue Tits were recruited into the woodlot in the autumn and subsequently joined the breeding population in the following year (Figure 20–11).



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DATA FROM DHONDT AND EYCKERMAN 1980

Figure 20–11 Experimental demonstration of interspecific competition. When Great Tits were excluded from nest boxes (from 1976 to 1978) in the experimental area at Gontrode, Belgium (blue circles), more Blue Tits established themselves there than in a control area at Zevergem (orange circles) that had the normal number of Great Tits.

The measurable competitive interactions between Great Tits and Blue Tits affect their annual successes. Although it does not result in the exclusion of one species from a woodlot by the other, competition favors different foraging behaviors, body sizes, and nest-site preferences. Segregation by habitat is another potential consequence in some species.

Habitat Segregation

Local separation by habitat and feeding stations is another way that species can partition resources. We have already described how segregation among congeners can be mediated by interspecific territoriality, but these cases may be in the minority. One of the best-known cases of habitat segregation occurs in titmice. In Europe, the

Great Tit, Blue Tit, and Marsh Tit inhabit broadleaf forests. The Crested Tit and Coal Tit live primarily in coniferous forest used by the other three species only as a suboptimal habitat. The species that live together feed in different places: Great Tits on the ground, Marsh Tits on large branches, and Blue Tits on the smaller twigs. Differences among European titmice in their feeding locations are associated with differences in body mass and beak size. Larger species feed at a lower level and on larger insects and harder seeds than do smaller species. Species that live in coniferous forests have longer and narrower beaks than those that live in broadleaf woods.

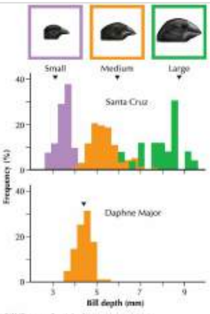
Each species of European tit has a counterpart in North America (Figure 20–12). However, only two of the North American species usually live together in the same habitat. In many areas, the small Carolina Chickadee coexists with the large Tufted Titmouse. Where two species of small chickadees coexist, they inhabit different habitats. In New England, the Boreal Chickadee inhabits dark conifer stands, whereas the Black-capped Chickadee inhabits more open, mixed deciduous and conifer forest. On the West Coast, Chestnut-backed Chickadees and Black-capped Chickadees similarly separate by habitat.

(A) Tufted Titmouse: Jerry Goldner. (B) Great Tit: StockPhotoAstur/Shutterstock.com.
(C) Chestnut-Backed Chickadee: Tim Zurowski/Shutterstock.com. (D) Coal Tit: Bildagentur Zoonar GmbH/Shutterstock.com

Figure 20–12 Certain species of North American (top row: A, C) and European (bottom row: B, D) chickadees and titmice act as ecological equivalents (left and right columns).

If competition actually restricts a species, one would expect shifts in the distribution, habitat use, or foraging behavior of a species when it is not limited by a competitor. The absence of a competitor allows ecological release. On the San Juan Islands of the Pacific Northwest, where there are no Black-capped Chickadees, the Chestnut-backed Chickadees inhabit broadleaf forests used elsewhere by the Black-capped Chickadees. Shifts in habitat use in the absence of other species are well documented among European tits. Marsh Tits, for example, inhabit pine plantations only in Denmark, where Willow Tits are absent from this habitat. In Ireland, Coal Tits feed regularly in the understory of evergreen forests in the absence of the Marsh Tits, Willow Tits, and Crested Tits that normally preempt this niche.

Evolutionary Consequences of Interspecific Competition: Character Displacement



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Data from Grant 1986

Figure 20–13 Three species of ground finches that coexist on the Galápagos island of Santa Cruz have bills of different depths (top), which enable them to feed on different seeds. Certain islands, such as Daphne Major, have only one species. In the absence of other species, the solo populations on this island evolved intermediate-sized bills.

Community interactions, such as interspecific competition, can also play a role in speciation. Darwin’s finches of the Galápagos Islands provide a classic example of the apparent role of competitive exclusion and character displacement (Figure 20–13). The adaptive radiation of these finches has propagated species with a variety of bill sizes that relate directly to seed sizes. Ground finches and cactus finches with distinctly different bill sizes inhabit every island. The differences in the average bill size of coexisting species are consistent with the hypothesis of interspecific competition for food. Species with similar-sized bills replace one another on various islands, and the bills of various species are more alike when they do not live together.

Simple ecological displacements as a result of competition should lead to evolutionary reinforcement in the form of morphological character displacement or enhanced differences (e.g., in size) where two species coexist. On the Swedish island of Gotland, in the absence of larger competitors—specifically, Crested Tits and Willow Tits—Coal Tits are larger than on the mainland (Alatalo et al. 1986). Their larger size on Gotland coincides with a shift in foraging niche from the outside of the tree and on needles, where small size is advantageous, to the inner parts of the pine trees (Box 20–2).

Box 20–2

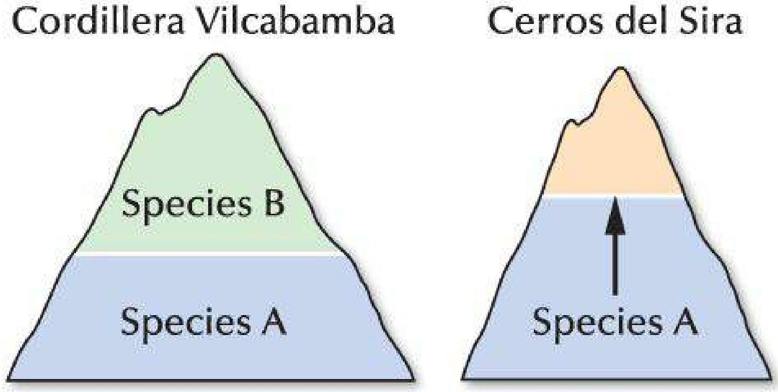
Competition Affects the Use of Foraging Sites by Tits

The ornithological literature contains many, often anecdotal observations of apparent niche shifts in the absence of a competitor. Controlled experimental demonstrations with the use of free-living birds in natural populations, however, are few. One exception is the study of foraging tits and Goldcrests in the coniferous forests of central Sweden (Alatalo et al. 1987). These small birds exploit nonrenewable insect and seed resources in their group territories during the long, cold winter. Two smaller and socially subordinate species, the Coal Tit and the Goldcrest, forage on the outermost branches and needles, whereas two larger and dominant species, the Willow Tit and the Crested Tit, forage inside the trees.

In this experiment, the ornithologists removed the Coal Tits and Goldcrests from three of six flocks to test whether Willow Tits and Crested Tits would change their foraging behavior. They did. In late winter, Crested Tits moved farther out on the spruce branches in experimental flocks than in control flocks. Willow Tits did so in pine trees but not in spruce trees.

The Swedish team concluded that exploitative competition directly based on food depletion, without any interference, influences the use of foraging sites by tits that coexist in coniferous forests.

Range Boundaries



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DATA FROM TERBORGH AND WESKE 1975.
COURTESY OF SCOTT ROBINSON

Figure 20–14 Ecological release in the Peruvian Andes. Lowland Species A expand into higher elevations of the Cerros del Sira, where competing highland Species B are fewer. An estimated 80 to 82 percent of the species would have occupied the summit zone of the Sira had it been a portion of the main body of the Andes.

Community interactions can also affect the geographical distributions of entire species. The abrupt replacement of one species by another at various altitudes in the Andes and in New Guinea suggests that competition from one species limits the distribution of another. Indirect evidence that competition restricts species to narrow elevations comes, once again, from studies of potential ecological release. In the isolated Sira Mountains of eastern Peru, where most species characteristic of higher mountains in the adjacent Andes are absent, most lowland species expand their elevational ranges upward, suggesting ecological release from competitors (Figure 20–14). Many of these species are moving into niches in the absence of a closely related competitor, at least some of which may be dominant members of interspecifically territorial species pairs (Jankowski et al. 2013; Freeman et al. 2016).

Smaller subordinate species of higher elevations may be severely endangered by upslope range expansions of larger, dominant species in response to global warming (Jankowski et al. 2010). This phenomenon is especially likely to be problematic in the tropics where many congeners are confined to narrow elevational distributions that are bounded by those of congeners. The same phenomenon, however, may also be occurring in the temperate zone. The subordinate Bicknell’s Thrush, for example, is confined to the highest elevation forests in the northeastern United States and Canada. This species is being replaced by the dominant Swainson’s Thrush, which has been expanding its range upward in recent years as the climate has been warming (Freeman and Montgomery 2015).

Predation

As we discussed in previous chapters, predation is a nearly ubiquitous selective pressure that affects sociality, plumage, communication, and life histories. Here we explore how predation, both on nests and on adults, affects the composition of bird communities. This topic has been the subject of lively debate between those who favor bottom-up processes, such as resource availability and competition, and those who emphasize the importance of “top-down” processes, such as predation. This debate can be difficult to resolve because humans have so severely altered top-down processes in most ecosystems that there is no reliable baseline for evaluating natural predator–prey dynamics (Pauly 1995). In particular, top predators are often eliminated, which can cause an increase in “mesopredators,” such as foxes and raccoons, many of which depredate bird eggs and nestlings (see Chapter 16). Increasing populations of mesopredators is generally considered to be one of the main reasons why fragmented habitats lose so much of their diversity. Indeed, introduced predators have greatly reduced community diversity on many islands; a single species of introduced snake essentially wiped out the entire native bird community of Guam (Savidge 1987; Figure 20–15).

(A) John Mitchell/Science Source. (B) Michael Fitzsimmons/Shutterstock.com

Figure 20–15 Brown Tree Snakes (A) accidentally introduced to the western Pacific island of Guam decimated and endangered the native populations of the

Micronesian Kingfisher (B).

High rates of nest predation, however, help maintain or even promote community diversity by preventing any one species from becoming too dominant. Some of the most diverse habitats on earth, such as those in the Neotropics, have extremely high nest predation rates (Robinson et al. 2000). Variation in predation rates along elevation gradients, in particular, may be an underlying cause of the extremely high beta diversity of tropical mountains (Jankowski et al. 2013). There, predation rates drop precipitously at middle elevations, which have fewer snakes and primates, two of the dominant groups of predators in the lowland Tropics.

Although we have focused mainly on the role of nest predation, the role of predators such as *Accipiter* hawks also undoubtedly play a crucial role in community structure. The mixed-species flocks that are such a dominant feature of most forest bird communities have evolved at least partly in response to the risk of predation. Many studies have documented the role of cover from predators in dictating which species can live in a habitat and how they behave (Box 20–3). Adding small piles of vegetation where seedeaters could escape predators changes the community composition of open-grassland species (Lima and Valone 1991).

Box 20–3

Distance to Cover Defines the Niches of Sparrows

Distance to protective cover affects the variety of sparrows that can coexist in open, simply structured grassland habitats (Pulliam and Mills 1977). In southeastern Arizona, four species of sparrows inhabit open grasslands that have scattered mesquite trees, which provide some protection from predators, such as Prairie Falcons. From the sparrows' point of view, this habitat offers concentric rings of increasing distance from the nearest cover. The Vesper Sparrow stays closest to the mesquite trees (within four meters), the Savannah Sparrow feeds farther out (4–16 meters) and the Grasshopper Sparrow still farther out (8–32 meters), and the Chestnut-collared Longspur feeds far from the trees in the most open grassland.

The behavior of these species when flushed corresponds to the risks of flying increasing distances to cover. Vesper Sparrows fly quickly to nearby cover. Savannah Sparrows fly to an exposed perch the first time they are flushed and then to full cover if flushed again. Rather than face the risks of a longer flight, Grasshopper Sparrows usually drop back into the grass when flushed, but they fly for cover if repeatedly flushed. Longspurs, however, either crouch to the ground to hide or fly off in tight flocks that help thwart predators.

Parasites and Pathogens

Parasites and pathogens can affect community composition, especially in situations in which there is not a long history of coevolution between parasites and their hosts. We discussed how the recent expansion of the Brown-headed Cowbird into new areas may be altering bird communities by reducing or even eliminating many species that have no evolved responses to combat brood parasitism (see Chapter 14). The introduction of new diseases, such as avian malaria, to islands such as Hawaii (see Chapter 18) has also resulted in a severe reduction in community diversity caused by extinctions. Virtually all continental bird communities are exposed to a wide array of parasites and pathogens, most of which seem to have little effect on populations, although they may play a crucial role in sexual selection (see Chapter 13). Continental birds, however, have effective immune systems and the capacity to recover even from severe losses. Consequently, invasions of continents by new diseases, such as West Nile virus, cause only temporary changes on communities.

Mutualistic Interactions

To this point, we have emphasized the role of negative interactions, such as interspecific competition and predation as processes that limit which species can coexist in a community. Mutualistic interactions, however, may also be crucial processes underlying community composition. In theory, mutualistic interactions, such as those between plants and their pollinators and fruit dispersers, can increase community richness by promoting the evolution of specialization. Plants benefit from having reliable, specialized pollinators and long-distance dispersers for their fruit. The comparative stability of resources and climate in tropical forests may lead to the evolution of more specialized pollinators and fruit dispersers, which leads to greater diversity compared with unpredictable and temporary fruit and nectar availability in the temperate zone.

Woodpeckers can also promote community diversity through mutualistic and commensal interactions. They and their dead trees are a resource that supports a healthy diversity of vertebrate and invertebrate species that depend on one another. The foraging and nest-excavation activities of woodpeckers determine how dead trees actually decay and become available for use by other species (Farris et al. 2004). For example, more than 50 percent of the woodpeckers sampled in the ponderosa pine forests of northern California carried fungal spores on their bills. They transport these spores from tree to tree, causing new trees to decay and to become suitable for excavation of their new nest holes. Many species of hole-nesting birds and small mammals use the diversity of nest holes that result, building guilds (sets of ecologically similar species) of interdependent nest-cavity species (see Box 15–3).

20.4 History and Biogeography

History and biogeography play major roles in dictating community composition. Evolutionary processes add new species to the potential pool of colonists available to occupy a community. Biogeographical factors limit the extent to which species disperse among communities (or **metacommunities,** defined as communities connected by dispersal). We begin this section by reviewing island bird communities, which have long been an intensive focus of studies of biogeography and historical processes dictating community composition. We then conclude with a brief discussion of patterns within continental communities for comparison.

Islands

Because islands are such discrete places, island birds provide many of our clearest examples of community dynamics as well as the process of speciation (see Chapter 19). We can deduce and sometimes actually document the arrivals of new colonists and their subsequent adaptations, expansions of distribution, and disappearances in time.

The active dispersal from and colonization of isolated places are trademarks of bird behavior. The dynamics of colonization are most apparent on oceanic islands, such as the West Indies, which receive periodic arrivals of new visitors dispersing over water from larger source areas. Water barriers favor colonization by highly mobile species that travel in small groups. Bananaquits in the West Indies and white-eyes in the Indian and Pacific Oceans are superb island colonists —or “supertramps” (Diamond 1974). Their extraordinary dispersal abilities enable them to be the most predictable first colonists on newly formed islands. Successful colonization of one island may be followed by the colonization of adjacent islands and continued spread throughout a region.

A colonist’s ecological flexibility and its competitive ability to fit into the local community increase its chances of establishing a population on a new island. Bananaquits and white-eyes are generalized opportunists that are able to take advantage of local situations. They breed readily and repeatedly. After they are established, their populations thrive and grow rapidly in an environment with few enemies—specialized predators, competitors, diseases, or parasites.

Population growth under such conditions of so-called ecological release leads to large, dense populations and to the use of a wider variety of habitats than is the case on the mainland. Resident birds of the Pearl Islands off western Panama, for example, achieve densities from 20 to 40 percent higher than those reached on the adjacent mainland. They also forage over a greater vertical range and use more habitats than do their mainland counterparts (MacArthur et al. 1972). Both the average number of habitats used by a species and the density of each species in a particular habitat may double on small islands with few species, such as St. Lucia and St. Kitts of the Caribbean (Table 20–1).

Table 20–1 *Relative Abundance and Habitat Distribution* *Birds in Five Tropical Localities*[a]

Locality	Number	Average	Habitats	Relative	Relative	Relati

	of Species Observed (Regional Diversity)	Number of Species per Habitat (Local Diversity)	per Species	Abundance per Species per Habitat[b] (Density)	Abundance per Species[b]	Abunda of all Specie
Panama	135	30.2	2.01	2.95	5.93	800
Trinidad	108	28.2	2.35	3.31	7.78	840
Jamaica	56	21.4	3.43	4.97	17.05	955
St. Lucia	33	15.2	4.15	5.77	23.95	790
St. Kitts	20	11.9	5.35	5.88	31.45	629

[a] Based on 10 counting periods in each of nine habitats in each locality.

[b] The relative abundance of each species in each habitat is the number of counting periods in which the species was seen (maximum 10); this number times the number of habitats gives relative abundance per species; this relative abundance times the number of species gives relative abundance of all species together.

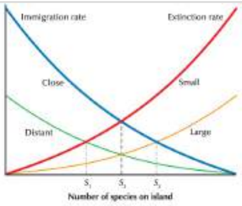
Data from Cox and Ricklefs (1977).

Populations on different islands diverge from one another as they adapt to local niches. The divergence of allopatric populations was discussed as part of the speciation process for Darwin’s finches in Chapter 19. Generalized colonists, such as white-eyes, may take over the specialized niches of species that are missing from island communities. The increased specialization of the first colonists then contributes to their ability—as well as to that of their descendants—to coexist with later arrivals. On the island of La Réunion in the Indian Ocean, where there is no nectar-feeding sunbird, the Reunion Olive White-eye has become a specialized nectar-feeding species in both bill morphology and behavior (Gill 1971). It coexists there with a second, generalized white-eye, the Reunion Gray White-eye (see Chapter 19). In the tropical Pacific, unusually large species of white-eyes have evolved independently on 12 small islands that have few other species. These large white-eyes often coexist with one or more other, smaller species of white-eyes (Figure 20–16).

(A) Joel Sartore, National Geographic Photo Ark/Getty Images. (B) Stubblefield Photography/Shutterstock.com

Figure 20–16 White-eyes are excellent island colonists that occupy many, diverse niches on remote islands that have few other birds. Shown here are (A) a typical species, the Bridled White-eye, and (B) a large, thrushlike species, the Giant White-eye. These species are found together on Belau (Palau) in the Caroline Islands.

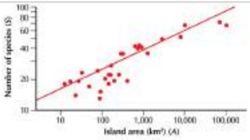
Island Biogeography



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
Data from Ricklefs 1976

Figure 20–17 The number of species found on an island reflects the balance between the rate of immigration (colonization) and the rate of extinction. Immigration rates on islands that are distant from source areas are lower than rates on islands close to source areas. Extinction rates on large islands are lower than those on small islands and increase as the number of species present on an island increases. The point of intersection of the two curves for any particular island defines the expected equilibrium number of species, S.

The number of species present on islands theoretically reaches a balance between gains due to immigration and losses due to extinction (MacArthur and Wilson 1967). The predictable balance between gains and losses is known as the **equilibrium theory of island biogeography.** By this theory, the point of intersection between the immigration curve and the extinction curve defines an equilibrium species number (Figure 20–17). The rate of extinction increases with the number of species on an island because there are more species with competition-reduced population sizes. Conversely, the rate of immigration falls as the number of species increases. Fewer new species from source areas are possible, and the colonization of an island full of competitors is more difficult.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
Data from Ricklefs and Cox 1972

Figure 20–18 The number of species, S, found on islands increases in direct relation to island area, A. This graph is plotted for islands of the West Indies.

Rates of extinction and colonization vary among islands of different sizes and degrees of isolation. In general, the observed relations between the number of species and island size are in accord with the model (Figure 20–18). Indeed, the relationship between island area and community richness is also documented on the mainland and is sometimes considered to be one of the “laws” of ecology. Prior to human colonization, however, islands were much more diverse and interesting places for birds than they are now. We now see only the remnant species that survived massive prehistoric extinctions caused by humans, such as the Polynesian colonists on the Hawaiian Islands and elsewhere in the South Pacific (Steadman 2006).

Recent examinations of the fossil record and molecular analyses suggest that extinction may limit species composition on islands less than we had realized. Because most island ecosystems have been so altered by the recent arrival of humans, it is difficult to infer historical processes from current species distributions. New molecular studies are showing that many of the birds in the West Indies, such as todies, are remnants of ancient, once-widespread lineages of birds that have disappeared from the mainland (Figure 20–19). Rather than being bird communities that represent an equilibrium balance of extinction and colonization, West Indian bird communities appear to be more akin to museums where ancient lineages have escaped the processes that drove their continental counterparts to extinction. These results suggest that extinction rates on islands, especially large ones, may be lower than on the mainland, an interpretation strengthened by the apparent long-term stability of island bird communities in the prehuman fossil record of the Pacific.

FOTOREQUEST/SHUTTERSTOCK.COM

Figure 20–19 Todies, tiny relatives of kingfishers, were once found over much of North America and even Europe but are now confined to the larger islands of the West Indies.

The roles of extinction and colonization, however, are well documented for islands that were once connected to the mainland. The number of equilibrium species for large so-called land-bridge islands, which were once part of a mainland with a full complement of species, is much greater (often three times) than that for large distant oceanic islands, which depend solely on colonists that cross the seas. Land-bridge islands have lost species steadily since they were isolated by rising sea levels at the end of the Pleistocene epoch (10,000 years ago). Small land-bridge islands have lost a greater proportion of their initial populations of birds than have large land-bridge islands of comparable age (Table 20–2).

Table 20–2 ***Present and Probable Past Land-Bird Faunas of Five Major Land-Bridge Islands***

		Number of Species			
Island	**Area (km^2)**	**Original**	**Present**	**Extinct**	**Extinct Species (%)**
Fernando Po	2,036	360	128	232	84
Trinidad	4,834	350	220	130	37
Hainan	33,710	198	123	75	38
Ceylon	65,688	239	171	68	28
Tasmania	67,978	180	88	92	51

Data from Terborgh and Winter (1980).

Barro Colorado Island in Panama is a land-bridge island that was separated from the mainland in recent times by the opening and flooding of the Panama Canal in 1914. The island is home to the prestigious Smithsonian Tropical Research Institute. Its scientists thoroughly documented the species that were present and how they fared in 85 years of isolation (Robinson 1999). The result: 65 bird species have disappeared from the island. Once gone, sedentary forest-dwelling species, in particular, have not recolonized the island. Many of them were lost before 1970. At least 14 species disappeared after 1970, and three others (Slate-colored Grosbeak, Speckled Mourner, and Rufous Piha) that were abundant in 1970 now persist only in small numbers.

What has been causing this loss of bird species from Barro Colorado Island? Several changes contribute to the loss, including successional changes in the vegetation that was present on the island, but one of them highlights the importance of large predators, such as jungle cats and eagles. These predators disappeared soon after isolation, leading to increases in their prey—small forest mammals and other predators of ground-nest birds. Similarly, mainland forests are increasingly reduced to small island fragments that are subject to loss of species in what is sometimes called the small-island effect (Chapter 21).

Continental Patterns

Differences in the numbers and relative abundances of the species in communities on continents relate to regional and historical processes as well as to local forces such as productivity and seasonal stability. Diversity in tropical communities, in particular, relates to their long, stable histories of accumulation of specialized species (Moreau 1966). Ancient communities may be the most species rich of all. For example, the forest faunas of Panama are richer than those of Africa, but the grasslands and savannas of Panama are relatively impoverished. The lowland forests in Africa were restricted in extent during the Pleistocene period, which prevented the development of rich forest avifaunas (Karr 1976). The man-made grasslands in Panama are quite young (15,000 years) relative to the ancient, natural grasslands and savannas of Africa. As a result, grassland communities in Africa are species rich, whereas those in Central America are species poor.

Community ecology is one of the most difficult subdisciplines of ornithology. Understanding the number of species and their patterns of abundance requires studies of resources, climate, several different kinds of biotic interactions (competition, predation, parasitism, and mutualisms), and the historical context under which the communities have evolved. Few studies have attempted to address all of these issues simultaneously. Yet there are some promising new approaches, such as ecological niche modeling and phylogenetic community ecology, that may enable us to disentangle the roles of these factors and predict how future human-induced changes in the environment will affect biodiversity. With the immense amount of data available on birds and their comparative ease of study, ecologists and conservation biologists can generate much stronger predictive models for bird communities than they can for other taxa.

REVIEW KEY CONCEPTS

20.1 Patterns of Species Diversity

Bird communities are sets of species that coexist in local combinations drawn from a larger pool of possible colonists. They range in composition from independent collections of species that overlap in space and time (open communities) to integrated sets of mutually compatible species (closed communities).

Local species diversity, which is highest in the Tropics, peaks in the northern Andes of South America. Hundreds of species coexist locally in the Amazon rain forests compared to dozens in temperate forests. Habitat heterogeneity increases species diversity in mountainous regions.

Key Terms: open (Gleasonian) communities, closed (Clementsian) communities, environmental filtering, species richness, community diversity, alpha diversity, beta diversity, gamma diversity

20.2 Resources and Climates

Each species has specific habitat, food, and climatic requirements, called its fundamental ecological niche. Species diversity in an area therefore increases with diversity of key resources, including sizes of prey or other food items, and physical structures of habitats.

Climatic variables, such as temperature and rainfall, filter which species can coexist in extreme environments that require evolutionary adaptations. Ecological niche modeling can predict future distributions due to climate change. Increased climatic stability and reduced seasonality of temperatures in the Tropics favor species that are physiologically more specialized than temperate species.

Key Terms: trophic levels, fundamental ecological niche

20.3 Biotic Interactions

Biotic interactions, such as interspecific competition, predation, parasitism, and mutualisms, limit which species can occur in a community. Competition is a key community structuring force that increases directly to overlapping use of limiting, shared resources. It may involve physical aggression (interference competition) or depletion of limiting resources (exploitative competition).

Competition leads to evolutionary reinforcement of morphological differences and segregation of species distributions. The differing bill sizes of Darwin’s finches on the Galápagos Islands are a classic example of character displacement.

Key Terms: foraging guild, Hutchinsonian ratios, Gause’s competitive exclusion principle, interference competition, exploitative competition

20.4 History and Biogeography

Turnover—the addition and loss of species—drives the changing compositions of avifaunas. The compositions of island avifaunas are due not only to ancient history but also to ongoing cycles of colonization and extinction, the frequency of which depends on the isolation and the size of the island. Small, isolated islands have the smallest equilibrium number of species, whereas large islands near continental source areas have the highest number of species.

Key Terms: metacommunities, equilibrium theory of island biogeography

APPLY YOUR KNOWLEDGE

1. Discuss the differences between communities of benign and extreme habitats relative to species diversity and abundance.
2. Describe the changes that occur in alpha, beta, and gamma diversity in a forest community during the succession that follows a "leveling" disturbance, such as fire or logging.
3. Describe differences in the climax (final) forest community structure after succession for a tropical and temperate forest community.
4. How does the elimination of top predators result in decreased community diversity?
5. Compare and contrast biotic and abiotic factors as determinants of community composition.
6. Discuss the possible outcome of "ecological release" that would occur during a warming climate and how this would influence range boundaries and species divergence in a temperate and a tropical mountainous region.
7. Define "character displacement" and explain its effect on competing species in a community.
8. How do habitat segregation and character displacement differ with respect to resource partitioning?

9. Explain why small, isolated islands tend to have population densities greater than their counterparts on continents. How does this differ between historically isolated islands and islands once connected to a continental landmass?
10. Explain the differences between interference competition and exploitative competition that might be acting in a foraging guild.

CHAPTER 21 *Conservation*


MARC SHANDRO/GETTY IMAGES

Early experiences with birds can fuel participation in ornithology and change lives.

> Never have I seen such wonders, or met landlords so worthy of their land. They have

> had, and still have, the power to ravage it; and instead they have made it a garden. [FISHER, P. 418 in *Wild America* by R. T. PETERSON and J. FISHER, 1955]

Birds have enormous conservation power, a power that can be harnessed for the conservation of all biodiversity. Their public appeal motivates millions of people to take time to observe them, to count them, to care about their well-being, and to act on their behalf. Their appeal adds economic value. Both public appeal and economic value translate into political power.

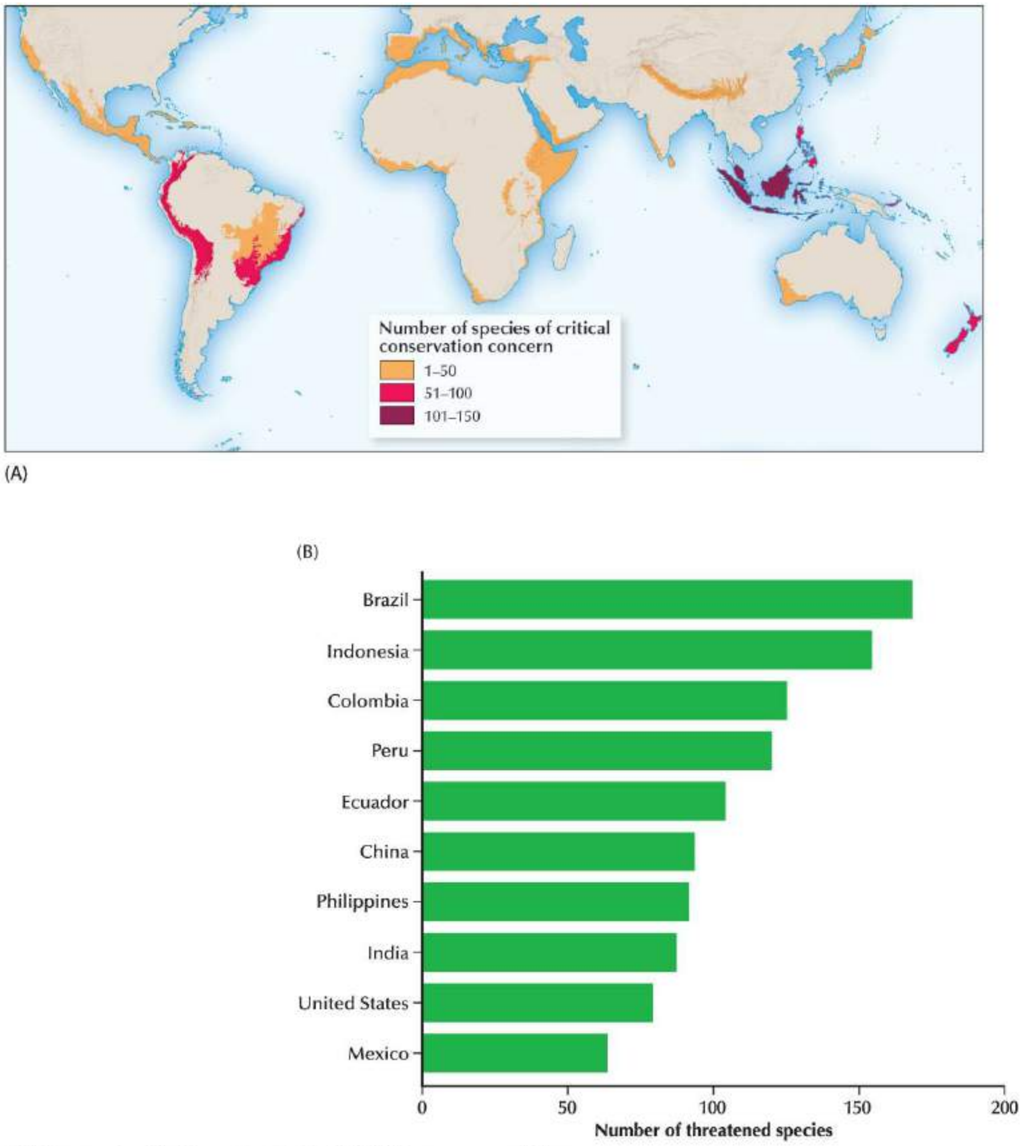
Birds also play a major role in ecosystem function (Sekercioglu et al. 2016). They pollinate many plants, disperse the fruits of most trees and shrubs (especially in the Tropics), and play critical roles in the control of insect outbreaks. The loss of birds can affect entire ecosystems.

The single-minded goal of modern bird conservation initiatives is to conserve and restore avian biodiversity by stabilizing bird populations worldwide and preventing more extinctions. For any bird-watcher and much of the public, the extinction of a species, such as the Ivory-billed Woodpecker, is almost unbearable. The best way to save species is while they are still common; wise management of healthy bird populations can preempt future costly rescue efforts and protect the ecosystems on which our societies depend.

Our preceding chapters highlighted many conservation implications of the biology of birds. This final chapter reviews specific bird conservation efforts—past, present, and future. The first three sections discuss the state of birds, the threats that they face, and some historical perspective on the excessive exploitations that they suffered. Then follow successful initiatives that inspire hope, including those that catalyzed the modern conservation movement. Science-based stewardship of the intact ecosystems and habitats that remain is critical. Conservation by design includes not just the geometry of wildlife preserves but also how best to maximize the viability of populations on fragmented or even urban landscapes through sound restoration initiatives. In the end, public support and community participation will determine which initiatives succeed.

21.1 The State of Birds

The past plights of our most majestic bird species—Whooping Cranes, California Condors, and Ivory-billed Woodpeckers in North America, to name a few—are renowned. Beyond them are substantial historical losses. At least 156 extinctions of birds diminished life on Earth from 1600 to the present time with another 21 species presumed extinct. The vast majority of these extinctions were island species exterminated by introduced species, habitat loss, diseases, and excessive human predation. By some estimates, human colonization of islands caused the extinction of more than 2,000 species of birds, many of them flightless rails (Steadman 2006). These processes continue unabated; in spite of intensive conservation efforts, the Hawaiian Islands have lost more than 10 species in the past decade; most of the remaining native Hawaiian honeycreepers on the island of Kauai face imminent extinction (Paxton et al. 2016). Virtually every region of the world, islands and continents alike, has endangered species, but just a few regions and countries contain most of them (Figure 21–1).



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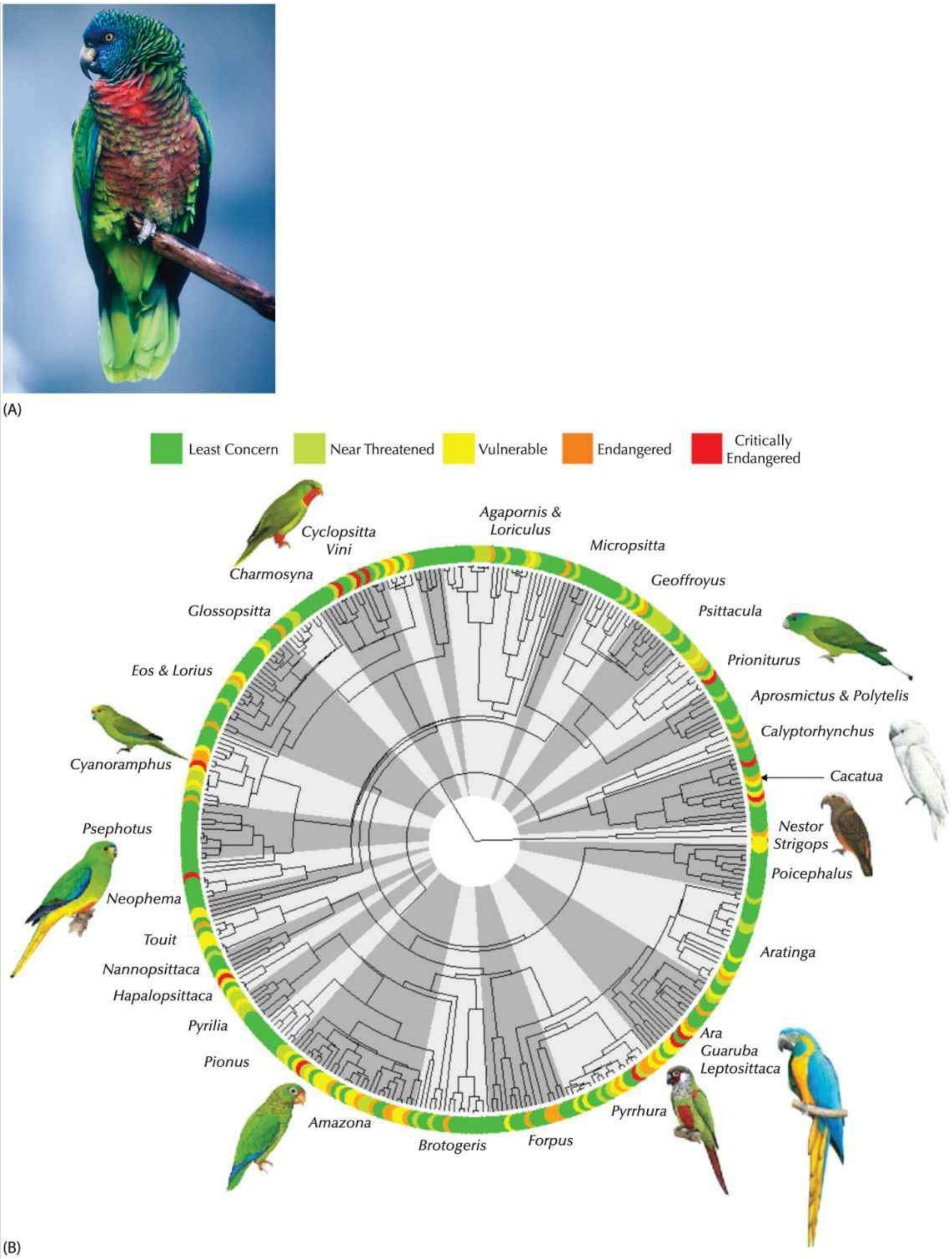
DATA FROM WIKIMEDIA COMMONS, BIRDLIFE INTERNATIONAL 2017

Figure 21–1 (A) Global hot spots map of bird species in trouble. (B) Countries with the highest numbers of threatened bird species populating restricted geographical ranges.

The authoritative **Red List** of the International Union for Conservation of Nature (IUCN) classifies species in accord with their risk of extinction. The 2016 Red List classifies 673 bird species as globally endangered and an additional 787 species as vulnerable. Another 66 species are “data deficient,” meaning that we know too little about them to assess their level of endangerment. Parrots (Psittaciformes) are among the most threatened major group of birds (Olah et al. 2016; Figure 21–2). Twenty-eight percent (111 of 398) of extant species are classified as threatened under IUCN criteria: 56 percent are in decline; only 9 percent have increasing populations. Agriculture, hunting, trapping, and logging are the most frequent threats to parrots worldwide. Although there are success stories (see below), the number of globally threatened and endangered species continues to increase annually.



(A) Michel Gunther/Getty Images. (B) Republished with permission of Springer Science+Business Media, from G Olah, SHM Butchart, et al., "Ecological and socio-economic factors affecting extinction risk in parrots," Biodiversity and Conservation, 2016, February; 25 (2) 205–222. Permission conveyed through Copyright Clearance Center, Inc.

Figure 21–2 (A) The endangered St. Lucia Parrot or Jacquot. (B) Phylogeny of parrots indicating IUCN Red List status of each species. Colors at the tip of the branches represent the IUCN Red List category of each species; gray shading inside the circle represents major genera and groups of related genera as labeled outside the circle.

History warns us not to take even common birds for granted. The once-widespread Bewick’s Wren, for example, disappeared from the eastern United States with little notice. Early danger signs prevail in Neotropical migrants and grassland and savanna species, migrant shorebirds, the seabirds of the Southern Hemisphere, and songbird species with restricted ranges.

One-third of North American bird species need urgent conservation action (North American Bird Conservation Initiative 2016). Grassland species are high on this list. Eastern Meadowlarks, for example, have been declining throughout their range since 1966, especially in the developed northeastern states, where annual declines approach 8 percent (see Figure 18–20). Declining also are Loggerhead Shrikes, Greater Prairie Chickens, and five species of quail. Once-abundant birds of old fields, abandoned farmlands, shrublands, and young or second-growth forests, such as the Eastern Towhee and Field Sparrow, are also declining. The conversion of their shrubland habitats into manicured yards of suburban sprawl and the maturation of young woods into mature forests are among the causes of these declines.

Not surprisingly, many species that adapt well to man-made environments are increasing. Introduced Common Pigeons, Common Starlings, and House Sparrows are now successful human associates, although even they have shown steep declines in some regions (Shaw et al. 2008). A redistribution of native species able to coexist with human societies also is under way. Canada Geese are thriving along urban streams and on golf courses. Ospreys and Monk Parakeets nest on telephone poles and power lines (Figure 21–3). Other raptors such as Red-tailed Hawks and Cooper’s Hawks are colonizing our cities and suburbs. Turkey Vultures benefit from the increasing densities of road kills, especially car-struck deer. American Crows, known for 200 years as shy, rural birds in the United States, are invading suburban backyards and city parks as House Crows and Common Mynas did in Asia centuries ago. Indeed, many of the most successful invasive species have spread worldwide, at least in part because they readily use human structures for their nests.

(A)

(B)

(A) James_Gabbert/Getty Images. (B) MICHELLE MCLOUGHLIN/AP Images

Figure 21–3 (A) The Osprey is a species benefiting from human structures that provide safe nest sites. (B) Monk Parakeets nest among power lines.

21.2 Threats

Despite a growing conservation ethic, expanding human populations continue to threaten native bird populations. Habitat loss is the primary threat. Other challenges to bird populations range from direct exploitation by hunting, overfishing, or commercial pet trading to the poisoning of food supplies with pesticides and other chemical contaminants. Added to these sources of mortality is the annual attrition due to predation by pets and collisions with cars, windows, and towers.

Human activities have profoundly changed the populations of predators in most landscapes. The loss of many top predators has had a cascading effect on medium-sized predators, such as raccoons and foxes, which are probably far more abundant than they were. All these "mesopredators" prey opportunistically on bird eggs and nestlings and may be one of the principal causes of population declines, especially in fragmented habitats (see below). In residential areas, domestic house cats in North America may kill hundreds of millions of songbirds each year and can even be major nest predators in urban environments (Stracey 2011). Some estimates indicate that about a billion birds are killed annually by domestic and feral cats (Loss et al. 2013). Keeping pet cats inside is best for their own well-being and for the future of backyard birds. Cats allowed outside have short life spans and higher risks of rabies, distemper, and toxoplasmosis.

Collisions and Conservation

Collisions with human-made objects of all kinds in the aggregate are a significant source of bird mortality (Figure 21–4). At the top of the list, collisions with plate-glass windows of homes and office buildings kill hundreds of millions of songbirds annually throughout the United States (Klein 2006). Systematic monitoring for one year registered 61 collisions at a house in Illinois and 47 collisions at a house in New York. Roughly half of the birds die of skull fractures and intracranial hemorrhaging. Collisions at single homes multiplied by the number of homes in suburban America projects to a truly huge annual loss of birds. We see only a fraction of these casualties because cats, raccoons, skunks, and opossums remove carcasses promptly. Such sources of bird deaths are of great concern because they augment natural processes of substantial annual mortality.

Photo Courtesy The Fatal Light Awareness Program (FLAP)

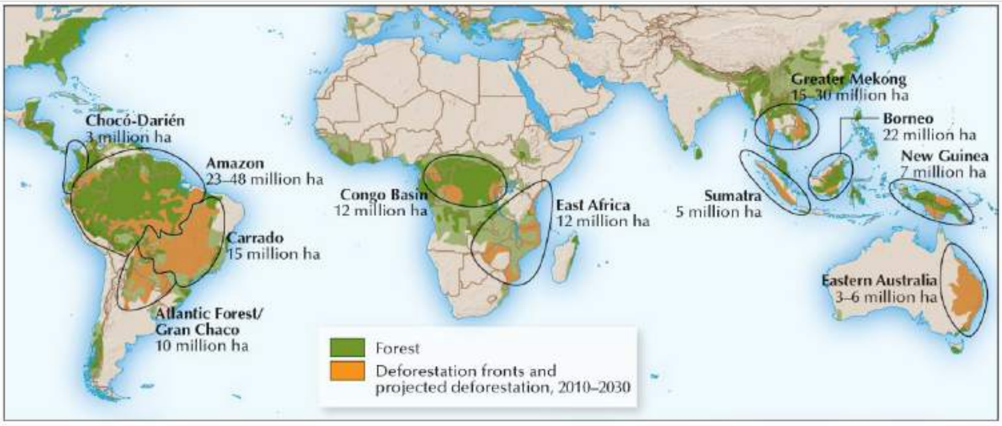
Figure 21–4 A display of 2,100 birds of many species killed by collisions with buildings in Toronto 2016 and collected by a network of volunteers. The Fatal Light Awareness program (FLAP) promotes awareness of this major source of bird mortality.

Bird populations potentially compensate for losses of individual birds through increased (density-dependent) reproduction or survival (see Chapter 18). Healthy populations of birds typically produce surplus young. For many species, especially songbirds, at least half of the total numbers of birds, swollen by the annual addition of young, die each year. That is half of the roughly 20 billion birds present at the end of the breeding season in North America alone. So each dead bird, although disturbing, is not a conservation problem. Rather, population problems are conservation problems. Conservation problems arise when breeding productivity is reduced by the lack of food, loss of habitat, thinning of eggshells due to pesticides, or excessive mortality of young and adults, especially in long-lived species, such as cranes and albatrosses. The accidental deaths of large, long-lived species, such as cranes, condors, and albatrosses, threaten the future of their slow-reproducing populations. The losses of large numbers of albatrosses that drown after being hooked on the lines meant for fish, for example, are causing severe declines of these grand seabirds (section 21.3).

Habitat

Paramount among the threats that challenge wildlife everywhere is the rapid destruction of the natural habitats of the world. Examples include the replacement of virgin rain forest by pastures and coffee or banana plantations, the conversion of rich grasslands into agricultural monocultures or croplands, the draining of wetlands, and the consumption of diverse biological habitats by urban sprawl. The complete loss and severe degradation of habitats now affect the landscapes of all continents, even in Antarctica, where the huge ice sheets used by Emperor Penguins for nesting are threatened by global warming.

The accelerating destruction of tropical rain forests, both lowland and montane, has deservedly the highest profile as a global conservation problem because these forests are the most diverse terrestrial ecosystems on the planet. They cover less than 7 percent of the Earth’s landmass but contain 66 percent of all species. Originally, rain forests covered about 12 percent of the Earth’s landmass, but commercial logging; conversion to cattle pastures and into croplands for soy, banana, and coffee; and expanding civilizations reduced their extent by nearly half in recent decades (Figure 21–5). Half again of the remaining rain forests on Earth will be gone by 2022 if their destruction continues at the present rate (50 million acres annually). This loss extinguishes or dooms to extinction about 27,000 species each year, including many birds (Wilson 1992).



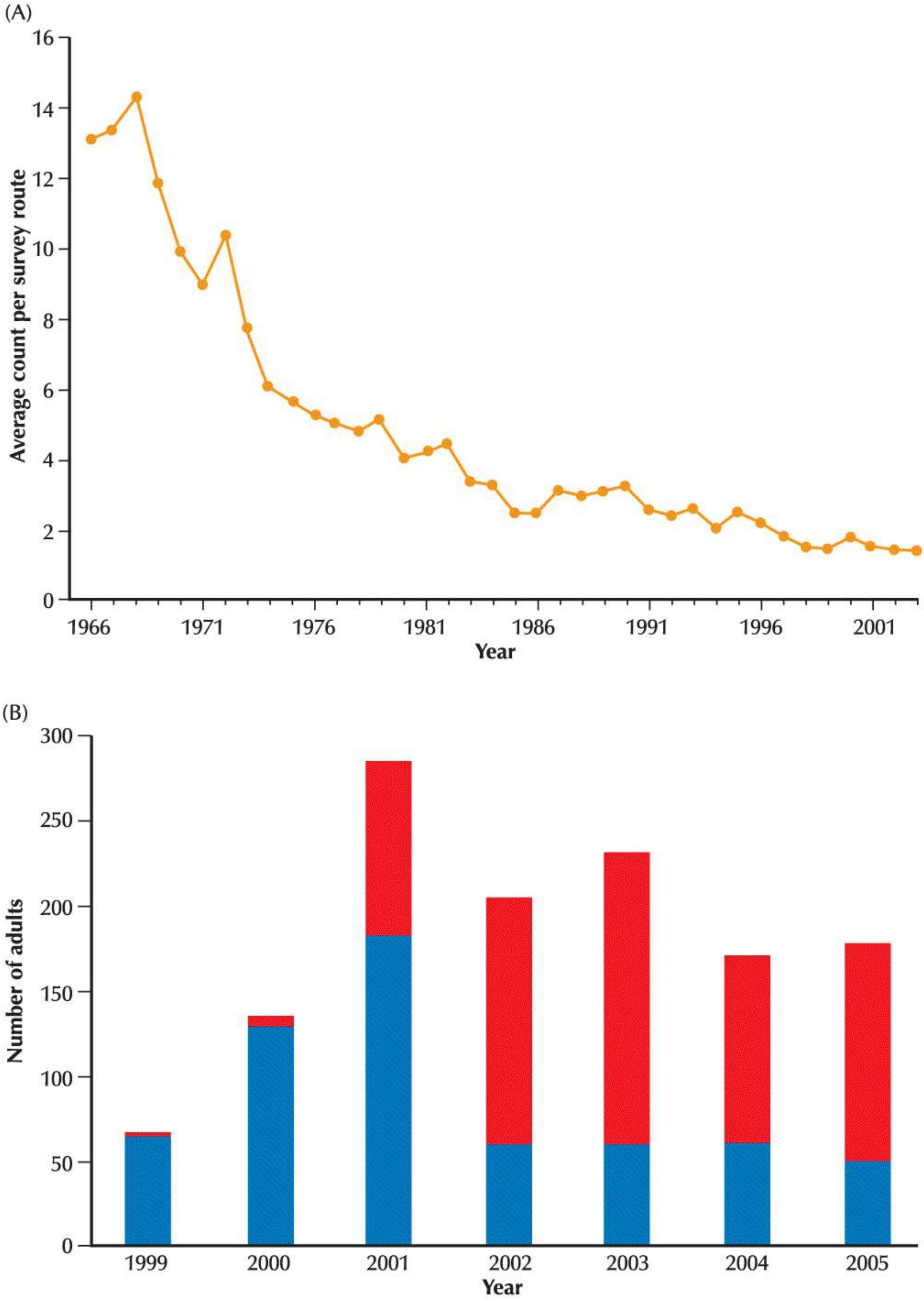
Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
Data from World Wildllfe Fund 2015

Figure 21–5 Roughly half of the planet’s rain forests have been destroyed or degraded in the past 50 years. Shown here are the major “deforestation fronts” where the World Wildlife Fund projects that 80 percent of ongoing deforestation will take place between 2010 and 2030.

The challenges of habitat loss exist not only in distant tropical settings but throughout North America and Eurasia as well. Preceding the cutting of tropical rain forests by more than a century was our consumption of North American forests for fuel, lumber, and agriculture. The forests of the northeastern United States—east of the Finger Lakes in New York—were virtually cleared by 1800 (Foster and Aber 2004). The bottomland forests of the Southeast, home to the Ivory-billed Woodpecker, and the giant old-growth forests of the West Coast, home to the Spotted Owl, were next.

The good news is that birds, especially migratory species and dispersing young ones, quickly find and use newly restored habitat. The regrown forests of New England, for example, now support large populations of once-extirpated Broad-winged Hawks and Pileated Woodpeckers. Success stories of grassland restoration, beach protection, wetland management, and reforestation fuel the conviction that we can stabilize and rebuild many bird populations.

Many grassland species are acutely sensitive to grassland management practices, such as grazing, the timing of haying, and government policy. The Grasshopper Sparrow, for example, declined throughout the eastern United States due to the loss of their grasslands. Yet conversion of fields on the eastern shore of Maryland from row crops into warm-season grasses attracted hundreds of them within two years (Figure 21–6) as well as Dickcissels and robust wild populations of Northern Bobwhites. The Henslow’s Sparrow, for another example, almost disappeared from much of its historical breeding range due to annual mowing of their fields. This species recovered rapidly and recolonized new areas when large areas of grassland were set aside in the government’s Conservation Reserve Program (CRP). This program protects highly erodible farmland and allows fields to grow for several years and to meet the sparrow’s special requirements (section 21.5). CRP grasslands also foster robust populations of Common Pheasants, Bobwhite Quail, and nesting ducks.



Gill/Prum, *Ornithology*, 4e, © 2019 W. H. Freeman and Company
(A) Data from Sauer et al. 2005. (B) Courtesy of D. Gill

Figure 21–6 Grasshopper Sparrows find restored grasslands at Chino Farms in Maryland. (A) Breeding Bird Survey data document the decline of Grasshopper Sparrows in Maryland. (B) Numbers of adult Grasshopper Sparrows found breeding in a 250-acre restored grassland at Chino Farms near Chestertown, Maryland, starting two years after the conversion of row crops into grasslands. Blue parts of bars indicate new arrivals, and red parts indicate banded birds returning from preceding year.

Some species and the ecosystems on which they depend require disturbances. As we review below, many species depend on habitats created by fire, flooding, and grazing. Grazing, for example, benefits species such as the Upland Sandpiper and Grasshopper Sparrow as well as most of the species that depend on the short-grass prairie. Indeed, the Mountain Plover has become a threatened species largely because of the loss of bison herds that created extensive areas of bare ground, such as buffalo wallows. The management of eastern forests to provide areas of second growth and saplings favored by game species, such as the Ruffed Grouse and American Woodcock, also attract declining songbird species, such as Golden-winged Warblers and Field Sparrows.

Many species that depend on floodplain habitats also depend on disturbances to create their habitat. Least Terns and Piping Plovers, for example, need large open sandbars on rivers in the central United States for their nesting (Sidle et al. 1992). Without massive spring floods, these habitats quickly become overgrown with willows and other woody vegetation. Indeed, several extinct and endangered birds, such as the Ivory-billed Woodpecker (Figure 21–7), Bachman’s Warbler, Southwestern Willow Flycatcher, and Least Bell’s Vireo, owe their imperiled status mostly to water management practices, such as levees and water diversion, that prevent or reduce flooding.

JOHN JAMES AUDUBON/GETTY IMAGES

Figure 21–7 Ivory-billed Woodpecker, the signature species of the bottomland forests of the southeastern United States, was last seen (for sure) in 1944.

Emerging Challenges

Conservation threats will increase steadily in the years ahead with new and emerging challenges. Some challenges stem from the globalization of world health and economies, which can cause global homogenization of wildlife communities (Qian and Ricklefs 2006). Others come from the growing perception of urban dwellers that the woods and fields are dangerous places to explore. Extreme climate events—heat waves, droughts, and extreme rainfall sessions—are increasing in frequency and intensity because of global warming. These climate events foster local outbreaks of disease vectors, such as mosquitoes, and local amplifications of viruses, such as West Nile virus, which then spread rapidly throughout the world. Fast-spreading new diseases affect local populations of both common birds, such as American Crows and Great Horned Owls, and endangered birds, such as Sage Grouse and California Condors.

Wild birds tend to be victims rather than agents or primary vectors of disease. But there is historical precedence for new disease as well as understandable public fear of it. The high-level concerns about Asian bird flu (H5N1), for example, include the role of migratory birds in its spread. Such concerns challenge the bird conservation community to be sensitive to the needs of both people and birds. In reality, high-density poultry farms and the globalization of human transportation systems are spreading the Asian bird flu, with migratory birds playing only a secondary, minor role (see Box 18–3).

Pollution comes in new and challenging forms. Certain chemicals disrupt the normal course of embryonic development, often without obvious manifestations until adulthood. This class of chemicals, called **xenobiotics,** includes fungicides, herbicides, and insecticides plus assorted industrial chemicals; synthetic products, including soy and pet-food products; and some metals, including cadmium, lead, and mercury (Colborn and Clement 1992). The effects include but are not limited to thyroid dysfunction, compromised immune systems, decreased fertility, decreased hatching success, gross birth deformities, metabolic and behavioral abnormalities, and sex reversal.

Studies of Western Gulls breeding in California and Herring Gulls breeding on Lake Ontario and Lake Michigan showed some of the effects of these contaminants, including a high incidence of clutches with extra eggs, female–female pairings, and the feminization and high mortality of males (Gilbertson et al. 1991; Fox 1992). Gulls in these colonies also suffered from embryonic and chick mortality, edema, growth retardation and deformities, and altered nest-defense and incubation behaviors. All of these effects severely reduced reproductive success. Chemicals that impair birds in these ways can also affect human health.

World health officials worry about new forms of drug pollution. A major episode surfaced on the Indian subcontinent, with birds—specifically vultures—serving once again as leading indicators of environmental problems (Figure 21–8). Starting in 1997, three abundant species of vultures of the genus *Gyps* underwent severe, rapid, and widespread declines in India and neighboring Pakistan. Their populations crashed to just 3 to 5 percent of their starting numbers. The vultures were dying of renal failure and visceral gout, but the cause was mysterious. Disease was ruled out. Government concern escalated because the vultures were essential to public health. They reduced the risk of disease by cleaning up waste and carcasses on the landscape, aiding particular religious sects to whom cattle were sacred and could not be eaten or for whom cremation of their own dead was not allowed. Packs of wild dogs formed in the absence of vultures, adding new threats to local communities.

Geoffrey K Brown/Pantheon/Superstock

Figure 21–8 Indian vultures (*Gyps indicus*) promptly consume dead livestock, an important ecological service. Residual painkilling chemicals within the meat caused high mortality and endangered this once-abundant species.

A veterinarian and his colleagues at the Peregrine Fund in Idaho and the Ornithological Society of Pakistan discovered the cause (Oaks et al. 2004). All three species of vultures were extremely sensitive to the anti-inflammatory drug diclofenac. Veterinarians in Pakistan and Indian used this drug with increasing frequency to relieve the suffering of dying sacred cattle. Diclofenac is a kind of ibuprofen (as in Advil) for pain relief. Vultures feeding on carcasses of recently treated cattle ingested the fatal drug as well. With little delay, an international team of scientists announced a solution in 2006, just two years after the diagnosis of diclofenac poisoning. An alternative drug named meloxicam, which is safe for vultures, was developed to replace diplofenac. The transition to meloxicam as the veterinary choice of drugs for dying cattle is under way.

Social challenges also loom large for the future of the environment and healthy bird populations. Urbanized societies are increasingly disconnected from the outdoors and, hence, tend not to value nature as much as earlier rural generations. That disconnect leads to fear of the woods and of nature generally called **ecophobia.** It also leads to a spiritual or psychological handicap, recognized formally as “nature deficit disorder” (Louv 2005). The challenge, therefore, is to help young children of all backgrounds and communities discover birds, value nature, and take ownership of these resources for their own good health. Bird-watching is an excellent remedy to this disorder; birds can be found even in the heart of some of the world’s largest cities—thousands of bird-watchers, for example, regularly cover Central Park in New York City, especially during the spring migration.

Before progressing to ongoing and increasingly successful conservation initiatives, let’s first consider the early effects of human expansions on bird populations. These human excesses provide an essential historical perspective.

21.3 Past Excesses

The plight of birds and other wildlife worldwide due to human activities is not just a recent circumstance. Rather, global expansions of human civilizations started to transform landscapes and ecosystems more than 50,000 years ago (Fitzpatrick 2004). The effects of humans on natural landscapes intensified and then escalated starting about 10,000 years ago.

Birds as Food

Bird flesh helped to fuel the global expansions of humans. Fossil records suggest that more than 9,000 species of birds were lost to the first hungry waves of human civilization (Steadman 1995). That is roughly the same number of species as now prevail. By modern times, therefore, early human civilizations already had claimed half of the birds of the world that survived the last Ice Age.

Losses of island birds account for 90 percent of bird extinctions during historical times. Pioneering human colonists everywhere found abundant, tame, and edible birds, especially on oceanic islands. The extermination of the Dodo and other flightless birds on the Indian Ocean island of Mauritius in the late 1600s is a classic example of the loss of vulnerable island birds (Box 21–1). Dodos were slaughtered and salted to provision continued global exploration and colonization.

Box 21–1

Symbol of Extinction: The Dodo

The legendary Dodo is a symbol for the process of extinction of vulnerable bird species by human beings. Not just a whimsical character in Lewis Carroll’s *Alice in Wonderland*, the Dodo was a real bird that once lived on the remote tropical island of Mauritius, one of three Mascarene islands in the western Indian Ocean. The Dodo was a large, flightless, turkey-sized pigeon, assigned to the Family Raphidae. Cohabiting Mauritius with the Dodo was an amazing array of flightless pigeons, rails, parrots, waterfowl, and other birds. Almost all were exterminated in the seventeenth century (Hachisuka 1953).

The Dodo ate fruit, became extremely fat, and was easily captured (hence the use of the name Dodo to indicate stupidity). It was prized as a readily available source of food. In the early 1600s, a few living Dodos were sent to Europe, where they captured public interest as a great curiosity. Few survived to the middle of the century, however.

The last eyewitness account of wild Dodos comes from the journal of Volquard Iversen, who was shipwrecked and stranded on Mauritius for five days in 1662 before being rescued (as seen in Cheke 1987). He found no Dodos on the mainland but discovered some on a small islet accessible by foot at low tide, which he described:

> Amongst other birds were those which men in the Indies call doddaerssen; they were larger than geese but not able to fly. Instead of wings they had small flaps; but they could run very fast. [Cheke 1987, p. 38]

Perhaps the last Dodos learned to fear human hunters. But they did not run fast enough. Only fossils and a few preserved specimens remain as evidence of this odd species.

ENCYCLOPAEDIA BRITANNICA/UIG/GETTY IMAGES

The Dodo.

More recently, men had harvested the Great Auk of the North Atlantic to extinction by 1840. Valued as food to resupply ships that had crossed the Atlantic, these flightless birds were easy to catch and kill. One enterprising crew built a bridge of sail canvas from shore to ship and herded the helpless auks directly into the ship's cargo hold (Matthiessen 1959).

Dodos and Great Auks are the most famous birds lost to extinction in human history but not the only ones. The Maori peoples who colonized New Zealand consumed giant, flightless moas. Similarly, Indonesian peoples who colonized Madagascar more than 14,000 years ago downed the amazing elephant birds—three meters tall with nine-liter eggs—plus a host of other species found only there.

These examples are only a few from the broad pattern of destruction of island avifaunas by early human colonists. Similar waves of extinctions of birds of all kinds followed the settlement of the Caribbean islands 3,000 to 4,500 years ago (Pregill and Olson 1981). Early camp garbage pits on islands throughout the South Pacific contain the bones of many species no longer there (Steadman 2006).

In one way or another, humans destroyed most of the unique original avifaunas of the Hawaiian Islands. The early Polynesians leveled the lowland forests after landing there roughly 1,500 years ago. Eliminated were at least 39 species of land birds, including seven geese, two flightless ibises, three owls, seven flightless rails, and 15 species of honeycreepers (James 1995). Captain James Cook then brought European civilization, mosquitoes, and diseases to the islands in the eighteenth century. Island birds lose resistance to mainland diseases in addition to losing their fear of predators and their ability to fly. Consequently, bird pox and malaria destroyed the remaining lowland populations of the Hawaiian honeycreepers when mosquitoes that carried these diseases were accidentally introduced.

In North America, the wholesale consumption of wildlife was a national pastime in the new nation of the United States in the eighteenth century and, especially, in the nineteenth century (Matthiessen 1959). The earliest settlers of the United States lived off the abundant game, severely depleting local stocks of turkey and deer. Larks, bobolinks, robins, and many other songbirds also were fair game. Full-scale market gunning took its toll later in the mid-1800s. First, the great bison herds and other large mammals of the Great Plains were exterminated. Then cannonlike punt guns mounted on low close-approaching “sinkboats” dropped flocks of waterfowl. Examples of the slaughter include 5,000 ducks shot in a day on the Susquehanna Flats of Pennsylvania, 1,300 mallards killed by one man in seven hours, and 3 million ducks killed in one year in Louisiana (Sawyer 2013). By 1900, only 150 million ducks and geese survived in the United States, down from an estimated 500 million in 1700.

Populations of the most common birds number in the hundreds of millions or more, but such abundance did not prevent extinction. Legendary are the estimated 1 billion Passenger Pigeons that flew over colonial America. Advancing European colonists cut down the beech forests that provided abundant food for the pigeons. Aided in the late nineteenth century by telegraph communications about the locations of the flocks and by new railroads that enabled transport to major city markets, market hunters harvested and sold vast numbers of the pigeons for food. The seemingly unlimited flocks of Passenger Pigeons disappeared. The last wild Passenger Pigeon was killed in Ohio in 1900. The last captive birds died soon after.

Shorebirds fell, too, particularly the vast flocks of American Golden Plovers and Eskimo Curlews that migrated north in the spring through the Great Plains and then south in the fall from maritime Canada to South America. John James Audubon reported millions of American Golden Plovers near New Orleans in the early nineteenth century and compared curlew flights with those of the Passenger Pigeon. Occasionally, southbound plover and curlew flocks appeared on the New England coast.

> On August 29, 1863, both curlew and plover appeared on Nantucket in such numbers as to “almost darken the sun”; seven or eight thousand were destroyed before the island’s supply of powder and shot gave out. [Matthiessen 1959, p. 162]

Excessive exploitation continues in modern times. The commercial fishing industry, for example, challenges not just fish populations but also the future of many seabirds, both indirectly and directly. The depletion of fish stocks—anchovy off the coasts of Peru and South Africa and in the North Sea—has caused major seabird colonies to decline. More directly, gill nets catch large numbers of diving seabirds as well as fish. In the North Pacific, an estimated 750,000 seabirds, including the threatened Marbled Murrelet, drown in gill nets each year. The Yellow-breasted Bunting of Asia, which was once so abundant that it was considered a crop pest, is now an endangered species as a result of ongoing trapping for the food trade.

The long-lived, slow-reproducing albatrosses of the world’s oceans

UNIVERSAL IMAGES/SUPERSTOCK

Figure 21–9 Large numbers of albatrosses drown as incidental bycatch of longline fishing industries.

are particularly vulnerable to accidental mortality when they are caught on the hooks meant for large pelagic fish, such as tuna. Albatrosses traditionally follow fishing ships for food and can’t resist the baited hooks tossed out on miles of longlines. Mortality due to drowning when hooked on longlines is estimated to be roughly 100,000 albatrosses each year (Figure 21–9). Nineteen of the 21 species of albatross in the world are threatened with extinction largely because of longline fishing. Fortunately, the fishing industry is starting to implement practical solutions. Adding weights to the baited hooks to sink them before the surface-feeding albatross can get them significantly reduces fatal bycatch rates.

Commercial harvesting of horseshoe crabs on the mid-Atlantic coast is another high-profile modern conservation problem. Red Knots and other shorebirds are the victims in this case. Thousands of horseshoe crabs emerge each spring from the depths of the inshore bay waters to lay their nutritious eggs in the beach sand. Those eggs are fuel for the final stages of the Red Knot’s northbound migration (see Chapter 10). Coasts of the Delaware Bay of New Jersey, Delaware, Maryland, and Virginia provide traditional stopover sites, where horseshoe crabs and shorebirds have converged each spring for thousands of years. Horseshoe crabs are also harvested locally for fertilizer and for bait. Intensive harvesting has caused the numbers of crabs emerging to decline each year. In parallel, the Atlantic population of the Red Knot has declined 80 percent in the past 10 years. Regulations that start to control the harvest rates are now in effect in most states.

Birds as Decorations

As the flocks of shorebirds and pigeons fell as sources of food in the late nineteenth century, another threat materialized—plume hunting for the millinery trade. The mounting of bird feathers, as well as whole birds, onto ladies’ hats became the height of fashion in the 1870s and 1880s. Entrepreneurs killed an estimated 5 million birds for this purpose alone.

At first, the breeding plumes of large wading birds—egrets, herons, and spoonbills—were prized, with devastating effect on their nesting colonies. The millinery trade next turned to gulls and terns and then to a full array of species, ranging from brightly colored songbirds to crows. Drawing rave reviews was an entire crow—beak, feet, and all—seen on a hat in New York City in 1886. Frank M. Chapman, distinguished ornithologist at the American Museum of Natural History and an early officer of the budding Audubon Society, amused himself by identifying the species on hats as he strolled through New York City. In one census, 542 of 700 hats sported mounted birds of at least 20 species, including a Ruffed Grouse and a Green Heron (Matthiessen 1959).

Few people are aware of the dimensions of the modern caged-bird industry and its effect on the populations of wild birds. Millions of birds are harvested from the wild as decorative pets. The exotic pet-bird trade is a mega-industry, much of it illegal. From 2 million to 5 million birds move annually from tropical habitats to the living rooms of developed countries. The United States, currently the largest importer of exotic birds, legally imported nearly 1 million birds annually throughout the 1980s. Forty-three percent were parrots, and the remainder represented various other birds of the world—no fewer than 77 different taxonomic families. Parrots command especially high prices. At the top of the price list are rare macaws, such as the Hyacinth Macaws. A pair sells for $5,000 to $30,000. Several species, including the Red Siskin, Bali and Black-winged Mynas, and Straw-headed Bulbul, are currently endangered as a result of the pet-bird trade.

Controlling the international pet trade is the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In response to a list compiled by this organization, the U.S. Congress passed the Wild Bird Conservation Act of 1992 in an effort to eliminate the importation of endangered wild bird species. By 1994, imports of cage birds dropped to 80,000 birds annually. Captive breeding stocks increasingly satisfy the appetites of the pet market.

21.4 Hope

There is hope despite the catastrophic losses of species, the ongoing declines, and the continuing excesses. Birds are amazingly resilient and will rebound if given half a chance. Remember the remarkable recovery of the Short-tailed Albatross (see Box 18–1).

Rediscoveries of species thought to be extinct energize conservation initiatives (Table 21–1). Last seen for sure in 1944 in the Singer tract of Louisiana, the majestic Ivory-billed Woodpecker, or Lord God Bird, is the signature species of the old-growth bottomland forests of the southeastern United States (see Figure 21–7). One of the largest woodpeckers in the world, the Ivory-bill, was first hunted by Native Americans and then collected as a desirable rarity by early ornithologists. Critical bottomland forests were cut. Despite regular reports of sightings of Ivory-billed Woodpeckers, in the absence of any confirming photograph, Ivory-bills became as legendary and as elusive as Elvis himself. Then a report by a kayaker in southeastern Arkansas on February 11, 2004, sparked fevered excitement and renewed hope (Fitzpatrick et al. 2005). Field teams searched the bottomlands—but to no avail.

Table 21–1 *Some Rediscovered Bird Species Thought to Be Extinct for at Least 50 Years*

Species	Location	Year Rediscovered
White-winged Guan	Peru	1977
Gurney's Pitta	Thailand	1986

Jerdon’s Courser	India	1986
Madagascar Serpent Eagle	Madagascar	1988
Night Parrot	Australia	1990
Sao Tome Grosbeak	Gulf of Guinea	1991
Cebu Flowerpecker	Philippines	1992
Edwards’s Pheasant	Vietnam	1996
Congo Bay Owl	Democratic Republic of the Congo	1996
Kinglet Calyptera	Brazil	1996
Forest Owlet	India	1997
Cherry-throated Tanager	Brazil	1998
Chinese Crested Tern	China Sea	2000
Kalinowski’s Tinamou	Peru	2000
White-masked Antbird	Peru	2001
Long-legged Thicketbird	Fiji	2003
Ivory-billed Woodpecker	United States	2004?

Restoration

We have the knowledge and the ability to stabilize threatened bird populations and to reverse their declines. Among the modern highlights are the remarkable comebacks of signature species, such as Bald Eagles, Brown Pelicans, and Sandhill Cranes decimated by pesticides, and colony-nesting herons, egrets, and ibises decimated 100 years ago by the plume hunters. Protection, combined with deliberate restoration programs, rebuilt the populations of iconic species, such as the Whooping Crane (Box 21–2).

Box 21–2

Saving the Whooping Crane

Cooperation between the governments of the United States and Canada has restored hope for the future of the stately black-and-white Whooping Crane, an endangered species that inspired international concern and constructive action. The population of Whooping Cranes, which once nested widely in the upper midwestern states and prairie provinces during the nineteenth century, declined to a low of only 18 birds (in 1939) that wintered at Aransas National Wildlife Refuge on the Texas coast (U.S. Fish and Wildlife Service 1986; McMillen 1988). In addition, three nonmigratory cranes lived year-round in southwestern Louisiana, but they had not bred since 1939, when the conservation efforts began.

International concern about this endangered species impelled the governments of the United States and Canada to work together to prevent the extinction of the Whooping Crane. This accomplishment overcame many setbacks—accidental deaths, fatal diseases in captive flocks, the consequences of imprinting on foster-parent Sandhill Cranes, and the need to teach young birds how to migrate to Florida (see Chapter 10). The total population of Whooping Cranes increased slowly at first but then dramatically to 442 birds in four free-living populations, plus an additional 161 in captivity (U.S. Fish and Wildlife Service 2015).

Most populations have the potential to rebound from severe reductions. The return of the Wood Duck was one of the early conservation triumphs in North America (Figure 21–10). Uncontrolled hunting and the destruction of the bottomland forests that also supported the Ivory-billed Woodpecker had almost eliminated this abundant species by 1900. In 1918, the U.S. government closed the hunting season. The Wood Duck population rebounded vigorously by the 1930s. Nest boxes supplemented natural production in tree holes and allowed the reopening in 1941 of carefully controlled hunting with limited daily bag limits in 14 states. Wood Ducks are now common throughout their original range with a total population size of more than 2 million. In addition, Wood Ducks are expanding widely into new parts of the continent. Annual harvests of Wood Ducks are now second only to those of Mallards.


LARRY JON FRIESEN

Figure 21–10 Male Wood Duck in breeding plumage. Wood Ducks made a comeback in the twentieth century after overhunting and habitat destruction led to their decline.

The DDT story offers further testimony to our ability to remove threats and rescue declining bird populations. Human poisoning of the environment has had a devastating effect on the fecundity of some birds, directly endangering them (see Chapters 12 and 18). DDT affects all animals, including human children, with symptoms ranging from growth deformities to neurological damage. After the effects of DDT were recognized, its use was widely banned, with dramatic positive results.

Given a chance by the banning of DDT and related pesticides, Bald Eagles and Ospreys recovered strongly. Bald Eagle populations now nest in growing numbers throughout most of the continent. Also a signature of success, Peregrine Falcons now nest on almost every traditional cliff in the northeastern United States as well as on every suitable bridge that crosses major rivers, such as the Hudson, the St. Lawrence, and the Mississippi. Less well known is the return of the Aplomado Falcons, among the fanciest of all falcons. Extirpated from southern Texas, New Mexico, and Arizona, Aplomado Falcons are back nesting on the South Texas Coast and in southwestern New Mexico thanks to a major reintroduction program.

Rescue of the Peregrine Falcon

CHRIS HILL/SHUTTERSTOCK

Figure 21–11 Peregrine Falcon, a raptor whose extinct populations have been replaced by local restoration programs releasing captive-raised young birds.

Restoration programs have the goal of reestablishing self-sustaining natural populations of a species. The successful effort to restore the Peregrine Falcon to eastern North America engaged the public as well as professionals (Figure 21–11).

Peregrine populations in North America, particularly in the eastern United States and Canada, virtually disappeared in the 1950s and 1960s, primarily as a result of reproductive failure due to DDT pesticide poisoning. The ban on DDT for most uses in the United States removed the immediate problem and set the stage for a bold conservation initiative. The goal was to rebuild a free-living population of eastern Peregrines by raising young falcons in captivity and then releasing them into the wild in a procedure called **hacking.** Private falconers joined the program led by Thomas Cade to help breed the large numbers of young birds necessary for the success of the hacking effort.

To reestablish a self-sustaining breeding population in midwestern North America, one group of volunteer conservationists, led by Bud Tordoff and Pat Redig of the University of Minnesota, worked with local business communities of the major cities. Peregrines were hacked from boxes on the window ledges of the cities' finest office buildings and then returned to nest themselves on these ledges. In all, the communities hacked 1,249 young falcons and fledged 3,178 wild young from 1,140 successful pairs between 1982 and 2005. This effort produced 169 territorial pairs that fledged 421 young themselves in 2005. Fecundity of the new midwestern Peregrines now averages the same as in healthy, wild Peregrine populations: 1.5 fledged young per pair annually. From a genetic standpoint, the rebuilt population also is healthy. Minnesota Peregrines are mixing with populations to the west, north, and east, fostering increased genetic variability.

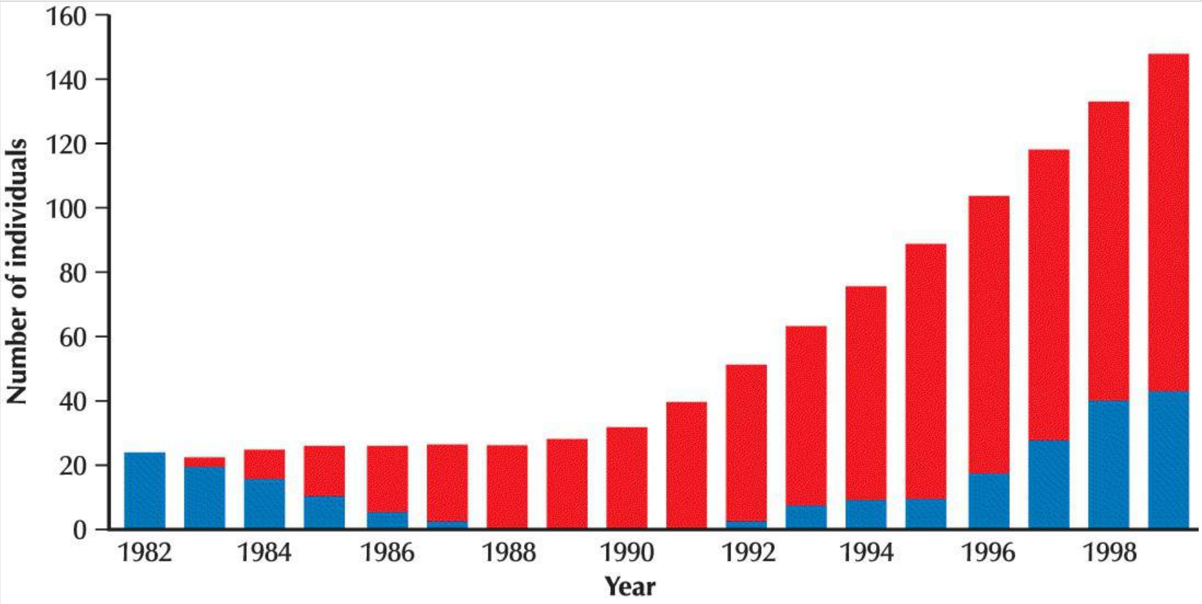
The cost of such restoration programs is significant but modest because of the volunteer contributions. In the entire Midwest, hacking 1,265 young falcons at $2,500 each cost $3,162,500. In the whole of North America, about 7,000 peregrines were produced and hacked, for a total cost of $17,500,000, less than the cost of a single fighter plane. One F-16, the least expensive of modern U.S. fighter planes, cost $28,000,000 in 2001.

Rescue of the California Condor

The California Condor, North America's largest vulture, is a relict of the Pleistocene. Other condor species, many of them much larger, once prospered along with the continent's prehistoric large mammals. Today, only two species remain: the Andean Condor of South America and the California Condor of North America. The California Condor once roamed widely across the United States as far east as New York in search of carrion. Through the millennia, the large populations shrank to a single remnant population in southern California. Illegal shooting, power-line collisions, and lead poisoning from bullet fragments in deer carcasses were the main terminal causes.

The rescue of the California Condor illustrates some of the conflicts between using a species as a symbol for habitat preservation and saving a species for its own sake (Kiff 2000; Snyder and Schmitt 2002). The initial efforts to save the California Condor polarized two political factions. In one camp were those who considered the condors an untouchable symbol of the remaining wilderness expanses of southern California threatened by expanding populations of people. Protecting it would also protect the wilderness reserves. No protection in captivity should take place. At worst, they reasoned, the condor should be allowed a noble death that would conclude an era of Earth's history. In the other camp were those who believed that intervention was both warranted and essential to save the species, even if only as captives in zoos, because we ourselves brought the condors to their sorry state.

With the wrenching decision to capture the last free-living condor in 1987, the prospects for their return to the skies of southern California shifted to the release and successful rehabilitation of condors hatched and raised in captivity (Figure 21–12; see Box 16–5). The first six young condors were released back into the wild in January 1992. One of the first ones released died after drinking water contaminated with antifreeze, an unfortunate accident. Despite the setbacks, increasing numbers of condors now fly over the Grand Canyon from the nearby Vermillion Cliffs release site in Arizona and over Big Sur of central California.



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DATA FROM KIFF 2000

Figure 21–12 California Condor numbers in the wild (blue part of bar) and in captivity (red part of bar) from 1982 to 1999.

The future success of this high-profile initiative will depend not only on teaching naïve young condors to forage and survive on their own but also on a new political challenge—the ability of conservation groups and government agencies to reduce the use of lead bullets in release areas. Soon after their release, some young condors die of poisoning by lead fragments that they ingest from carcasses of deer and wild pigs shot by hunters. Lead is a poison that has been banned from our homes and office buildings and from waterfowl marshes. In April 2015, the California Fish and Game Commission also banned the use of lead ammunition when hunting wildlife with a firearm.

Special Facilities

Other success stories stem from the provision of special nesting facilities. Eastern Bluebirds responded to the network of well-designed nest boxes on the bluebird trails pioneered by Thomas Musselman of Quincy, Illinois, in 1926, now a nationwide network of trails maintained by members of the North American Bluebird Society. Aided by regular cleaning and maintenance of the nest boxes in backyards, on farmlands, and in parks and refuges, Eastern Bluebirds are now widespread and common to the delight of all. Mountain Bluebirds and Western Bluebirds also respond to bluebird boxes erected in the western states.

Nest platforms also aid waterbirds, such as the Common Loon, by reducing nest predation by raccoons and nest flooding due to rising lake levels (Piper et al. 2002). This initiative started on Squam Lake, New Hampshire, as a local conservation initiative of volunteer "Loon Rangers." It caught on. Summer-camp owners now proudly protect their loons as a feature of the vacation experience on northern lakes.

Like the California Condor, however, loons now also must contend with lead poisoning (Box 21–3).

Box 21–3

Loons and Lead

Lead poisoning is a significant source of mortality of Common Loons on the lakes where they nest in the northern United States and Canada. Lead poisoning causes from 25 to 50 percent of documented cases of death on some lakes. Lost lead fishing tackle—jigs and sinkers—is responsible for this mortality.

How does fishing tackle poison birds? Loons ingest small pebbles as “grit” to help digest fish bones in their gizzards. They pick up lead fishing tackle by mistake, sometimes large sinkers and jigs. More than 20 other species of waterbirds accidentally ingest lead fishing tackle while feeding.

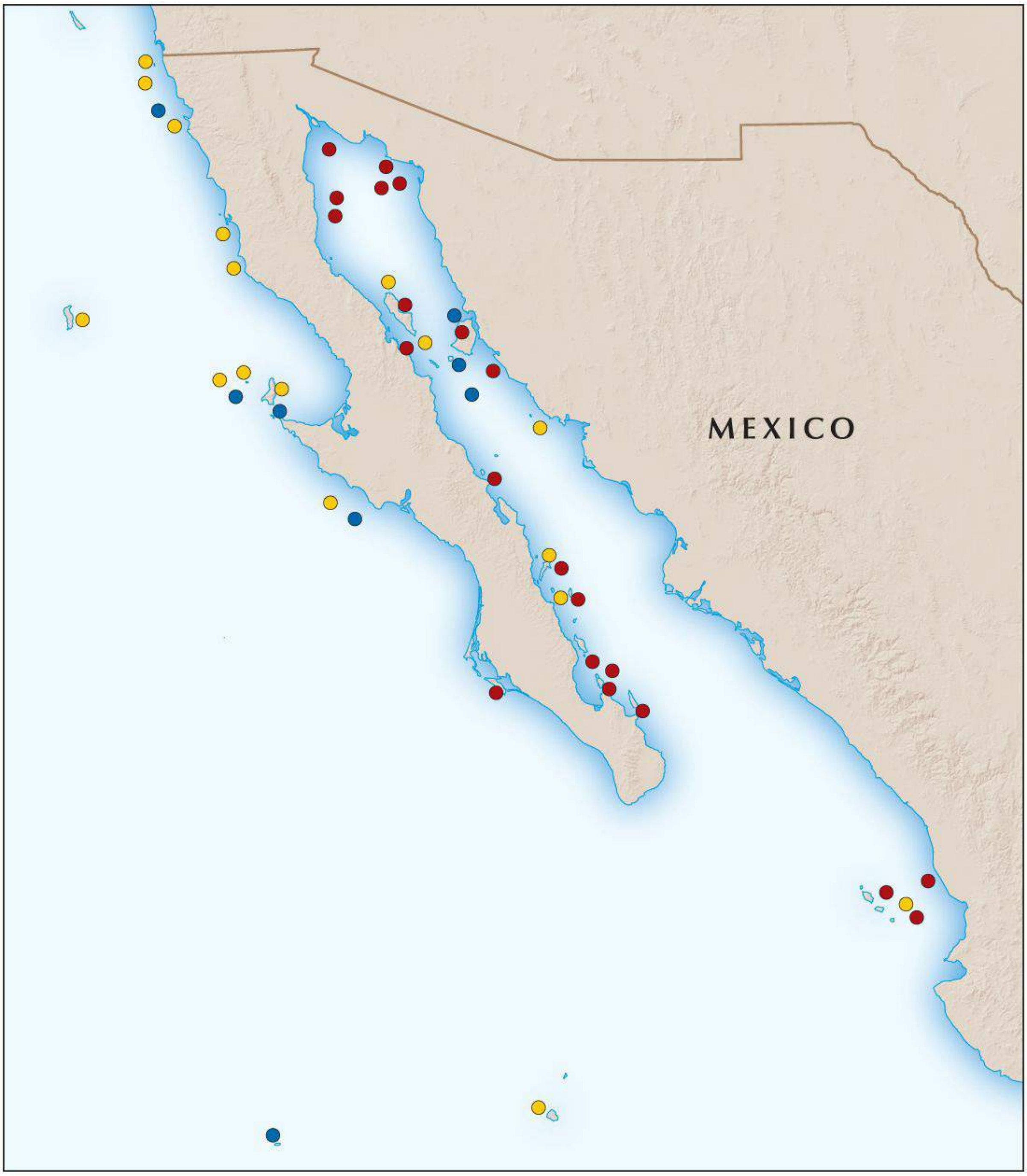
Under way are many educational and political campaigns to reduce the use of lead fishing tackle. In 2004, New York State passed legislation banning the sale of small lead sinkers weighing less than 0.5 ounce. Some New England states (New Hampshire, Maine, and Vermont) also have legislation regulating the use or sale of lead fishing tackle. They also promote educational programs for anglers about nontoxic alternatives. More broadly, the use of lead sinkers has been banned in national parks and wildlife refuges across the United States.

Island Conservation

Island-bound birds and nesting seabirds are particularly vulnerable to hogs and goats, cats and rats, and other such exotic mammals brought to once-safe islands by ships and sailors. Hogs and goats eat everything down to bare rock. Introduced predators, such as rats and cats, are directly responsible for the extirpation of many island populations of birds—landbirds and seabirds alike. Rats, which infest most (80 percent) of the islands of the world, participated in roughly half of the historical extinctions of island birds (and reptiles). One pregnant cat imported in the 1950s onto Kerguelen Island in the southern Indian Ocean multiplied into 3,500 cats in 30 years. They killed 1.2 million seabirds each year (Krajick 2005).

New Zealand's Department of Conservation pioneered the conservation of endangered island bird species, especially their own shattered avifauna, through aggressive eradication of invasive species. Other organizations, government and private, are following suit. The U.S. Fish and Wildlife Service, for example, eradicated Arctic foxes introduced onto the Aleutian Islands. Fork-tailed Storm Petrels, eiders, and native geese increased fivefold within 10 years after the foxes were gone.

A similarly aggressive and model program eradicated invasive mammals from the hundreds of islands in the Sea of Cortez and off the coast of Baja California in northwestern Mexico (Figure 21–13). The array of more than 250 islands supports diverse plants and animals, including 180 endemic terrestrial vertebrates and 50 kinds of seabirds. Invasive alien mammals—rats, cats, goats, rabbits, and so on—are responsible for the disappearance of 22 endemic vertebrate taxa (species and subspecies) and the local extinction of seabirds from 10 islands.



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DATA FROM TERSHY ET AL. 2002

Figure 21–13 Islands off northwestern Mexico with invasive mammals in 1994. Orange circles indicate islands that suffered local extinctions of seabird species. Blue circles indicate islands that lost endemic vertebrates. Red circles indicate islands that have not lost species.

A consortium of organizations supported by Island Conservation, a small nonprofit organization in California, developed a master collaborative plan that ranked islands by their level of threat and prospects of recovery (Tershy et al. 2002). They then deployed teams of hunters, trappers, and Jack Russell terriers to systematically eradicate one or more invasive mammals from 23 small islands. As a result, 27 seabird taxa, such as the Black-vented Shearwaters on Natividad Island, and 38 endemic terrestrial vertebrates are protected and on the rebound. Lessons learned from these initial experiments enable even more ambitious eradication efforts on large islands.

Many colonial seabirds that nest on islands require social stimulation to breed. Audubon's Steve Kress (1997) pioneered the use of social attraction to bring Atlantic Puffins back to the coast of Maine (Figure 21–14). Harvesting of their eggs and young had extirpated these colonies by the 1880s. Now, Atlantic Puffins are back as nesting species. The formula required transplanting nestlings from Great Island, Newfoundland, and hand-rearing them in specially constructed burrows. Between 1973 and 1986, they successfully fledged 914 puffin chicks from Eastern Egg Rock. Fledged young puffins then wait from two to three years to return to their home island to nest. Prospecting young puffins flew by but did not stop and stay. They prefer not to be the first of their kin to settle down on an empty island. But broadcasts of puffin calls, combined with decoys placed on prominent rocks, tempted young puffins to land and then consort with, even court, the decoys. Real puffins now thrive in robust colonies on many of the islands. Summer communities on the shores of the Gulf of Maine are thrilled to have their puffins back. So are growing numbers of tourists eager to pay for boat rides to see them.

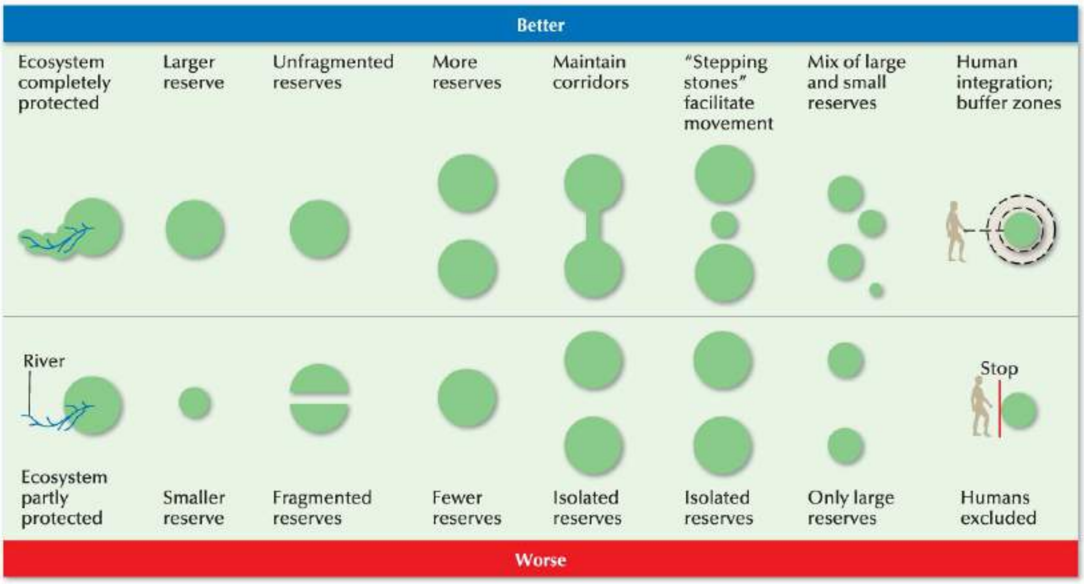
Photo Courtesy of Dr. Stephen W. Kress, Seabird Restoration Program

Figure 21–14 Decoys were the key to attracting sociable Atlantic Puffins back to deserted islands in the Gulf of Maine.

21.5 Conservation by Design

Conservation biology is an essential scientific discipline that sets priorities and then integrates specific objectives into large-scale plans of ecosystem management. These plans address both the integrity of healthy ecosystems and the broad spectrum of plants and animals that will benefit from scientifically smart management. Birds are often the signature species of projects that foster biodiversity as a whole.

With commitments for the protection and restoration of habitat come the significant challenges of designing effective networks of conservation reserves. The basic guidelines for reserve networks in fragmented landscapes are now well established (Figure 21–15). For purposes of bird conservation, the geometry and scale of the design must take into consideration the substantial movements of birds and meet their seasonal requirements. Corridors are an essential part of that geometry to facilitate dispersal among reserves so as to maintain genetic variability and to reduce the probability of extinction due to the small-island effect. Efforts to improve the habitat quality in the matrix surrounding patches are also under way (Karp et al. 2011).



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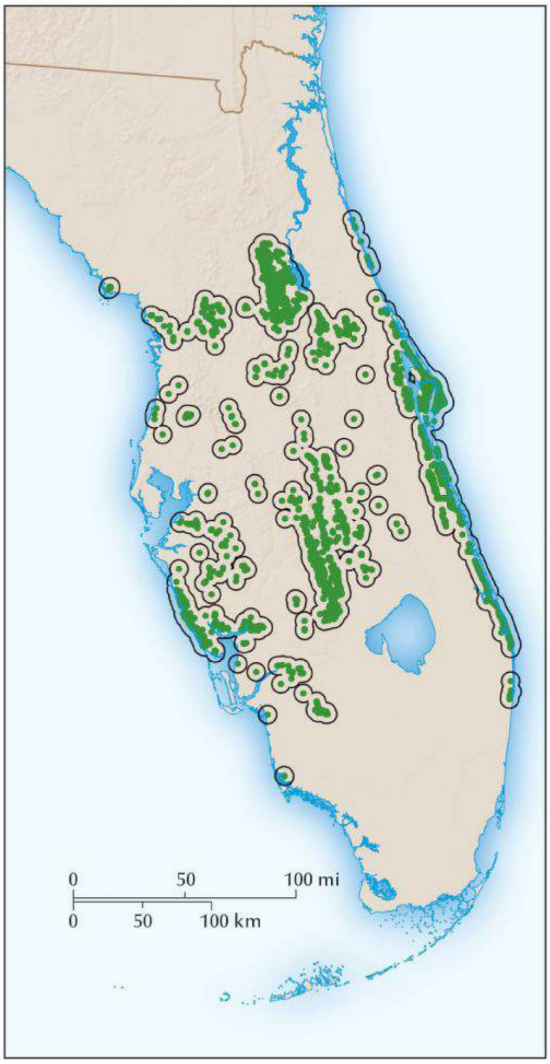
DATA FROM SHAFER 1997, FITZPATRICK 2004

Figure 21–15 Guidelines for designing networks of nature reserves. Attention to their size, shape, and arrangement on the landscape increases their conservation effectiveness.

Looking ahead, we see that global warming challenges the past designs and locations of reserves. Coastal reserves on the Norfolk coasts of Britain, for example, will be under the North Sea in this century because of rising sea levels and the continued downward tilting of the land itself, causing a net loss of freshwater and brackish habitat of about 4,000 hectares (Lee 2001). In response, the Royal Society of Bird Preservation built new marshland preserves inland to restore declining populations of threatened marsh species, such as the Eurasian Bittern. The projected costs of freshwater and brackish habitat replacement will be roughly £50 million to £60 million. Parallel efforts are also under way to locate new reserves in areas where future projected climates will be suitable for species in California and elsewhere (see Figure 20–8).

Population Viability

Populations of plants and animals typically comprise numerous local populations distributed across the landscape in patches, or fragments, of preferred habitat. Dispersal and gene flow between the local populations unites them into so-called **metapopulations** (Figure 21–16). Small, local **“sink” populations** prone to extinction disappear temporarily and then reappear when new colonists arrive from nearby or larger source populations.



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Data from Fitzpatrick 2004

Figure 21–16 Metapopulation map of Florida Scrub Jays. Each green dot indicates one or more family groups of this cooperatively breeding species. Solid outlines group sets of territories into 42 separate metapopulations within which dispersal offsets local extinctions.

Metapopulation structures are an intrinsic property of the Biological Species Concept (see Chapter 19). Understanding them is central also to conservation plans that ensure the viability of populations that occupy fragmented habitats. Two elements are most important: (1) the probability of the extinction of populations of different sizes and (2) maintaining adequate genetic diversity.

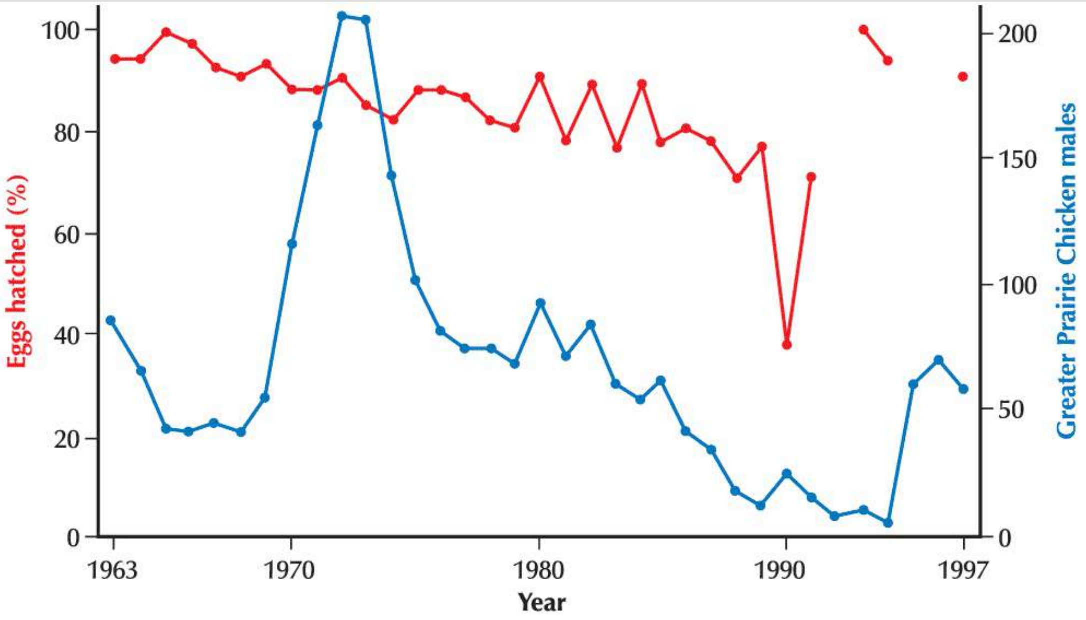
Population viability analysis is a standard tool of conservation planning by which computer models incorporate life-table statistics (age-specific birthrates and death rates; see section 17.1) of the species under study to simulate rates of growth or decline of populations of different sizes through time. The simulated population trend leads to extinction in some runs but not others. These results define their probability of extinction. For example, populations of the Florida Scrub Jay with only a single family group territory are likely to disappear within 50 years, but populations with 100 territories will last for hundreds of years (Fitzpatrick et al. 1991). These analyses can be executed for single populations or, with more assumptions about dispersal, for multiple local populations that represent a metapopulation.

Recovery plans for endangered species incorporate estimates of population size that ensure their long-term viability. The recovery plan for the Black-capped Vireo, which lives in the troubled oak–juniper habitats of Texas, Oklahoma, and Mexico, has the goal of downlisting this species from endangered to threatened (U.S. Fish and Wildlife Service 1991). Four criteria must be fulfilled: (1) all existing populations must be protected and maintained; (2) a minimum of six viable breeding populations of 500 to 1,000 pairs must exist in Texas, Oklahoma, and Mexico; (3) sufficient winter habitat must exist to support the priority breeding populations; and (4) the designated breeding populations must be maintained for at least five consecutive years with evidence of continued viability.

Small fragmented, or remnant, populations lose genetic diversity due to chance and to increased inbreeding. The loss of genetic diversity affects survival and fertility and, hence, the ability of a population in trouble to recover. If natural dispersal does not offset local losses of genetic diversity, conservation biologists can offset these losses themselves by adding birds imported from other populations.

The conservation of the Greater Prairie Chicken in the midwestern United States provides an example of this process. The current distribution of the Greater Prairie Chicken is only a small fraction of its original range throughout the central and much of the eastern United States. In the early nineteenth century, native prairie covered most of Illinois. By 1994, only a few small patches remained in the state. The same was true in Wisconsin. Greater Prairie Chickens and other grassland birds declined along with their prairies. The remnant population of prairie chickens in southeastern Illinois dropped from 2,000 birds in 1962 to fewer than 50 by 1994 (Westemeier et al. 1998). Genetic diversity dropped significantly in both states.

Projections of continued loss of genetic variation suggest that, in 40 years, these prairie chicken populations would reach the reduced genetic diversity of the related Heath Hen 30 years before its extinction on Martha’s Vineyard in 1932 (Johnson and Dunn 2006). In Illinois, egg fertility and hatchability declined significantly along with genetic diversity, a prelude to extinction (Figure 21–17). The good news is that conservation biologists were able to offset these handicaps and to increase egg viability in Illinois by importing prairie chickens from large and genetically diverse populations in other states.



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DATA FROM WESTEMEIER ET AL. 1998

Figure 21–17 Population trends and fertility in a remnant population of Greater Prairie Chickens in southeastern Illinois. Counts of males on the lek (blue line) declined steadily after a short-lived peak in 1972 until extra males were introduced from other larger populations. Genetic diversity and egg-hatching rates (red line) declined in this small shrinking population but then rebounded after birds from other populations were introduced in 1990.

Fragmentation and Corridors

Many human activities—cutting forests for timber, converting grasslands into croplands, and dividing shorelines for buildings—divide major blocks of quality habitat into remnant islands of habitat, or fragments (Figure 21–18). The small sizes and extensive edges of habitat fragments lead to increased predation, limited space, and invasion by exotic species. Reduced nest success and adult survival in fragments, compared with large intact blocks of habitats, are predictable results. Small fragments become unsustainable population sinks, with poor reproductive success and high mortality.

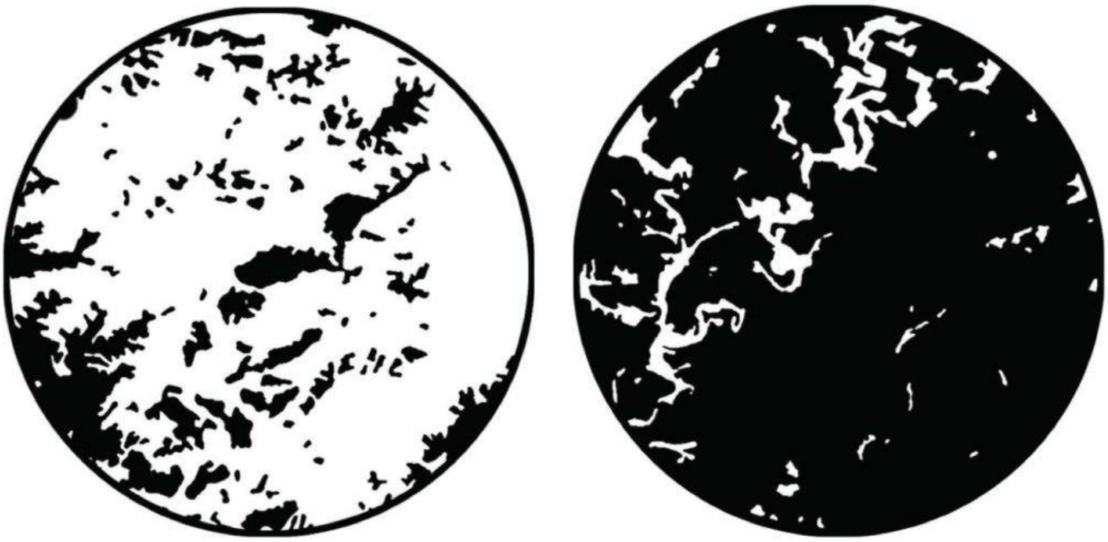

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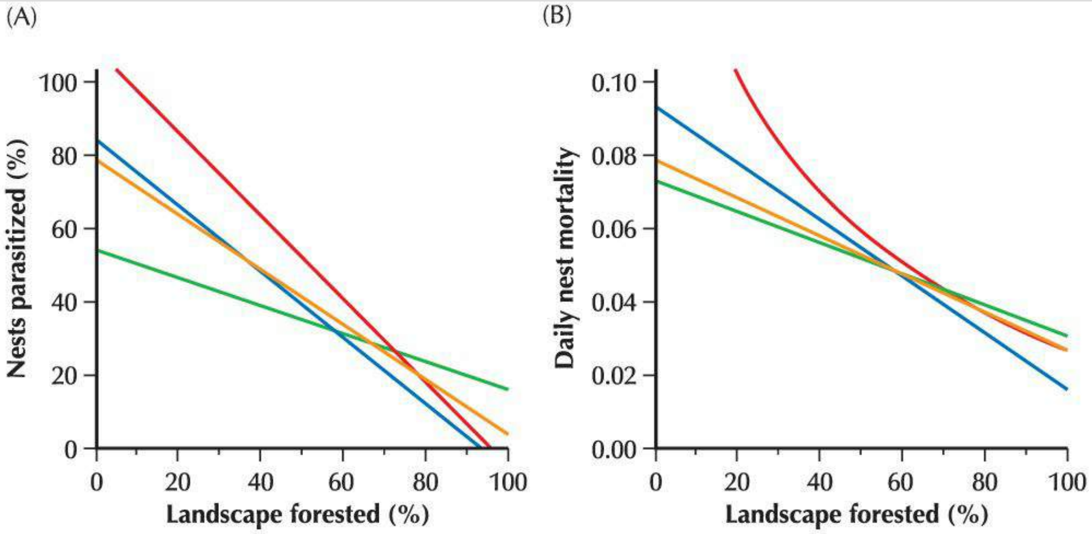
Figure 21–18 Forest fragmentation in Missouri. Computer maps of a nonforested landscape (*left*) and a forested landscape (*right*). Dark areas are forested.

Unfragmented core areas of habitat, therefore, are an essential element of conservation planning. Forest fragmentation in North America, for example, promotes local reproductive failure due to increased nest predation and brood parasitism by Brown-headed Cowbirds (Figure 21–19). The highly fragmented landscapes of northern Missouri, southern Wisconsin, and Illinois are population sinks. Those populations cannot sustain themselves without the immigration of young birds from the extensive source forests of the Missouri Ozarks, northern Wisconsin, and south-central Indiana, respectively. These costs are most severe within 100 to 200 meters of the forest edge (Figure 21–20). The interiors of large blocks, on the other hand, are relatively safe.



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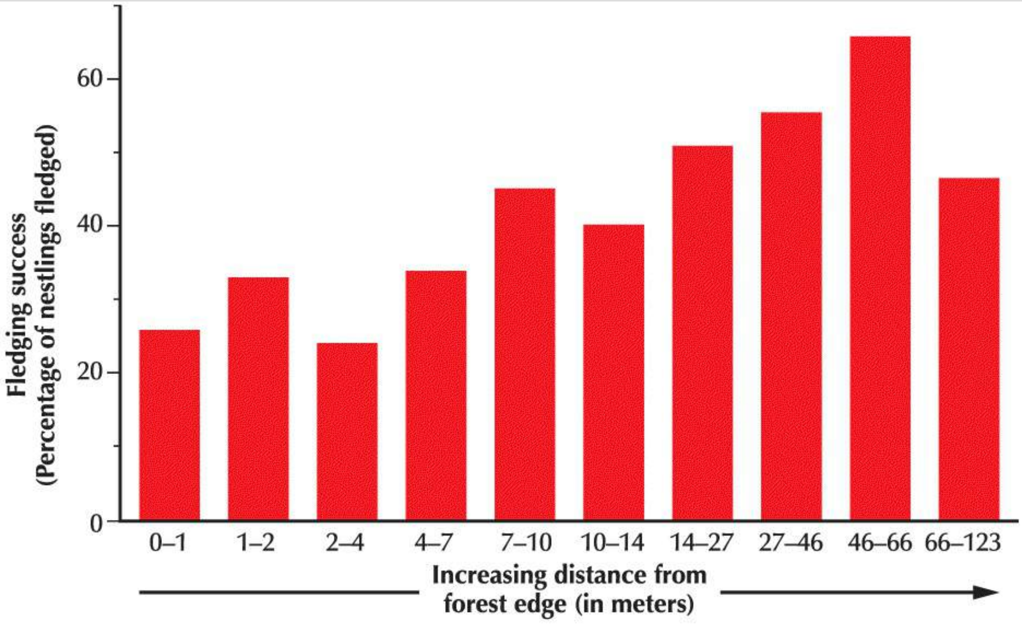
DATA FROM ROBINSON ET AL. 1995

Figure 21–19 Forest cover improves nest success in the midwestern United States, but such cover is diminished in landscapes where forests are fragmented. (A) Correlations of the proportion of nests parasitized by Brown-headed Cowbirds and the percentage of forest cover. (B) Correlations of daily nest mortality and the percentage of forest cover. Species: Indigo Bunting (blue); Worm-eating Warbler (red); Ovenbird (orange); Kentucky Warbler (green).



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DATA FROM WILCOVE ET AL. 1986

Figure 21–20 Songbird nesting success increases with distance (10 categories from 0 to 123 meters) from the forest edge, where nest predation and parasitism (by Brown-headed Cowbirds) is greatest.

Like islands in the ocean, fragments of habitat lose species at predictable rates because of fluctuations in population size and the costs of edge effects. Small fragments lose species faster than large fragments. In southern Brazil, for example, intact subtropical woodlands support about 220 bird species (Willis 1980). Fragmentation of the woodlands for coffee plantations in the past century caused reductions of species to 202 species in a large, isolated woodlot (1,400 hectares), 146 species in a medium-sized woodlot (250 hectares), and only 93 species in a small woodlot (21 hectares). The birds lost from the largest plots were mostly large species found in low densities, such as eagles, macaws, parrots, toucans, and tinamous. The birds most likely to disappear from the small woodlots were primarily large, canopy, fruit-eating birds and large, ground, insect-eating birds.

Recent analyses suggest that the ability to disperse may constrain the capacity of some species to recolonize habitat fragments (Claramunt et al. 2012). Birds with rounded wings, which are not designed for sustained flight, have difficulty crossing gaps between forest patches and do not recolonize deserted patches. Other species with eye physiologies adapted to low light levels may also have difficulty crossing large open areas that separate forest fragments (Dolan and Fernandez-Juricic 2010).

In 1979, Thomas Lovejoy and his colleagues launched a landmark project to document the specific effects of forest fragmentation on tropical biodiversity in the Amazon rain forests near Manaus, Brazil (Bierregaard et al. 1992). In an alliance with the government, farmers left blocks of forest of different sizes and configurations as they cleared the land. Teams of experts then monitored dramatic losses of species from tropical forest islands less than 10 hectares in size. Especially vulnerable were specialized birds that follow army ants to catch flushed prey because the ants themselves disappeared. Three species of obligate army ant followers disappeared immediately on the isolation of small fragments. Also vulnerable were birds that participated regularly in mixed-species foraging flocks. Most of these species disappeared from all small rain-forest fragments in one to two years.

Local landscapes, the teams concluded, should include one or more forest tracts larger than 1,000 hectares. Large source tracts would produce surplus birds to help populate smaller fragments. Corridors between isolated fragments of original habitat, however, are needed as an essential element of conservation planning. Corridors just 100 to 300 meters wide between blocks of forest helped to maintain species diversity in forest fragments as large as 100 hectares in area. Small forest fragments also require connections by corridors of rain forest to facilitate the dispersal of young birds among them.

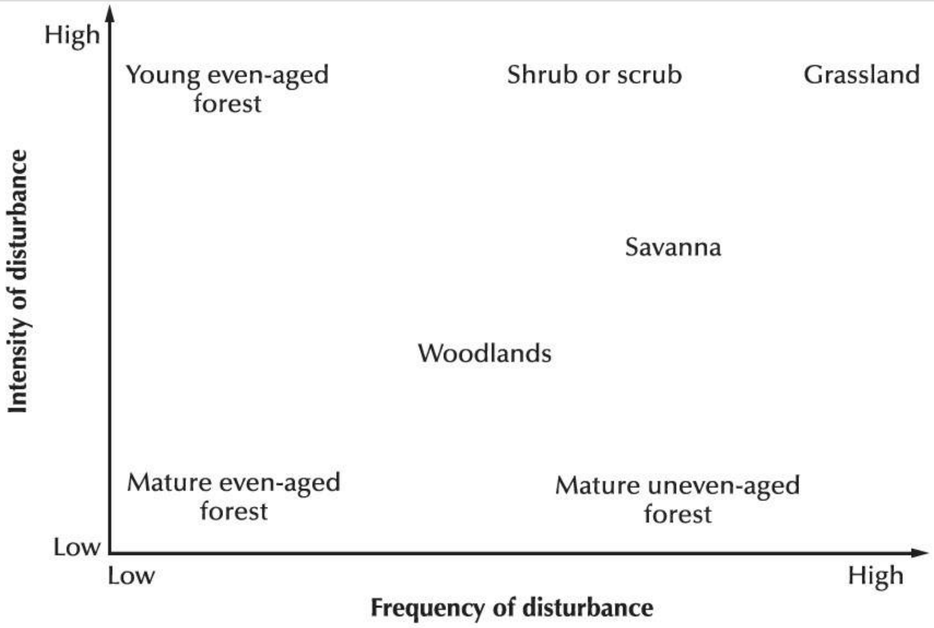
Species of tropical mountain forests require corridors for seasonal altitudinal migration between separated living areas. One of the most dramatic of all tropical birds, the Resplendent Quetzal, a trogon of the cloud forests of Central America, is iridescent green and scarlet in color with lacy, two-foot-long upper tail coverts (Figure 21–21). It feeds and breeds in mountain preserves, such as the popular 28,000-hectare Monteverde Cloud Forest Preserve in Costa Rica. But the quetzals also migrate downslope to find food during the nonbreeding seasons. By tracking the seasonal movements of quetzals wearing radio transmitters, George Powell and his colleagues (1995) discovered that the mountain slopes between 615 and 1,540 meters altitude were critical corridors and nonbreeding residences for the quetzal. The preserve now provides a network of habitats required by the quetzal throughout the year.

Jim Cumming/Getty Images

Figure 21–21 Resplendent Quetzal. Conservation reserves for the quetzal and other mobile species of the cloud forests of Central America must include different sites for different seasons and corridors that connect them.

Disturbance

Many habitats and their birds require regular ecological disturbances, especially by fires or floods, to maintain their vitality (Askins 2000; Brawn et al. 2001). Both the intensity and the frequency of local disturbance govern the character of habitats (Figure 21–22). In particular, the suppression of fires and floods is responsible for losses or declines of bird species in addition to those lost on a broad scale to outright loss of habitat. On a landscape level, healthy ecosystems are those that include a mixture or mosaic of habitats in various stages of recovery from disturbance. Good stewardship of ecosystems, therefore, requires deliberate programs of burning and the flooding of floodplains.



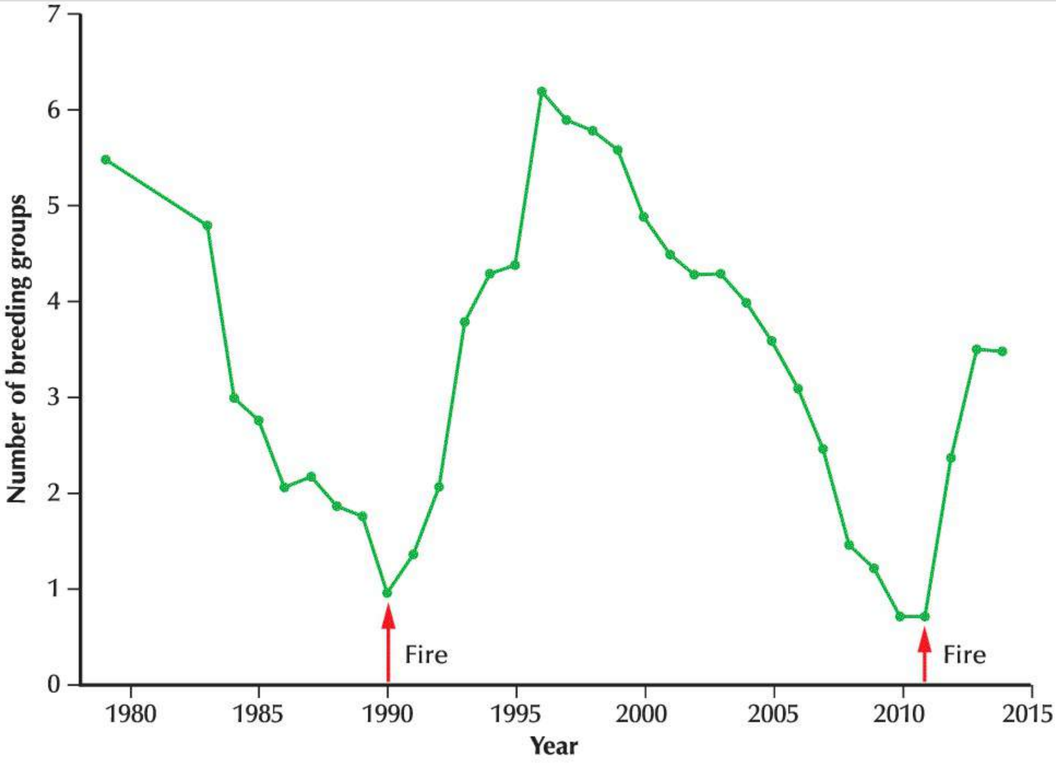
REPUBLISHED WITH PERMISSION OF ANNUAL REVIEWS, FROM JEFFREY D. BRAWN, SCOTT K. ROBINSON, AND FRANK R. THOMPSON III, "THE ROLE OF DISTURBANCE IN THE ECOLOGY AND CONSERVATION OF BIRDS," ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS, 2001, NOVEMBER; 32: 251–276, FIGURE 2. PERMISSION CONVEYED THROUGH COPYRIGHT CLEARANCE CENTER, INC.

Figure 21–22 Intensity versus frequency of disturbance on selected terrestrial habitats. Fire, floods, severe winds, and forestry practices create even-aged forests by promoting growth of replacement saplings over large areas. Frequent fires of light to moderate intensity structure woodlands and savannas. Grazing and frequent, intense fires control the structure and species compositions of grasslands.

Fire

Fire is an essential element in the ecological health of almost all habitats. It naturally affects the plant structure and species compositions of forests, grasslands, and scrublands and thereby what bird species will also be present. California's coastal chaparral, the longleaf pine forests of the southeastern United States, Yellowstone's scenic ponderosa pine forests, and Illinois's remnant prairies all require regular fires to sustain their special suites of species. Before the colonization of the United States by Europeans, regular fires started accidentally by lightning and deliberately by Native Americans swept unchecked across the landscape. One-half of the continental United States burned every one to 12 years (Brawn et al. 2001).

Many bird species also are fire-dependent specialists. Among them, Black-backed Woodpeckers target the wood-boring beetles that flourish in scorched conifer trees from two to three years after fires in the boreal forests of Canada and Alaska. The endangered Kirtland's Warbler specializes in young jack pines that grow after fire releases seeds from mature pines in Michigan. Fire also controls critical longleaf pine habitat for Red-cockaded Woodpeckers and Bachman's Sparrows of the southeastern United States, two species that are endemic to the United States. Florida Scrub Jays also are a fire-dependent species. They survive only in the remnant scrub habitats of the sandy ridges of central Florida, along with other endangered species. They depend on regular fires at eight- to 15-year intervals to refresh territories with optimal habitat (Woolfenden and Fitzpatrick 1996; Figure 21–23).



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DATA FROM FITZPATRICK AND BOWMAN 2016

Figure 21–23 Beneficial effects of fire on habitat use by Florida Scrub Jays. The quality of the habitat and the number of territories in the 55-hectare study site declined from 1980 to 1991 as the scrub habitat grew in the absence of fire. A prescribed burn in 1991 promoted increased occupancy through 1997. A second prescribed burn in 2010 replicated the population cycle.

Specifically, active fire suppression from 1980 to 1990 caused the number of territories on a 55-hectare (136-acre) study plot to decline from more than five to just one. Competition from Blue Jays and predation by hawks and snakes increase in the absence of fire. To improve the quality of the habitat, the station's staff burned the study plot in a carefully controlled "prescribed burn" in 1991. Scrub jays returned to the plot, reestablishing more than six territories by 1997. Repeating the cycle, they then started to decline, awaiting the next burn.

Grassland birds most of all respond to different regimes of prescribed burns to replace the lightning-sparked natural fires that once governed grassland ecology. Local populations of Henslow’s Sparrows in the midwestern states prefer postburn grasslands two to four years of age (Herkert and Glass 1999; Figure 21–24). Such burns allow the development of thick protective ground cover for the nests as well as the growth of small flowering plants (forbs) that enhance the diversity of insect prey. More generally, regular burns of grasslands favor a variety of native grass species and thwart the growth of woody plant species that start to prevail through natural succession if left unchecked.

In addition to disturbance by fire, grasslands are subject to disturbance by grazing—originally by great herds of buffalo, antelope, or elk and now, mostly, by domestic livestock. Overgrazing, especially on leased government lands, converts rich grasslands into deserts. Savvy ranchers, however, guard the health of grasslands and the sustainability of their ranges by rotating their livestock. A variety of widespread birds, including Horned Larks and Lark Buntings, as well as specialized local birds, such as Montezuma Quail in Arizona, benefit from moderate grazing regimes.

NATURE PHOTOGRAPHERS LTD/ALAMY

Figure 21–24 Henslow’s Sparrows require fire regrowth grasslands.

Floods

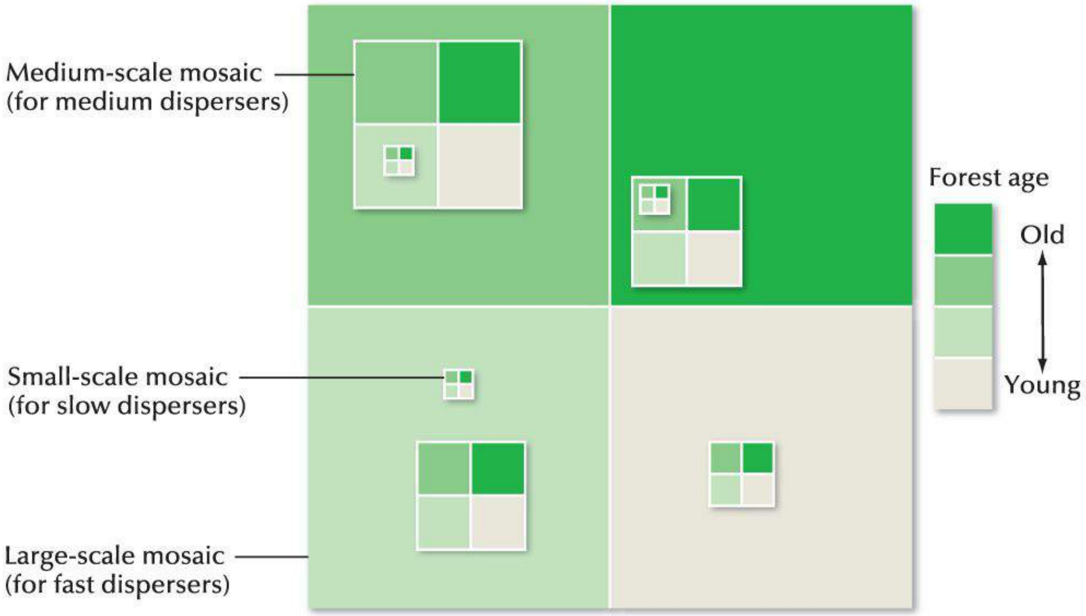
The flooding of bottomlands along rivers is an essential source of disturbance (Brawn et al. 2001). Historically, seasonal flooding, sometimes severe and sometimes not, created backwater lakes and habitats, replenished vital nutrients, and reset the initial stages of plant succession on new soils. Now, however, floodplain habitats are under severe threat due to the “protection” from normal flood regimes by dams, channels, and levees and other changes, such as excessive siltation.

Changes in flooding disturbance affect the riparian forests of southwestern North America and the large river systems of central North America. The floodplain forests of the Southeast once supported species such as Carolina Parakeets (extinct), Bachman’s Warblers (extinct?), Swainson’s Warblers (declining), and the Ivory-billed Woodpecker. The Amazon and Orinocan river systems of South America still undergo major cycles of disturbance by flooding. Many little-known bird species, such as the Black-and-white Antbird and the White-bellied Spinetail, benefit from these cycles. They inhabit only the early-succession-stage vegetation on ever-changing sandbars and river islands (Ridgely and Tudor 1994). Nesting populations of some endangered species, such as the Interior Least Tern and the Piping Plover, have largely disappeared because flood control caused the bare sandy beaches where they breed to become overgrown by woody vegetation. Allowing the spring flood pulse in recent years increased their populations by scouring the beaches clean of vegetation (Sidle et al. 1992).

Forestry

Timber harvests vary from clear-cuttings to highly selective logging and from uneven-aged to even-aged methods of tree removal. The sizes, distributions, and characters of the resulting timber harvests lead to landscape-scale mosaics of disturbed and successional habitats. These mosaics can be managed to ensure the sustained presence of disturbed forests of different ages, albeit at different locations, in the mosaic.

Shifting forest mosaic designs accommodate the needs of species with different habitat preferences and different dispersal tendencies, supporting diverse bird communities that use them dynamically (Brawn et al. 2001; Figure 21–25). Some species, such as Winter Wrens, Eastern Bluebirds, and Northern Flickers, quickly colonize cutover regeneration stands. They use open slash piles, herbaceous undergrowth, or residual snags. Within two to three years, additional species, such as Mourning Warblers, Common Yellowthroats, and Swainson’s Thrushes, start using the regrowth saplings. About half of the Neotropical migratory bird species that breed in the hardwood forests of the central United States prefer early succession stands of harvest regrowth. Well-designed forest regeneration mosaics can thus support high diversities of bird species that include clear-cut colonists and mature forest residents.



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From: Hagan, J.M. 1996. The Shifting Mosaic Model: an ecological approach to private industrial forest management. Unpublished report. Manomet Observatory, Manomet, MA.

Figure 21–25 The shifting forest mosaic model. Forestry cutting of trees creates a variety of successional stages in the landscape. Different shades denote four stages of forest age from young to old. The stages “move around” over time as the forest grows and is cut in different years. Ideally, a full complement of plant and animal species adapted to a particular stage will colonize each stage. Different dispersal and colonization abilities enable some species to keep up and leave others behind. The inclusion of different-sized shifting mosaics in the landscape ensures the continued presence of fast dispersers, such as birds, and slow dispersers, such as some plants. Small-scale mosaics should be embedded within large-scale mosaics to accommodate different kinds of dispersers and to maintain large blocks of adequate habitat.

Forest management plans that protect old-growth forests are extremely important and also controversial. Intense logging in the twentieth century reduced the old-growth forests in the Pacific Northwest to about 10 percent of their original extent. The environmentalists were eager to protect the remnant of what remained,

MICHAEL SEWELL VLSUAL PURSUIT/GETTY IMAGES

Figure 21–26 The Spotted Owl, a threatened species that came to symbolize old-growth forests of the Pacific Northwest and that are reduced to less than 10 percent of their original extent.

and the loggers were eager to continue harvesting timber as the main source of their livelihoods. One species in particular—the Spotted Owl (Figure 21–26)—occupied the center of the controversy as the symbol of the endangered old-growth forest ecosystem and its biodiversity, including an endangered seabird—the Marbled Murrelet (Box 21–4). Conservation research on the biology of Spotted Owls ultimately improved land-use policy generally in the United States (Noon and Franklin 2002).

Box 21–4

A Seabird of the Old-Growth Forest

Few birds have been as mysterious and have eluded study for as long as the quail-sized Marbled Murrelet, a declining and threatened species. The murrelet was the last North American species to have its nest discovered. By accident, a tree surgeon named Hoyt Foster discovered a moss nest containing one downy young murrelet 45 meters off the ground in a tall Douglas fir 16 kilometers from the ocean in California's Santa Cruz Mountains. These small seabirds, it turns out, fly inland to nest in tall, old-growth forest. Like the Spotted Owl, they depend on the disappearing old-growth forests of the Pacific Northwest (Nelson 1997).

The dependence of Marbled Murrelets on the old-growth forests from northern California to Alaska adds an extra threat to their future because they are also highly vulnerable to coastal oil spills and to drowning in underwater fishing nets.

The Spotted Owl's typical habitat in the Pacific Northwest consists of low- to middle-elevation old-growth forests dominated by Douglas fir trees. These forests include large trees that are more than 200 years old, plus an abundance of dead trees and branches. The owls' preference for old-growth forests relates to the availability of large, old dead trees for nesting; the availability of small mammalian prey, especially flying squirrels; and protection from predators. Each pair requires from 500 to 2,000 hectares of mature forest, depending on location. Among the challenges facing these owls, the fragmentation of continuous stretches of old-growth forest increases competition from larger and more aggressive Barred Owls that thrive in adjacent regrowth areas. Fragmentation also increases predation by Great Horned Owls, which frequent the forest edges and openings created by logging.

Required by law to ensure viable populations of all native vertebrate species in the national forests, the U.S. Forest Service developed guidelines for the management of the Spotted Owl in consultation with a blue-ribbon advisory panel of ornithologists convened by the National Audubon Society. They recommended protection of a minimum of 1,500 breeding pairs by setting aside habitat areas with 2,100 hectares each in Washington, 1,100 hectares each in Oregon and northern California, and 650 hectares in the Sierra Nevada (Dawson et al. 1986).

The Spotted Owl was listed as threatened in 1990, and a draft recovery plan was published in 1992. The Northwest Forest Plan of 1994 became the cornerstone for conserving and recovering the Spotted Owl on 24.4 million acres of federal land. Ongoing analyses of the viability of the scattered populations of the Spotted Owl confirm the original projections of their declines and sensitivity to habitat quality. These analyses also suggest that the declines of some populations are accelerating because of decreased adult survival. Larger blocks of forest than originally projected may be needed to stop the declines.

Huge logging programs challenge conservation efforts in southeastern Asia (Wilcove et al. 2013). Repeated logging of the Dipterocarp forests there has reduced avian community diversity. Yet, even twice-logged forests retain large proportions of their original bird communities and are far more diverse than in the surrounding agricultural matrix. This distinction is important—heavily logged forests have been targeted for conversion to oil palm plantations, a habitat of almost no value to birds. It is far better to retain even heavily logged forests rather than allow them to be converted to intensive agriculture.

Hot Spots and Important Bird Areas

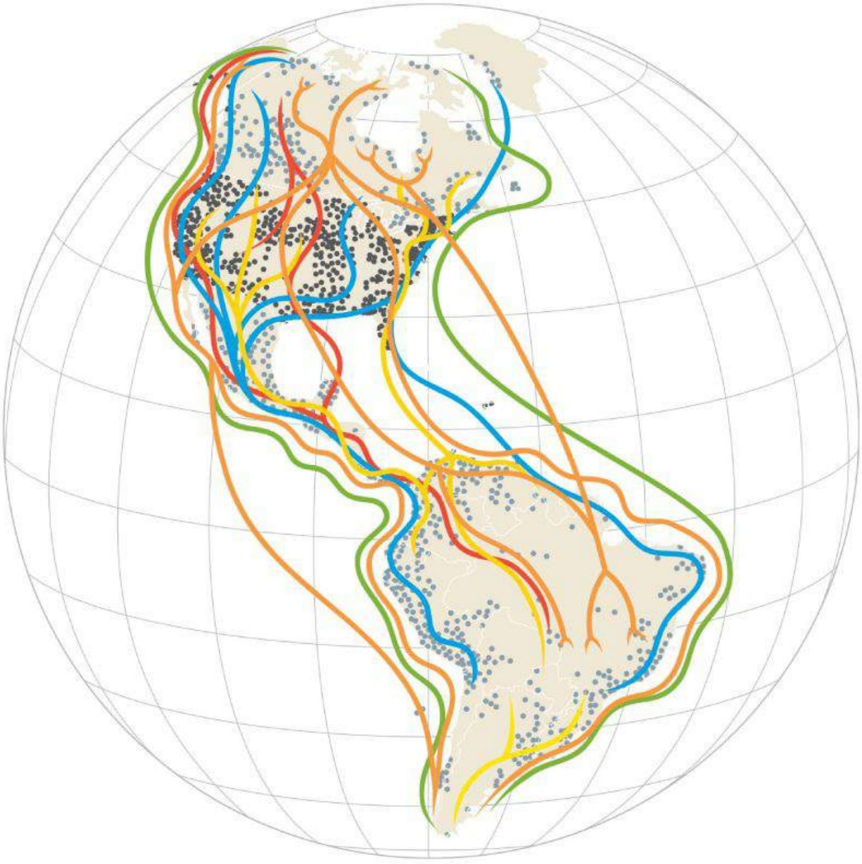
Setting priorities is an essential first step in the process of conservation by design. Limited resources must be directed wisely to conservation programs at the highest-priority places among the many places that are under threat and for the species that are declining.

To focus conservation resources on places of greatest need, conservation biologists identified “hot spots” of biodiversity. **Hot spots** are those places under threat in the world that have the greatest concentrations of biodiversity, defined by the largest total number of species, the most threatened and endangered species, and the most endemic species. The initial selection of hot spots was based on measures of the richness of plant species, but birds also stand out as one of the best indicators of biodiversity and ecosystem health. In the broad spectrum of biodiversity, birds are the most visible and accessible indicators of the interconnectedness of life on Earth.

By using computerized maps of the geographical distributions of all extant bird species, David Orme and his colleagues (2005) identified the places that host the greatest bird diversity on the basis of the same three principal criteria. The tropical Andes of South America topped the list of avian hot spot regions by all three criteria. Important in regard to species richness were other parts of South America (Amazon Basin, Atlantic Coastal Forest, and Guyana highlands), the Himalayas, and the Rift Valley of Africa. Regions with high numbers of threatened species also included the Philippines, Indonesia, New Zealand, and Madagascar. New Guinea ranked high among the regions with lots of endemic species.

Responding to the challenge of protecting global diversity, the partnership alliance of Birdlife International created the **Important Bird Areas (IBA)** program. The IBA program is now the global paradigm for site-based conservation using the power of birds. It sets conservation priorities and provides a unified framework for national bird conservation initiatives. The goal is to protect a vast, well-designed, worldwide network of sites that stabilize bird populations and their essential ecosystems. Realizing their full potential, IBAs will keep common birds common, stop and reverse current declines, and prevent the extinction of our most imperiled bird species.

The IBA network includes protected public lands, such as federal wildlife refuges, as well as private and local community lands important for birds. The network features sites in the tropical Andes that harbor the most endangered forest species, wetland sites that are critical to stopover during seasonal migrations of shorebirds, including Western Hemisphere Shorebird Reserve Network sites (see Chapter 10) and the major wintering grounds of Arctic waterfowl. BirdLife partners have identified and documented over 12,000 IBAs in 200 countries and territories worldwide. This global network will likely comprise around 15,000 IBAs covering some 10 million square kilometers (7 percent of the world's land surface) under the supervision and conservation stewardship of nearby local communities (Figure 21–27).



Audubon Annual Report 2017, National Audubon Society

Figure 21–27 Important Bird Areas and flyways in the Western Hemisphere.

The future of IBAs as primary conservation sites depends partly on the local management and restoration of quality habitat and on the abatement of major threats to those habitats. The future wildlife value of IBAs also depends on the care of the larger landscape of which they are a part. Most IBAs are surrounded by working lands of agriculture, high-impact human activities, or urban development. What home owners do in their own backyards affects the quality of watersheds, flooding regimes, pollution, and frequency of predation by pets. The entire matrix of human activities thus governs the future value of sites in the network and of the network as a whole. Conversely, IBAs add value to the communities as recreational spaces for families and as magnets for ecotourism that brings revenue to the community.

Public Support

Public and community support of conservation programs is an essential ingredient for their success. Therefore, conservation initiatives must incorporate economic and social variables as well as tenets of landscape ecology.

Local pride is key to getting public support. It can convert a community into an effective conservation force in just one year. The conservation organization RARE uses the power of local pride creatively to integrate conservation into the cultural, economic, and political aspects of community life. One of its initial programs in the Caribbean demonstrated the power of fully engaging public participation on behalf of an endangered parrot, the St. Lucia Amazon, known locally as the Jacquot (see Figure 21–2A). The Jacquot population declined to a precariously small size as a result of being hunted for food and captured for the pet trade. Its mountain forests had been cut for firewood and for farming. RARE’s conservation blitz heightened awareness everywhere, with special attention given to schoolchildren who educated their parents (Nielsen 1993). The parrot’s colorful image appeared on billboards, bumper stickers, T-shirts, and St. Lucia passports. A lively combination of classroom visits (featuring a person dressed up like a parrot), reggae songs, music videos, church sermons, and puppet shows made saving the Jacquot a cause célèbre with all age-groups on the island. As a result, the parrot not only stopped its slide toward extinction but also nearly doubled its population to about 350 birds. Now the island’s national bird and center of pride, the Jacquot is increasing in numbers. As the island’s conservation spokesman, the Jacquot exhorts fellow St. Lucians to save the island’s forests, keep the water clean, and protect their island’s coral reefs.

21.6 The Conservation Movement

The roots of conservation initiatives in North America, as well as in other parts of the world, go deep into past practices of uncontrolled exploitation of the eighteenth and nineteenth centuries, outlined earlier in this chapter. Public opposition to the killing and exploitation of native birds in the nineteenth century was inevitable and then prevailed.

Leading the initial battles for bird conservation were several amazing women in Massachusetts. Fannie Hardy and Florence Merriam founded the first Audubon Society in 1887 at Smith College to rid the campus of feathered finery. A few years later, in 1896, Harriet Hemenway founded the Massachusetts Audubon Society with the mission of discouraging ornamental uses of wild bird feathers and protecting birds. From their first acts, the bird conservation movement grew steadily, led by more women.

Hawk Mountain

Rosalie Edge was a pioneer conservationist who believed that the time to save a species is while it is still common. In 1934, she challenged local traditions of shooting “bad” hawks for fun. Her private initiative at Hawk Mountain in southeastern Pennsylvania started the sport of hawk watching as an alternative to hawk shooting and created a model for the monitoring and conservation of migratory hawks and eagles worldwide (Bildstein et al. 1993).

On their way south in the fall, migrating hawks hug the tops of mountain ridges, riding favorable, rising air currents. They pass key sites in great numbers on days of favorable winds that deliver living targets to shooters. The annual toll—tens of thousands of Sharp-shinned Hawks and other species—was staggering. Determined to stop the shooting, Rosalie Edge raised the money to buy 567 hectares (1,400 acres) on Hawk Mountain (Figure 21–28). She installed a brave young naturalist warden, Maurice Broun, to protect the hawks and to share his recognition of raptors as beneficial rather than harmful members of natural ecosystems. Since its founding, the Hawk Mountain Sanctuary Association has played a key role in protecting North America’s raptors and their essential habitats by developing grassroots support for state and national legislation. Each year, over 70,000 visitors come to view the inspiring passage of hawks and eagles and leave Hawk Mountain with a greater commitment to conservation. Now, there is a continent-wide network of hawk watching and monitoring sites: Cape May, New Jersey; Duluth, Minnesota; and Vera Cruz, Mexico, complemented by others in Spain, Taiwan, Thailand, and many more.

Courtesy of Hawk Mountain Sanctuary Association

Figure 21–28 The lookout at Hawk Mountain near Reading, Pennsylvania.

Momentum

A series of environmental crises—fatal air-pollution events, rivers afire with debris and chemicals, birds dying of pesticides on lawns—and a powerful book by Rachel Carson—*Silent Spring* (1962)—awoke the country and launched the modern environmental movement. President Nixon's administration (1969–1974) accomplished more significant environmental legislation than any before or since, with the possible exception of Theodore Roosevelt (1901–1909).

The restoration of the declining waterfowl populations led modern government bird conservation initiatives. Faced with continuing wetland destruction and accompanying declines in waterfowl populations, the governments of the United States, Canada, and Mexico initiated new, intense efforts to protect wetlands and associated wildlife in 1986. Participants in the North American Waterfowl

Management Plan (NAWMP) vowed to protect millions of acres of important wetlands. The conceptual foundations of the NAWMP gave rise to two new remarkable initiatives in the 1990s: Partners in Flight, followed by the North American Bird Conservation Initiative. This coalition of government agencies, corporate leaders, nonprofit conservation groups, and academic professionals focused first on the growing plight of Neotropical migrant bird species, with the rallying cries “Keep common birds common” and “Birds are just like ducks.” It set priorities on action plans through consensus and mobilized new resources—federal, state, and private dollars—to protect bird populations throughout North America.

Bird conservation grew to be a local, national, and international priority as nonprofit organizations, national and local, complemented government initiatives. Local communities formed to coordinate and focus public concern about their birds. In North America, more than 1,000 independent bird clubs, bird observatories, professional coalitions, and Audubon chapters look out for the welfare of birds. They maintain sanctuaries, restore habitat, and advocate on behalf of birds. Each organization has its own proud stories of accomplishment. Uniting national bird conservation organizations worldwide in the common cause, the BirdLife International coalition of country partners spearheads the conservation of globally endangered and threatened bird species.

Birding and Citizen Science

Citizen science is research done by people from every level of society in collaboration with scientists; through direct participation, it fosters a deeper understanding, appreciation, and sense of stewardship for the natural world. By empowering voters and decision makers with science-based information, citizen science is central to the maintenance of a sustainable society and a healthy environment (Irwin 1995). The average citizen tends to take ownership of what he or she counts and then to act on their behalf (Flicker 2002).

Ever-increasing numbers of birders participate in citizen science projects and thereby in the local conservation of the birds that they count. Citizen science birding started with the efforts of Frank Chapman. When he was not censusing birds on women's hats in New York City, Chapman promoted winter bird-watching in the form of bird counts during the Christmas holidays to replace the traditional end-of-the-year bird-shooting parties. The Christmas Bird Count of the National Audubon Society is the largest and oldest citizen science project in the world (see section 18.6). It fostered the founding and growth of more than 1,000 bird clubs and Audubon chapters throughout the United States and Canada. It continues to expand throughout Central and South America. Armies of volunteers also monitor their local bird populations as indicators of environmental health through a growing array of substantial projects, including the Breeding Bird Survey and eBird.

The growth of public interest in birds has been extraordinary. It powers the modern conservation movement in many respects. Birding engages tens of millions of citizens (La Rouche 2001). The average birder is well educated, earns an income above the national average, and belongs to at least three conservation or birding organizations. On the basis of 15,300 interviews, the national survey estimates that 46 million U.S. citizens, 16 years of age or older, are birders. This projection defines birders as people who "closely observed or tried to identify birds around the home and/or took a trip a mile or more from home for the primary purpose of observing birds." Responsible birders observe a code of ethics for behavior that is good for both the birds that they watch and the places that host them (Box 21–5).

Box 21–5

Birding Ethics: American Birding Association

Everyone who enjoys birds and birding must always respect wildlife, its environment, and the rights of others. In any conflict of interest between birds and birders, the welfare of the birds and their environment comes first.

1. **Promote the welfare of birds and their environment.**
    - To avoid stressing birds or exposing them to danger, exercise restraint and caution during observation, photography, sound recording, or filming.
    - Limit the use of recordings and other methods of attracting birds and never use such methods in heavily birded areas or for attracting any species that is threatened, endangered, of special concern, or rare in your local area.
    - Keep well back from nests and nesting colonies, roosts, display areas, and important feeding sites.
    - Stay on roads, trails, and paths where they exist; otherwise, keep habitat disturbance to a minimum.
2. **Respect the law and the rights of others.**

  - Do not enter private property without the owner’s explicit permission.
  - Follow all laws, rules, and regulations governing use of roads and public areas, both at home and abroad.

3. **Ensure that feeders, nest structures, and other artificial bird environments are safe.**

  - Keep dispensers, water, and food clean and free of decay or disease. It is important to feed birds continually during harsh weather.
  - Maintain and clean nest boxes regularly.
  - If you are attracting birds to an area, ensure that the birds are not exposed to predation from cats and other domestic animals or to dangers posed by artificial hazards.

4. **Group birding, whether organized or impromptu, requires special care.**

  - Respect the interests, rights, and skills of fellow birders as well as those of people participating in other legitimate outdoor activities.
  - Freely share your knowledge and experiences. Be especially helpful to beginning birders.
  - If you witness unethical birding behavior, assess the situation and intervene if you think it prudent.
  - Please follow this code—distribute it and teach it to others.

Birding is an economic force for local communities and governments as well as for conservation. In Britain, the presence of a nearby bird reserve maintained by the Royal Society for the Protection of Birds substantially improves the economies of small rural towns by increasing sales of gas, beer, and pub lunches. In the United States, birders and other wildlife watchers spend an estimated $26 billion on binoculars, bird food, camping equipment, and related items and about $15 billion on travel (Carver 2013). These expenses leverage billions of dollars in overall economic output and in state and federal income taxes.

Wild America, A Closing Perspective

American bird-watching icon Roger Tory Peterson took British ornithologist James Fisher on an epic journey and survey of the birds across North America in 1953. Fisher saw North America for the first time and concluded their story of this journey in their book *Wild America* (Peterson and Fisher 1955) with the quote posted at the beginning of this chapter. Fifty years later, Scott Weidensaul took a second look and observed,

> I found the continent changed—for the better in some places, for the worse in others. Yet the land, the rugged heart of natural America, retains an essential timelessness. . . . Ours is still, at its core, a wild country. [Weidensaul 2005, p. xx]

Our knowledge of birds and our appreciation of them can ensure their future and "the rugged heart" of the planet. That has been the theme of this book. Each of us can make a difference. Please start now.

REVIEW KEY CONCEPTS

21.1 The State of Birds

More than 10 percent of the world’s bird species are either endangered or vulnerable. In the United States alone, about half of bird species are declining, some steeply. Species that adapt well to man-made environments are increasing.

Key Term: Red List

21.2 Threats

Rapid destruction of natural habitats worldwide, ranging from the tropical rain forests to grasslands, is the primary threat to the future of world bird species. Excessive exploitation and nesting failures caused by pesticides or introduced predators were primary causes of historical extinctions. Continuing and emerging threats include the commercial pet-bird trade, new diseases, and new forms of chemical pollution of the environment.

Key Terms: xenobiotics, ecophobia

21.3 Past Excesses

Wholesale slaughter of wild birds accompanied the expansions of human civilizations, especially the past 10,000 years. Island avifaunas especially were devastated. They account for over 90 percent of the known historical extinctions. Abundant birds, both flighted and flightless, were easy sources of meat that sustained local colonists, explorations of new lands, and the urban markets of Western societies.

Vast numbers of birds with fancy plumages were also taken to adorn fashionable head wear and to be decorative cage birds.

21.4 Hope

The goal of bird conservation is to stop declines and to prevent further extinctions. Attention to the habitat needs of birds also benefits a wide range of other species as well as the health of ecosystems on which modern societies depend. Conservation successes inspire hope and confidence that we can reverse negative trends. Determined restoration of populations on the brink demonstrate our ability to prevent extinctions. Bird populations respond spectacularly to the eradication of introduced mammals from islands and to the restoration of new grassland habitats.

Key Term: hacking

21.5 Conservation by Design

With the commitment to set aside critical habitat for endangered species comes the challenge of designing these reserves. Conservation design includes the geometry of reserve shapes and sizes and their arrangement on the landscape, including connections by corridors. Population viability analyses include attention to the dynamics of local populations within larger metapopulations. Conservation plans must incorporate or replace natural forms of disturbance, including fires, floods, and blocks of successional-stage forest that suit the dispersal behavior of both plants and animals.

Key Terms: conservation biology, metapopulations, “sink” populations, population viability analysis, hot spots, Important Bird

Areas (IBA)

21.6 The Conservation Movement

At first championed by local activists over a century ago, science-based bird conservation programs are hemispheric and global in scale. Ambitious partnerships of government agencies, nonprofit organizations, and universities make possible programs such as BirdLife International's global Important Bird Areas (IBA) program. The IBA network identifies and protects over 12,000 sites worldwide that are critical to the future of threatened birds.

The economic value of bird-watchers as ecotourists and the cultivation of local pride are powerful forces behind successful conservation projects. In addition to public concern, the key ingredients for the success of bird conservation programs worldwide are sound ornithological knowledge of a species' biology and the political will to help species prosper.

APPLY YOUR KNOWLEDGE

1. Human colonization has greatly reduced biodiversity and increased the rate of extinction, with island bird populations being extremely sensitive to human impact. What factors have made island bird populations susceptible to human colonization?
2. Consider the following habitats: prairie grassland, riparian woodland, chaparral, coastal wetlands, and open ocean. Describe the principal human-caused threat(s) to birds that use the resources of these areas.

3. Describe how fragmentation of habitats reduces biodiversity and how corridors help to sustain biodiversity.
4. How have biodiversity “hot spots” and “important bird areas” been defined? Where are they?
5. What aspects of bird biology make them ideal indicators of ecosystem health?
6. How did women’s fashion spawn an important bird conservation society?
7. What characteristics of amateur “birders” make them ideal citizen scientists?
8. Your local conservation group is charged with the protection of a small woodland bird in a forested area scheduled to be forested. Describe how you would gain public support and fund your protection plan by answering the following three questions:
   a. What activities would you initiate to educate the public and to gain support for protecting this bird?
   b. What activities would you employ on a local scale to raise money to support your endeavors?
   c. What are the characteristics of the protection plan you would attempt to negotiate with the forester?

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ABOUT THE COVER

Keel-billed Toucans (*Ramphastos sulphuratus*) live in lowland tropical forests, riparian forests, and second-growth woodlands from southern Mexico to northern Colombia and northwestern Venezuela. Males and females have the same bright colors, which are produced by a mixture of pigmentary (black, yellow, and red) and structural (blue and green) coloration mechanisms. Keel-billed Toucans eat mostly fruits, but also prey on arthropods and small vertebrates, including the eggs and nestlings of other birds. They grasp food items in the tips of their long bills, toss them up with a quick flick of the head, and swallow them whole.

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