Grzimek's
Animal Life Encyclopedia

Second Edition

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Volume 14
Mammals III

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AZA

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Grzimek's Animal Life Encyclopedia, Second Edition
Volume 14: Mammals III

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Foreword

Earth is teeming with life. No one knows exactly how many distinct organisms inhabit our planet, but more than 5 million different species of animals and plants could exist, ranging from microscopic algae and bacteria to gigantic elephants, redwood trees and blue whales. Yet, throughout this wonderful tapestry of living creatures, there runs a single thread: Deoxyribonucleic acid or DNA. The existence of DNA, an elegant, twisted organic molecule that is the building block of all life, is perhaps the best evidence that all living organisms on this planet share a common ancestry. Our ancient connection to the living world may drive our curiosity, and perhaps also explain our seemingly insatiable desire for information about animals and nature. Noted zoologist, E. O. Wilson, recently coined the term "biophilia" to describe this phenomenon. The term is derived from the Greek *bios* meaning "life" and *philos* meaning "love." Wilson argues that we are human because of our innate affinity to and interest in the other organisms with which we share our planet. They are, as he says, "the matrix in which the human mind originated and is permanently rooted." To put it simply and metaphorically, our love for nature flows in our blood and is deeply engrained in both our psyche and cultural traditions.

Our own personal awakenings to the natural world are as diverse as humanity itself. I spent my early childhood in rural Iowa where nature was an integral part of my life. My father and I spent many hours collecting, identifying and studying local insects, amphibians and reptiles. These experiences had a significant impact on my early intellectual and even spiritual development. One event I can recall most vividly. I had collected a cocoon in a field near my home in early spring. The large, silky capsule was attached to a stick. I brought the cocoon back to my room and placed it in a jar on top of my dresser. I remember waking one morning and, there, perched on the tip of the stick was a large moth, slowly moving its delicate, light green wings in the early morning sunlight. It took my breath away. To my inexperienced eyes, it was one of the most beautiful things I had ever seen. I knew it was a moth, but did not know which species. Upon closer examination, I noticed two moon-like markings on the wings and also noted that the wings had long "tails", much like the ubiquitous tiger swallow-tail butterflies that visited the lilac bush in our backyard. Not wanting to suffer my ignorance any longer, I reached immediately for my *Golden Guide to North American Insects* and searched through the section on moths and butterflies. It was a luna moth! My heart was pounding with the excitement of new knowledge as I ran to share the discovery with my parents.

I consider myself very fortunate to have made a living as a professional biologist and conservationist for the past 20 years. I've traveled to over 30 countries and six continents to study and photograph wildlife or to attend related conferences and meetings. Yet, each time I encounter a new and unusual animal or habitat my heart still races with the same excitement of my youth. If this is biophilia, then I certainly possess it, and it is my hope that others will experience it too. I am therefore extremely proud to have served as the series editor for the Gale Group's rewrite of *Grzimek's Animal Life Encyclopedia*, one of the best known and widely used reference works on the animal world. *Grzimek's* is a celebration of animals, a snapshot of our current knowledge of the Earth's incredible range of biological diversity. Although many other animal encyclopedias exist, *Grzimek's Animal Life Encyclopedia* remains unparalleled in its size and in the breadth of topics and organisms it covers.

The revision of these volumes could not come at a more opportune time. In fact, there is a desperate need for a deeper understanding and appreciation of our natural world. Many species are classified as threatened or endangered, and the situation is expected to get much worse before it gets better. Species extinction has always been part of the evolutionary history of life; some organisms adapt to changing circumstances and some do not. However, the current rate of species loss is now estimated to be 1,000–10,000 times the normal "background" rate of extinction since life began on Earth some 4 billion years ago. The primary factor responsible for this decline in biological diversity is the exponential growth of human populations, combined with peoples' unsustainable appetite for natural resources, such as land, water, minerals, oil, and timber. The world's human population now exceeds 6 billion, and even though the average birth rate has begun to decline, most demographers believe that the global human population will reach 8–10 billion in the next 50 years. Much of this projected growth will occur in developing countries in Central and South America, Asia and Africa—regions that are rich in unique biological diversity.

Finding solutions to conservation challenges will not be easy in today's human-dominated world. A growing number of people live in urban settings and are becoming increasingly isolated from nature. They "hunt" in supermarkets and malls, live in apartments and houses, spend their time watching television and searching the World Wide Web. Children and adults must be taught to value biological diversity and the habitats that support it. Education is of prime importance now while we still have time to respond to the impending crisis. There still exist in many parts of the world large numbers of biological "hotspots"—places that are relatively unaffected by humans and which still contain a rich store of their original animal and plant life. These living repositories, along with selected populations of animals and plants held in professionally managed zoos, aquariums and botanical gardens, could provide the basis for restoring the planet's biological wealth and ecological health. This encyclopedia and the collective knowledge it represents can assist in educating people about animals and their ecological and cultural significance. Perhaps it will also assist others in making deeper connections to nature and spreading biophilia. Information on the conservation status, threats and efforts to preserve various species have been integrated into this revision. We have also included information on the cultural significance of animals, including their roles in art and religion.

It was over 30 years ago that Dr. Bernhard Grzimek, then director of the Frankfurt Zoo in Frankfurt, Germany, edited the first edition of *Grzimek's Animal Life Encyclopedia*. Dr. Grzimek was among the world's best known zoo directors and conservationists. He was a prolific author, publishing nine books. Among his contributions were: *Serengeti Shall Not Die*, *Rhinos Belong to Everybody* and *He and I and the Elephants*. Dr. Grzimek's career was remarkable. He was one of the first modern zoo or aquarium directors to understand the importance of zoo involvement in *in situ* conservation, that is, of their role in preserving wildlife in nature. During his tenure, Frankfurt Zoo became one of the leading western advocates and supporters of wildlife conservation in East Africa. Dr. Grzimek served as a Trustee of the National Parks Board of Uganda and Tanzania and assisted in the development of several protected areas. The film he made with his son Michael, *Serengeti Shall Not Die*, won the 1959 Oscar for best documentary.

Professor Grzimek has recently been criticized by some for his failure to consider the human element in wildlife conservation. He once wrote: "A national park must remain a primordial wilderness to be effective. No men, not even native ones, should live inside its borders." Such ideas, although considered politically incorrect by many, may in retrospect actually prove to be true. Human populations throughout Africa continue to grow exponentially, forcing wildlife into small islands of natural habitat surrounded by a sea of humanity. The illegal commercial bushmeat trade—the hunting of endangered wild animals for large scale human consumption—is pushing many species, including our closest relatives, the gorillas, bonobos and chimpanzees, to the brink of extinction. The trade is driven by widespread poverty and lack of economic alternatives. In order for some species to survive it will be necessary, as Grzimek suggested, to establish and enforce a system of protected areas where wildlife can roam free from exploitation of any kind.

While it is clear that modern conservation must take the needs of both wildlife and people into consideration, what will the quality of human life be if the collective impact of short-term economic decisions is allowed to drive wildlife populations into irreversible extinction? Many rural populations living in areas of high biodiversity are dependent on wild animals as their major source of protein. In addition, wildlife tourism is the primary source of foreign currency in many developing countries and is critical to their financial and social stability. When this source of protein and income is gone, what will become of the local people? The loss of species is not only a conservation disaster; it also has the potential to be a human tragedy of immense proportions. Protected areas, such as national parks, and regulated hunting in areas outside of parks are the only solutions. What critics do not realize is that the fate of wildlife and people in developing countries is closely intertwined. Forests and savannas emptied of wildlife will result in hungry, desperate people, and will, in the long-term lead to extreme poverty and social instability. Dr. Grzimek's early contributions to conservation should be recognized, not only as benefiting wildlife, but as benefiting local people as well.

Dr. Grzimek's hope in publishing his *Animal Life Encyclopedia* was that it would "...disseminate knowledge of the animals and love for them", so that future generations would "...have an opportunity to live together with the great diversity of these magnificent creatures." As stated above, our goals in producing this updated and revised edition are similar. However, our challenges in producing this encyclopedia were more formidable. The volume of knowledge to be summarized is certainly much greater in the twenty-first century than it was in the 1970's and 80's. Scientists, both professional and amateur, have learned and published a great deal about the animal kingdom in the past three decades, and our understanding of biological and ecological theory has also progressed. Perhaps our greatest hurdle in producing this revision was to include the new information, while at the same time retaining some of the characteristics that have made *Grzimek's Animal Life Encyclopedia* so popular. We have therefore strived to retain the series' narrative style, while giving the information more organizational structure. Unlike the original *Grzimek's*, this updated version organizes information under specific topic areas, such as reproduction, behavior, ecology and so forth. In addition, the basic organizational structure is generally consistent from one volume to the next, regardless of the animal groups covered. This should make it easier for users to locate information more quickly and efficiently. Like the original Grzimek's, we have done our best to avoid any overly technical language that would make the work difficult to understand by non-biologists. When certain technical expressions were necessary, we have included explanations or clarifications.

Considering the vast array of knowledge that such a work represents, it would be impossible for any one zoologist to have completed these volumes. We have therefore sought specialists from various disciplines to write the sections with which they are most familiar. As with the original *Grzimek's*, we have engaged the best scholars available to serve as topic editors, writers, and consultants. There were some complaints about inaccuracies in the original English version that may have been due to mistakes or misinterpretation during the complicated translation process. However, unlike the original *Grzimek's*, which was translated from German, this revision has been completely re-written by English-speaking scientists. This work was truly a cooperative endeavor, and I thank all of those dedicated individuals who have written, edited, consulted, drawn, photographed, or contributed to its production in any way. The names of the topic editors, authors, and illustrators are presented in the list of contributors in each individual volume.

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy or biosystematics. Taxonomy is the science through which various organisms are discovered, identified, described, named, classified and catalogued. It should be noted that in preparing this volume we adopted what might be termed a conservative approach, relying primarily on traditional animal classification schemes. Taxonomy has always been a volatile field, with frequent arguments over the naming of or evolutionary relationships between various organisms. The advent of DNA fingerprinting and other advanced biochemical techniques has revolutionized the field and, not unexpectedly, has produced both advances and confusion. In producing these volumes, we have consulted with specialists to obtain the most up-to-date information possible, but knowing that new findings may result in changes at any time. When scientific controversy over the classification of a particular animal or group of animals existed, we did our best to point this out in the text.

Readers should note that it was impossible to include as much detail on some animal groups as was provided on others. For example, the marine and freshwater fish, with vast numbers of orders, families, and species, did not receive as detailed a treatment as did the birds and mammals. Due to practical and financial considerations, the publishers could provide only so much space for each animal group. In such cases, it was impossible to provide more than a broad overview and to feature a few selected examples for the purposes of illustration. To help compensate, we have provided a few key bibliographic references in each section to aid those interested in learning more. This is a common limitation in all reference works, but *Grzimek's Encyclopedia of Animal Life* is still the most comprehensive work of its kind.

I am indebted to the Gale Group, Inc. and Senior Editor Donna Olendorf for selecting me as Series Editor for this project. It was an honor to follow in the footsteps of Dr. Grzimek and to play a key role in the revision that still bears his name. *Grzimek's Animal Life Encyclopedia* is being published by the Gale Group, Inc. in affiliation with my employer, the American Zoo and Aquarium Association (AZA), and I would like to thank AZA Executive Director, Sydney J. Butler; AZA Past-President Ted Beattie (John G. Shedd Aquarium, Chicago, IL); and current AZA President, John Lewis (John Ball Zoological Garden, Grand Rapids, MI), for approving my participation. I would also like to thank AZA Conservation and Science Department Program Assistant, Michael Souza, for his assistance during the project. The AZA is a professional membership association, representing 215 accredited zoological parks and aquariums in North America. As Director/William Conway Chair, AZA Department of Conservation and Science, I feel that I am a philosophical descendant of Dr. Grzimek, whose many works I have collected and read. The zoo and aquarium profession has come a long way since the 1970s, due, in part, to innovative thinkers such as Dr. Grzimek. I hope this latest revision of his work will continue his extraordinary legacy.

Silver Spring, Maryland, 2001
Michael Hutchins
Series Editor

How to use this book

Grzimek's Animal Life Encyclopedia is an internationally prominent scientific reference compilation, first published in German in the late 1960s, under the editorship of zoologist Bernhard Grzimek (1909-1987). In a cooperative effort between Gale and the American Zoo and Aquarium Association, the series is being completely revised and updated for the first time in over 30 years. Gale is expanding the series from 13 to 17 volumes, commissioning new color images, and updating the information while also making the set easier to use. The order of revisions is:

Vol 8–11: Birds I–IV
Vol 6: Amphibians
Vol 7: Reptiles
Vol 4–5: Fishes I–II
Vol 12–16: Mammals I–V
Vol 1: Lower Metazoans and Lesser Deuterostomes
Vol 2: Protostomes
Vol 3: Insects
Vol 17: Cumulative Index

Organized by taxonomy

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy—the science through which various organisms are discovered, identified, described, named, classified, and catalogued. Starting with the simplest life forms, the lower metazoans and lesser deuterostomes, in volume 1, the series progresses through the more complex animal classes, culminating with the mammals in volumes 12–16. Volume 17 is a stand-alone cumulative index.

Organization of chapters within each volume reinforces the taxonomic hierarchy. In the case of the Mammals volumes, introductory chapters describe general characteristics of all organisms in these groups, followed by taxonomic chapters dedicated to Order, Family, or Subfamily. Species accounts appear at the end of the Family and Subfamily chapters To help the reader grasp the scientific arrangement, each type of chapter has a distinctive color and symbol:

● =Order Chapter (blue background)

=Monotypic Order Chapter (green background)

▲ =Family Chapter (yellow background)

△ =Subfamily Chapter (yellow background)

Introductory chapters have a loose structure, reminiscent of the first edition. While not strictly formatted, Order chapters are carefully structured to cover basic information about member families. Monotypic orders, comprised of a single family, utilize family chapter organization. Family and subfamily chapters are most tightly structured, following a prescribed format of standard rubrics that make information easy to find and understand. Family chapters typically include:

Thumbnail introduction
- Common name
- Scientific name
- Class
- Order
- Suborder
- Family
- Thumbnail description
- Size
- Number of genera, species
- Habitat
- Conservation status

Main essay
- Evolution and systematics
- Physical characteristics
- Distribution
- Habitat
- Behavior
- Feeding ecology and diet
- Reproductive biology
- Conservation status
- Significance to humans

Species accounts
- Common name
- Scientific name
- Subfamily
- Taxonomy
- Other common names
- Physical characteristics
- Distribution
- Habitat
- Behavior

Feeding ecology and diet
Reproductive biology
Conservation status
Significance to humans
Resources
Books
Periodicals
Organizations
Other

Color graphics enhance understanding

Grzimek's features approximately 3,000 color photos, including approximately 1,560 in five Mammals volumes; 3,500 total color maps, including nearly 550 in the Mammals volumes; and approximately 5,500 total color illustrations, including approximately 930 in the Mammals volumes. Each featured species of animal is accompanied by both a distribution map and an illustration.

All maps in *Grzimek's* were created specifically for the project by XNR Productions. Distribution information was provided by expert contributors and, if necessary, further researched at the University of Michigan Zoological Museum library. Maps are intended to show broad distribution, not definitive ranges.

All the color illustrations in *Grzimek's* were created specifically for the project by Michigan Science Art. Expert contributors recommended the species to be illustrated and provided feedback to the artists, who supplemented this information with authoritative references and animal skins from University of Michgan Zoological Museum library. In addition to species illustrations, *Grzimek's* features conceptual drawings that illustrate characteristic traits and behaviors.

About the contributors

The essays were written by scientists, professors, and other professionals. *Grzimek's* subject advisors reviewed the completed essays to insure consistency and accuracy.

Standards employed

In preparing these volumes, the editors adopted a conservative approach to taxonomy, relying on Wilson and Reeder's *Mammal Species of the World: a Taxonomic and Geographic Reference* (1993) as a guide. Systematics is a dynamic discipline in that new species are being discovered continuously, and new techniques (e.g., DNA sequencing) frequently result in changes in the hypothesized evolutionary relationships among various organisms. Consequently, controversy often exists regarding classification of a particular animal or group of animals; such differences are mentioned in the text.

Grzimek's has been designed with ready reference in mind and the editors have standardized information wherever feasible. For **Conservation status,** *Grzimek's* follows the IUCN Red List system, developed by its Species Survival Commission. The Red List provides the world's most comprehensive inventory of the global conservation status of plants and animals. Using a set of criteria to evaluate extinction risk, the IUCN recognizes the following categories: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Conservation Dependent, Near Threatened, Least Concern, and Data Deficient. For a complete explanation of each category, visit the IUCN web page at <http://www.iucn.org/>.

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Primates
(Primates)

Class Mammalia
Order Primates
Number of families 14
Number of genera, species 62 genera; 350 species

Photo: A white-throated capuchin (*Cebus capucinus*) forages in Costa Rica. (Photo by Animals Animals ©Mickey Gibson. Reproduced by permission.)

Introduction

The order name "Primates" (literally: "those of first rank") was introduced by Linnaeus in 1758 for a group that included man along with several non-human primates known at that time. Interestingly, Linnaeus also included bats in his order Primates, but this was soon abandoned by other taxonomists. The number of living primate species recognized in standard classifications has been steadily climbing and has reached at least 350. It is highly likely that additional species will be recognized, notably because of contributions from molecular studies and the discovery of further previously unrecognized "cryptic species" among the incompletely studied night-active (nocturnal) primates. The total number of extant primate species is therefore likely to settle at about 400. The living primates fall quite clearly into six "natural groups," based on a combination of geographical distribution and key characteristics: (1) lemurs (infraorder Lemuriformes), (2) lorises and bushbabies (infraorder Lorisiformes), (3) tarsiers (infraorder Tarsiiformes), (4) New World monkeys (infraorder Platyrrhini), (5) Old World monkeys (superfamily Cercopithecoidea), (6) apes and humans (superfamily Hominoidea). The last two groups—Old World monkeys, apes, and humans—are relatively close together, so they are given the status of superfamilies within the single infraorder Catarrhini. The first three groups of living primates (lemurs, lorises, and tarsiers) have all retained numerous primitive features, and these "lower primates" have therefore commonly been allocated to the suborder Prosimii (literally: "before the monkeys"). The remaining three groups (monkeys, apes, and humans) all share a set of advanced characters, and these "higher primates" have been allocated to the suborder Anthropoidea.

Evolution and systematics

The known fossil record of undoubted primates dates back to the beginning of the Eocene epoch, some 55 million years ago (mya). A group of fossil mammals from the preceding Paleocene epoch (55–65 mya), containing many North American and European representatives and allocated to the infraorder Plesiadapiformes (e.g., *Ignacius*, *Palaechthon*, *Plesiadapis*, *Purgatorius*), is commonly included in the order Primates. However, some authors have questioned the proposed link between Plesiadapiformes and Primates and the principal similarities involve the molar teeth. It is, in any case, generally agreed that the Plesiadapiformes branched away before the origin of modern primates. They are hence no more than a sister group and have accordingly been given the label "archaic primates." Modern primates and their direct fossil relatives ("primates of modern aspect" or Euprimates) can only be traced back to the basal Eocene. Close to 500 fossil primates of modern aspect have been recognized, and this total will surely increase. Surprisingly, the earliest representatives, from the Eocene epoch, have been discovered primarily in North America and Europe, where numerous species have been documented. This is unexpected, because primates today are very largely confined to the southern continents (South America, Africa, and Asia). Most of the Eocene primates that have been found are of course relatively primitive and hence most closely resemble modern prosimians. Indeed, it is possible to find both lemur-like species (infraorder Adapiformes) and tarsier-like species (infraorder Omomyiformes). Representatives of both of these groups are found in Europe and North America (e.g., European *Adapis* and American *Notharctus* among Adapiformes and European *Necrolemur* and American *Tetonius* for Omomyiformes).

A blue-eyed lemur (*Eulemur macaco flavifrons*) with its young. (Photo by Tom & Pat Leeson/Photo Researchers, Inc. Reproduced by permission.)

For a long time, the earliest known direct fossil relatives of higher primates dated back only to the beginning of the Oligocene, about 35 mya. These early Oligocene anthropoids are all derived from a single fossil site in Egypt, the Fayum, and include a dozen genera belonging to two distinct groups with different dental formulae (e.g., *Aegyptopithecus* versus *Apidium*). A few enigmatic Eocene forms with some monkey-like features had been reported from Asia (e.g., *Amphipithecus* and *Pondaungia* from Myanmar [formerly Burma]), but the remains were so fragmentary that their affinities were uncertain. Recovery of more complete specimens revealed that these Asian forms are, indeed, related to higher primates, and the discovery of monkey-like *Siamopithecus* from Eocene deposits in Thailand has provided additional confirmation. Thus, the earliest known relatives of higher primates come from Asia. Fissure fillings from the Chinese middle Eocene site of Shanghuang have also yielded several fossils that have expanded our understanding of early primate evolution. In addition to adapiforms and omomyiforms, the Shanghuang deposits contain a possible early anthropoid (*Eosimias*) and an apparent direct relative of modern tarsiers (*Tarsius eocaenus*).

Overall, an impressive range of early fossil primates of modern aspect is known from the Eocene and early Oligocene, primarily from the northern continents. However, there is a period of 6 million years during the middle of the Oligocene epoch (26–32 mya) from which not a single fossil primate species has been recovered. A few primate fossils have been discovered in late Oligocene deposits, and from the Miocene upwards (i.e., over the last 25 million years) the primate fossil record is again relatively good. Miocene deposits have yielded direct relative of modern lorises and bushbabies, of New World monkeys, of Old World monkeys, and of apes (hominoids). Nevertheless, there are still some marked gaps in the fossil record. For instance, no single fossil lemur has ever been discovered on Madagascar, although a score of subfossil lemur species (predominantly large-bodied forms) dating back just a few thousand years have been discovered.

The order Primates is one of a score of major groups that radiated from the ancestral stock of placental mammals that existed at some time during the Cretaceous. One key question therefore concerns the relationship between primates and other mammals. Primates of modern aspect undoubtedly constitute a monophyletic group. In other words, they are all derived from a single, distinct common ancestor. Various attempts have been made to link this monophyletic group of primates to other orders of mammals. For some time, the tree shrews (now allocated to the separate order Scandentia) were actually included in the order Primates, but it eventually emerged that the similarities between tree shrews and primates are attributable to retention of primitive mammalian features and convergent adaptations for arboreal life. There has also been much support for recognition of a superorder Archonta containing primates, tree shrews, colugos (Dermoptera), and bats (Chiroptera). (In the original proposal, Archonta also included elephant shrews, but they were subsequently quietly dropped.) One problem with recognition of the Archonta is that it perpetuates the disputed link between primates and tree shrews by other means. Furthermore, it continues the practice of suggesting links on the basis of likely retention of primitive mammalian features and convergent adaptations for arboreal life. A quite different suggestion, based on certain features of the visual system, is that primates are the sister group of fruit bats (Megachiroptera). Among other things, this "flying primate hypothesis" has the corollary that the bats are not monophyletic and that flight evolved twice, once in ancestral fruit bats and once in the ancestor of the remaining bats (Microchiroptera). Comprehensive analyses of relationships between mammalian orders using large molecular data sets have now fairly clearly ruled out any connection between tree shrews and primates or between bats and primates. Indeed, several molecular studies have indicated that tree shrews may have some link to rabbits, while a whole host of morphological and molecular evidence resoundingly indicates that the bats form a monophyletic group. Hence, the "flying primate hypothesis" has been largely discredited and there is little support for recognition of a superorder Archonta. On the other hand, there are indications from the molecular data that there might be some kind of link between colugos and primates.

Because the earliest known undoubted fossil primates are only 55 million years old, it has been widely accepted that the common ancestor of primates of modern aspect dates back only to the Paleocene, some 60–65 mya, thus post-dating the demise of the dinosaurs at the end of the Cretaceous. However, comprehensive phylogenetic trees for placental mammals based on molecular evidence suggest that many orders, including the Primates, began to diverge during the Cretaceous, about 90–100 mya. Furthermore, a statistical analysis that takes into account the numerous gaps in the primate fossil record indicates that these gaps have led to marked underestimation of the age of the last common ancestor of primates of modern aspect. Calculations suggest that ancestral primates existed at least 82 mya.

Relationships within the order Primates are now relatively well established, at least as far as the living representative are concerned. Numerous sources of evidence, including morphology, chromosomes, and molecular data, all point to a basic divergence between one lineage leading to lemurs and the loris group and another leading to tarsiers and higher primates. Modern lemurs, lorises, and bushbabies have retained the rhinarium (a hairless area of moist skin surrounding the nostrils) and are referred to as strepsirrhines. They uniformly exhibit a non-invasive (epitheliochorial) type of placentation. Furthermore, they are generally characterized by the development of a toothcomb in the lower jaw, in which the bilaterally flattened crowns of the lower incisors and canines have become almost horizontal. This distinctive dental specialization can be traced back over 40 million years. By contrast, modern tarsiers and higher primates have completely lost the rhinarium and are accordingly labeled haplorhines. They uniformly exhibit a highly invasive (hemochorial) type of placentation, and this in fact provided the first evidence of a link between tarsiers and higher primates. Haplorhine primates lack any dental development resembling the toothcomb of strepsirrhine primates. On the other hand, they all have a virtually complete bony wall (postorbital plate) behind the orbit, whereas strepsirrhine primates merely have a bony strut (postorbital bar) around the outer margin of the orbit. The relationships between Eocene primates and modern primates are uncertain. Although the Adapiformes resemble modern lemurs in many respects, this is mainly because both possess relatively primitive primate features. Significantly, the Adapiformes lack any dental development that can be linked to the distinctive toothcomb of modern strepsirrhines. Hence, it seems likely that the Adapiformes may be a sister group of the strepsirrhines or perhaps just a side-branch from the ancestral primate stock. Similarly, the relationship between Omomyiformes and modern tarsiers is tenuous. Although both groups show an intriguing similarity in possessing relatively large molar teeth and a bell-shaped upper dental arcade, the Omomyiformes merely have a postorbital bar and lack a postorbital plate. Thus, there is probably no more than a sister-group relationship between Omomyiformes and tarsiers. From the late Eocene through the lower Oligocene, there is increasing evidence of the development of higher primate characteristics in certain lineages. Deepening of the lower jaw (mandible) and the presence of a postorbital plate are identifiable in the late Eocene, and by the lower Oligocene there are fossil forms with spatulate (rather than peg-like) incisors and medial fusion of the right and left halves of the mandible. All of these are advanced features of the higher primates. From the beginning of the Miocene onwards, it is possible to identify representatives of all three natural groups of higher primates on the basis of defining characteristics.

A Japanese macaque (*Macaca fuscata*) eats phloem from the bark. (Photo by Nils Reinhard/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)

For many years, it was customary to classify the primates into two suborders: Prosimii and Anthropoidea. This reflected a classical, grade-based approach to classification in which the most primitive surviving forms are allocated to a basic group along with all early fossil forms. The suborder Prosimii hence included the fossil Adapiformes and the Omomyiformes along with the extant lemurs, lorises, and tarsiers, while the suborder Anthropoidea included the extant monkeys, apes, and humans along with any fossil forms showing certain advanced features that characterize this subgroup of primates. However, many authors now favor a cladistic type of classification in which the main subdivisions are designed to reflect directly the main divergences within the reconstructed phylogenetic tree. This has led to the widespread adoption of an alternative classification in which lemurs and lorises are allocated to the suborder Strepsirrhini and tarsiers and higher primates to the suborder Haplorhini. This approach is not followed here for entirely practical reasons. In the first place, if a classification directly matches an inferred phylogenetic tree, it must logically be changed every time the tree is changed. This is a prescription for classificatory instability. Secondly, most primate fossils (particularly the earlier representatives) are known only from isolated molar teeth and there is no known way of reliably distinguishing all strepsirrhines from all haplorhines on the basis of molar features alone. In any event, almost all primate classifications in general use have a primary subdivision into two suborders. The consensus view is that these contain a total of at least 14 families with extant representatives. Reflecting the diversity of the lemurs of Madagascar, five of these families belong to that group alone: Cheirogaleidae (dwarf and mouse lemurs); Lemuridae (true and gentle lemurs); Lepilemuridae (sportive

A greater dwarf lemur (*Cheirogaleus major*) feeds on ravenala in Madagascar. (Photo by Harald Schütz. Reproduced by permission.)

lemurs); Indriidae (indri group); and Daubentoniidae (aye-aye). The loris group can be divided into two families: Loridae (lorises); Galagonidae (bushbabies). There are only five species of modern tarsiers, and these are all allocated to the single family Tarsiidae. The New World monkeys have classically been divided into two families: Cebidae (true New World monkeys) and Callitrichidae (marmosets, tamarins and Goeldi's monkey). The Old World monkeys are all morphologically very similar and they are generally placed in the single family Cercopithecidae. However, some authors regard the leaf-monkeys as sufficiently different to place them in a separate family Colobidae. Finally, the hominoids have been traditionally divided into three families: Hylobatidae (lesser apes, or gibbons), Pongidae (great apes), and Hominidae (modern humans and their fossil relatives).

Physical characteristics

Living primates cover a very large range of body sizes, extending from 1 oz (30 g) for the pygmy mouse lemur (*Microcebus berthae*) to about 375 lb (170 kg) for a full-grown adult male gorilla. There is accordingly a more than 5,000-fold difference between the smallest and largest living primates. As a rule, fossil primates fall at the lower end of this size range, although some of the recently extinct subfossil lemurs of Madagascar were comparable in size to an adult female gorilla (175 lb [80 kg]). The earliest known fossil primates from the Eocene and Oligocene were generally quite small. Some of them were apparently even smaller than the pygmy mouse lemur, while the biggest probably did not exceed 22 lb (10 kg). Among living primates, it is notable that nocturnal species are generally markedly smaller than diurnal species. The average body weight for nocturnal primates is about 1 lb (500 g), whereas the average body weight for diurnal primates is approximately 11 lb (5 kg), representing a ten-fold difference.

The hands and feet of primates are typically adapted for grasping rather than grappling while moving around. A widely divergent big toe (hallux) provides the basis for a powerful grasping action of the foot in all primates except humans, while the hand usually exhibits at least some grasping capacity. In most primates, the digits (fingers and toes) typically bear flat nails rather than narrow claws, and in all cases the hallux bears a nail. On the ventral surfaces of the hands and feet there are tactile pads with skin ridges (dermatoglyphs) that serve an anti-slip function on twigs and branches. These skin ridges, in combination with special tactile sense organs (Meissner's corpuscles), also permit enhanced tactile sensitivity. Patterns of movement (locomotor sequences) are typically hindlimb-dominated. The location of the body's center of gravity is typically closer to the hindlimbs, with the result that the typical walking gait shows a diagonal sequence (forefoot precedes hindfoot on each side). In the foot, there is usually at least some degree of relative elongation of the distal segment of the heel bone (calcaneus). Primates also tend to have longer limbs, in relation to overall body size, than other mammals, and this results in increased stride length. The visual sense is greatly emphasized in primates. The eyes are relatively large and in the eye sockets (orbits) there is at least a bony strut (postorbital bar) on the outer margin. A large degree of binocular overlap is ensured by pronounced forward rotation of the eyes and orbits. The proportions of nerve fibers passing from the retina of each eye to the two sides of the brain are approximately balanced and they are organized in a very unusual way such that the opposite half of the visual field is represented in each half of the brain. The ventral floor of the bony capsule protecting the middle ear (auditory bulla) is formed predominantly by the petrosal bone, which is unusual among mammals. Partly because of the increased emphasis on vision, the primate brain is typically enlarged at least to some extent, relative to body size, in comparison to other living mammals. The brain of living primates always possesses between the frontal and the parietal lobes a true Sylvian sulcus (joining the rhinal sulcus) and a complex calcarine sulcus on the inside of the occipital lobe. Primates are unique among living mammals in that the brain constitutes a significantly larger proportion of body weight at all stages of fetal development. The dental formula exhibits a maximum of two incisors, one canine, three premolars and three molars on each side of upper and lower jaws, differing from ancestral mammals in the loss of one incisor and one premolar from each toothrow. In association with the reduction in the number of incisors, the premaxilla bone at the front of the upper jaw is very short, and the incisors are arranged more transversely than longitudinally. The cheek teeth are typically relatively unspecialized, although the cusps are generally low and rounded, while in the lower molars the heels (talonids) are raised and enlarged.

Golden snub-nosed monkeys (*Pygathrix roxellana*) are found along the Tibetan Plateau in China. (Photo by Christian Grzimek/OKAPIA/Photo Researchers, Inc. Reproduced by permssion.)

Distribution

Modern primates are very largely confined to tropical and subtropical regions of the world, hence occurring predominantly in the southern continents. The smaller-bodied prosimian primates are even more restricted in their distribution, while a few of the larger-bodied higher primates (notably macaques) can occur quite far north in regions where snow is found in winter (Barbary, rhesus, and Japanese macaques). The lemurs are confined to Madagascar and are the only primates to occur on that island. The lorises and bushbabies are an Afro-Asian group. However, whereas the lorises occur in both Africa and Asia, the bushbabies occur only in Africa. The tarsiers are restricted to various islands in Southeast Asia. The New World monkeys occur in South and Central America and are the only primates to be found in the Neotropical region. The Old World monkeys, like the lorises, are an Afro-Asian group with a very wide distribution. However, the guenons and their relatives primarily occur in Africa, with only the macaques as an essentially Asian offshoot, while the leaf-monkeys are primarily Asiatic and represented in Africa only by the colobus monkeys. Finally, the hominoids are also an essentially Afro-Asian group, although humans began to expand outside that range about two million years ago. The gibbons and the orangutan are found only in Southeast Asia, while chimpanzees and gorillas are confined to Africa.

In the distant past, during the Eocene epoch, primates occurred at very high latitudes in North America and Europe, in regions where they subsequently left no trace. One plausible explanation for this is that a marked increase in ambient temperatures at higher latitudes that marked the transition from the Paleocene to the Eocene led to a northward expansion of tropical and subtropical forests, thus expanding the potential geographical range of habitats available to primates. At the end of the Eocene, temperatures at higher latitudes declined markedly and this doubtless explains why primates virtually disappeared from the northern continents at that time, with only a few species surviving for a while into the Oligocene. In fact, it seems likely that primates also occurred widely in the southern continents during the Eocene, at least in Africa and Asia, but for various reasons we have very few fossils from those regions. The most likely interpretation for

An olive baboon (*Papio hamadryas anubis*) devours a freshly killed baby antelope. (Photo by Peter Davey. Bruce Coleman, Inc. Reproduced by permission.)

the current geographical distribution of primates is that they have always been present in the south and that their range expanded temporarily into the north during the Eocene when temperatures where higher, only to contract again at the end of the Eocene when temperatures declined. In the Old World, primates also occurred somewhat further to the north during the Miocene, as fossil apes and monkeys from that epoch have been documented for the circum-Mediterranean region, for southern Europe and as far north as Hungary and Czechoslovakia.

Habitat

Primates are typically tree-living (arboreal) inhabitants of tropical and subtropical forest ecosystems. Their grasping hands and feet represent adaptations for grasping twigs and branches while moving around in the trees. Ancestral primates, which were probably small-bodied creatures, were seemingly adapted for movement in the fine branches of trees and bushes, where they fed on a mixture of fruits and arthropods. The enlarged, forward-facing eyes of primates probably developed for visually oriented leaping among fine branches while seeking both fruits and animal prey.

Although they are generally restricted to tropical and subtropical forests, primates nevertheless occupy a remarkably wide range of habitats, ranging from evergreen tropical rainforest with year-round rainfall to quite dry scrub forest with strictly seasonal rainfall. Primates are also characteristic inhabitants of gallery forests along the banks of rivers running through otherwise relatively dry areas. Madagascar is a good example of the variety of habitats. Lemurs inhabit the evergreen rainforests extending along the eastern coast; the deciduous forests found on the northwestern and western coasts; the semi-arid, cactus-like forests in the southwestern and southern regions; and in the cooler forests on the central plateau. A general rule for primates is that the number of species living in any one area (sympatric species) tends to increase as the total annual rainfall increases. For example, the maximum number of sympatric lemur species in Madagascar is found in the eastern rainforest, while the minimum is found in the dry forests of the south and southwest.

Most primates are entirely arboreal in habits, living virtually all of the time in trees and rarely descending to the ground. The prosimian primates are almost exclusively typically arboreal. The only obvious exception to this rule is provided by the ringtailed lemur (*Lemur catta*), which spends approximately 25% of its time on the ground. The New World monkeys are also almost exclusively typically arboreal. However, even typically arboreal primate species descend to the ground occasionally. For instance, mouse lemurs, some bushbabies, and tarsiers commonly scan the leaf litter on the forest floor from some vantage point low down in the trees and then trap insects with sudden, rapid dashes to the ground. It is only among the Old World monkeys and apes that we find semi-terrestrial or terrestrial species that spend a significant amount of the time moving around and feeding on the ground, as is the case with baboons and gorillas.

Behavior

Primates generally live in well-developed social networks and this can be regarded as a defining characteristic of the order. Although species that are active by night (nocturnal) have commonly been described as solitary, field studies have revealed that there are intimate social links between individuals, maintained by intermittent contacts during the night and by sharing of nests during the daytime. Nevertheless, there is a major distinction between day-active (diurnal) primates and nocturnal species in that the former typically live in obvious cohesive social groups, whereas the latter usually move around and feed alone at night. In sum, while all primates have intricate social systems, as a general rule diurnal species are gregarious whereas in nocturnal species individuals are dispersed. Among nocturnal primates, the only exceptions to solitary behavior are found in a few species that are monogamous (pair-living), such as the avahis (*Avahi*) in Madagascar and the owl monkeys (*Aotus*) in the New World. Among diurnal primates, the only representative that is almost solitary like most nocturnal primates is the orangutan (*Pongo*) of Southeast Asia. Otherwise, the groups of gregarious diurnal primates can be classified into three main categories according to the composition of their groups: monogamous family units, one-male groups and multi-male groups. Monogamous groups typically consist of an adult pair living together with their immature offspring. Clear-cut examples of monogamy are found among lemurs (e.g., avahis, mongoose lemurs, red-bellied lemurs, and indri), among New World monkeys (e.g., owl monkeys, marmosets, tamarins and Goeldi's monkey), in a few Old World monkeys (e.g., Mentawai langur) and in all gibbons. Such groups are necessarily relatively small and may contain between two and a dozen individuals. One-male groups, also known as harem groups, contain a single adult male, several adult females and a variable number of immature individuals. The best-known examples of one-male groups are found among such Old World monkeys as Hamadryas baboons (*Papio hamadryas*), geladas (*Theropithecus*), guenons (*Cercopithecus* species), patas monkeys (*Erythrocebus patas*), and the majority of leaf-monkeys (e.g., black-and-white colobus and several langur species). Among the apes, gorillas also live in one-male groups. In many species that are characterized by harem groups, the surplus males join together in bachelor groups. Furthermore, in some cases several harem groups and bachelor male groups may move together in large herds that may contain over a hundred individuals, as is the case with Hamadryas baboons and geladas. Multi-male groups contain several adult males along with several adult females and a variable number of immature individuals. Examples of such social groups are widespread among primates and found in various diurnal lemurs like ringtails (*Lemur catta*) and some sifakas (e.g., *Propithecus verreauxi*); in most New World monkeys (e.g., capuchins, howler monkeys, spider monkeys, and woolly monkeys); in several Old World monkeys (e.g., plains baboons, vervet monkeys, and red colobus); and in chimpanzees. Various attempts have been made to reconstruct the evolutionary history of primate social systems. One key finding is that, although individuals are typically dispersed, nocturnal primates show social networks that exhibit parallels to the array of monogamous, one-male, and multi-male patterns found among diurnal primates. Reconstruction in comparison with other mammals suggests that the ancestral primates were nocturnal and lived in multi-male social networks similar to those found in most modern nocturnal prosimians.

A mouse lemur (*Microcebus griseorufus*) on a tree branch in Madagascar. (Photo by Harald Schütz. Reproduced by permission.)

Because they live in well-defined social networks, primates typically exhibit regular and relatively intense social interactions. One very common form of social interaction is grooming, which is frequently reciprocal. Even in nocturnal primate species that show dispersal of individuals at night, and in orangutans, which are usually dispersed by day, social grooming is a prominent feature of occasional encounters between familiar individuals. In prosimians, social grooming is usually carried out mainly with the teeth, and in lemurs and lorises (strepsirrhines) the tooth-comb is actively used. In higher primates, by contrast, the hands usually play a more intense role in social grooming, particularly in Old World monkeys and apes. Although the visual sense is highly developed in primates, olfactory signals continue to play a role in social interactions, particularly in prosimians and New World monkeys. Nocturnal lemurs and lorises still have relatively large olfactory bulbs in the brain, and marking with urine and/or feces and with secretions from special skin glands (e.g., on the chest) is prominent. For dispersed nocturnal prosimians, olfactory marking may be the primary means of communication between individuals while active. Visual displays are particularly important in diurnal primates, some of which have developed quite striking coloration patterns of the fur (e.g., certain lemurs, Old World monkeys, and gibbons). In fact, ringtailed lemurs show an interesting display pattern that combines both olfactory and visual elements. During encounters between groups that have been labeled "stink fights," individuals anoint their tails with secretions from marking glands on the arms and then wave their tails in the air while strutting around. Perhaps the greatest diversity of color patterns on the face and elsewhere on the body is found in the African guenons, which often have characteristic head movements that emphasize any species-specific facial markings. Vocalizations are also generally important for social interactions among primates. Nocturnal primates usually have a relatively restricted vocal repertoire, but the calls that they do have are important for maintaining contact between dispersed individuals. Some of the smallest nocturnal primates (e.g., mouse lemurs, dwarf bushbabies) have calls that are in the ultrasonic range. Diurnal primates generally have richer vocal repertoires containing numerous calls in the audible range and their subtlety (e.g., through intergradation between call types) can be quite pronounced, particularly in certain Old World monkeys and chimpanzees. Many species like the lion tamarins and titi monkeys have long calls to maintain contact between neighboring groups.

A Japanese macaque (*Macaca fuscata*) in Jigokudani hot springs, Japan. (Photo by © Paoloa Ghirotti/Corbis. Reproduced by permission.)

Although it is often assumed that all primates show territorial behavior, defense of an exclusive territory is in fact comparatively rare among primates. Numerous nocturnal primates show range overlap between adults of both sexes, and diurnal primates that live in gregarious groups often show quite extensive overlap between group ranges. Some nocturnal prosimians, such as sportive lemurs (*Lepilemur*) in Madagascar and in a minority of diurnal primates, including some lemurs (e.g., certain populations of sifakas, *Propithecus*, and in the indri), show true territoriality in the sense of behavior shown to defend an exclusive area. There seems to be a general trend for primates that live in monogamous groups to show marked territorial behavior, and it has in fact been suggested that one of the factors promoting monogamy is joint defense of an area containing vital resources. Territorial behavior has been found in a variety of monogamous species, including such nocturnal lemurs as avahis (*Avahi*), such cathemeral lemurs as the mongoose lemur (*Eulemur mongoz*), such diurnal lemurs as the indri (*Indri*), most marmosets and tamarins (Callitrichidae), and all gibbons (Hylobatidae). In fact, the indri, the gibbons, lion tamarins, and titi monkeys show conspicuous, often melodious vocalizations that carry over great distances in the forest and seem to play a part in territoriality. These "great calls" of the monogamous indri and gibbons provide one of the most striking examples of convergent evolution to be found among primates.

Most primate species are either exclusively nocturnal (active at night between dusk and dawn) or clearly diurnal (active by day between dawn and dusk). The majority of prosimian primates are nocturnal in habits, whereas simian primates are typically diurnal. Indeed, the only nocturnal representatives among simian primates are the owl monkeys of South and Central America (*Aotus* species); all the rest of the monkeys and apes, like humans, are diurnal. Of the three natural groups of prosimian primates, two contain only nocturnal species (loris group; tarsiers) while the third (lemurs) contains mainly nocturnal species but also some diurnal species. Among the lemurs, there is also an unusual pattern known as cathemerality in which there is a combination of nocturnal and diurnal activity. This is found in most or all brown lemurs (*Eulemur* species) and gentle lemurs (*Hapalemur* species). It has been found that in such species the proportions of nocturnal and diurnal activity vary over the annual cycle, and it seems that seasonal variation in ambient temperatures plays a part in this. Cathemeral activity has also been reported for some owl monkey populations in South America. Compared to other mammals, all primates have relatively large eyes, but in nocturnal primates the eyes are generally even larger. As a further adaptation to nocturnal life, lemurs and lorises typically possess a special reflecting layer behind the retina of the eye, known as a *tapetum lucidum*. Unique among mammals, the reflecting properties of this structure are derived from flat crystals of riboflavin. Although they are also nocturnal, both tarsiers and owl monkeys lack a reflecting layer behind the retina and they compensate for this by having even larger eyes than nocturnal lemurs and lorises. This is just one indication that tarsiers and owl monkeys are secondarily nocturnal and have adapted in a different way to night-time activity.

Feeding ecology and diet

Primate species exhibit a wide range of diets, although most of them include at least some fruits in their food intake. If there is a typical dietary category for primates generally, it is surely fruit consumption, as this is found from the smallest to the largest species. Although most primates eat at least some fruits, primates can be classified into three main dietary categories representing at least 50% of food intake: (1) insectivores, feeding mainly on arthropods (e.g., tarsiers); (2) frugivores, feeding mainly on fruits (e.g., most forest-living monkeys); (3) folivores, feeding mainly on leaves (e.g., leaf-monkeys). There is a general trend among primates for the diet to shift progressively from insectivory through frugivory to folivory as body size increases. This is understandable because small-bodied mammals have relatively high-energy requirements per unit body weight and must eat foods with a rich, easily available energy content. Large-bodied mammals have relatively low energy requirements per unit body weight and can consume foods that have a poor energy content and require extensive digestion. As a general rule, insectivorous primates do not exceed 1.5 lb (700 g) in body weight, while folivorous primates tend to be quite large-bodied species. Sportive lemurs (*Lepilemur*) and avahis (*Avahi*), which weigh between 1.4 lb (650 g) and 2.2 lb (1 kg), are both exceptions to this rule, but they can cope with their relatively low-energy food intake because they have unusually low metabolic rates. In fact, a fourth dietary category known as gummivory must be recognized for primates whose food intake includes more than 50% of plant exudates (gums). Gums resemble fruits in that they are a major source of carbohydrates, but they resemble leaves in that the carbohydrates are polymerized and require extensive digestion. Many primate species include at least some plant exudates in their diets, but there are just a small number of gum-feeding specialists, such as the fork-

Crowned lemur (*Eulemur coronatus*) females feeding on bark. (Photo by Harald Schütz. Reproduced by permission.)

crowned lemur, the needle-clawed bushbaby and some marmoset species.

Most primates forage primarily in trees or bushes for insects, fruits, leaves and/or gums. Regardless of the diet, the visual sense plays a major part in searching for food. Nocturnal primates generally have only a very restricted capacity for distinguishing colors and must rely on other dietary cues, but diurnal primates usually have some form of color vision. Fully developed trichromatic color vision of the kind found in humans occurs in Old World monkeys and apes and a few New World monkeys. Most New World monkeys and all diurnal lemurs have fundamentally dichromatic vision, although in certain New World monkeys there is an unusual polymorphism of the gene coding for a retinal pigment on the X-chromosome, such that some females have a form of trichromatic vision. Prosimian primates generally collect their food primarily with the mouth, but in higher primates the hands play an increased role. As a rule, food items are consumed directly, but in some cases there is some pretreatment of food items. For instance, some capuchin monkeys break nuts by pounding them on branches or tree trunks, while certain chimpanzee populations show nut-cracking involving the use of some kind of hammer and anvil. Chimpanzees have also been reported to use twigs or stems as tools to extract termites from their mounds.

Most primates lack any obvious special foraging adaptations, but there are a few conspicuous exceptions. The tooth-comb in the lower jaw of strepsirrhine primates is, for instance, commonly used in gathering food as well as for grooming. Some lemurs, bushbabies and lorises use the tooth-comb to harvest gum, and many species use it to scoop out the pulp of large fruits. However, the tooth-comb is quite fragile, so it is typically used simply to scrape up plant exudates that seep out following insect damage to tree trunks and branches. In marmosets, by contrast, the lower incisors are elongated to match the canines and all of these stout teeth are used together as a dental tool to gouge holes in tree-trunks to promote the flow of gum. This dental adaptation distinguishes the marmosets from the closely related Goeldi's monkey and tamarins. Undoubtedly the most striking foraging adaptation in primates is found in the aye-aye (*Daubentonia*) of Madagascar, which has rodent-like incisors in both upper and lower jaws and a very thin middle finger in each hand. The gnawing incisors are used to open up channels occupied by wood-boring larvae in tree trunks, and the thin finger is used as a probe to extract the prey. Experiments have confirmed that the aye-aye can locate larvae in a tree trunk by tapping with the probe-like finger and listening to the echoes. It should also be mentioned that the leaf-monkeys (Colobinae) are unique among primates in that they have a complex stomach to permit efficient digestion of leaves.

A red mouse lemur (*Microcebus rufus*) feeds in the trees in Madagascar. (Photo by Harald Schütz. Reproduced by permission.)

Reproductive biology

A number of reproductive features are typical of primates. Male primates are characterized by permanent descent of the testes into a scrotum that is always located behind the root of the penis (postpenial position). Although several other mammal groups exhibit such descent of the testes, primates are unusual in that it occurs very early in life, usually by the time of birth. Female primates are characterized by the absence of a urogenital sinus, which is a shared canal for the urinary and reproductive systems that is primitively present in mammals. In all female primates, the urethra and the vagina have separate external openings. In all primates, placentation is relatively advanced in that involvement of the yolk sac in the circulation of the placenta has been partially or completely eliminated. Relative to maternal body size, primates typically have long pregnancies (gestation periods), and they produce a small number of well-developed (precocial) neonates that are characteristically born with a covering of fur and with their eyes and ears open. Both fetal and postnatal growth are characteristically slow in relation to maternal size, and lactation periods are also relatively long. Sexual maturity is attained late and life spans are correspondingly long relative to body size. In a nutshell, primates are adapted for slow reproductive turnover and intensive, long-term investment in individual offspring.

Another defining feature of primates is that the non-pregnant cycle of females is typically quite long, usually lasting about a month. (The only striking exception is the squirrel monkey, which has a cycle lasting only nine days or so.) Furthermore, ovulation during the female cycle occurs spontaneously and is not induced by the act of mating as in many other mammals. Lasting bonds between individual males and females are generally typical of primates, and the process of bonding may be quite intense and drawn out. However, the frequency and duration of mating show great variation between species. As a rule, mating is seen relatively rarely in monogamous primate species, whereas in multi-male species mating may be very frequent, often involving several males for any individual female. One conspicuous feature associated with the female cycle and mating that is found in several Old World monkey species and in chimpanzees is the occurrence of sexual swellings, which reach a peak of size and coloration at about the time of ovulation.

It has often been assumed that primate mating systems are directly related to the patterns found in social groups. For instance, with species living in social groups with a single adult male (monogamous or harem groups), it has been widely assumed that that male is the father of all offspring born in the group. However, in most cases such restricted paternity has not yet been confirmed with genetic tests. Furthermore, there are some harem-living species in which incursions by extra-group males are known to occur quite regularly. This has, for example, been reported for patas monkeys and certain guenons. It has also been widely assumed that in multi-male groups of primates often showing a relatively clear hierarchy among males, paternity is related to male rank. In some cases (e.g., long-tailed macaques and plains baboons), this expectation has been confirmed with genetic tests, but in others (e.g., Barbary and Japanese macaques; hanuman langurs) it has been found that paternity is unrelated to rank.

Intensive parental care is also a hallmark of the primates. In most cases, there is a single offspring, although some prosimian species and marmosets and tamarins typically give birth to two or three infants at a time. All primates have frequent suckling bouts, long lactation periods, and intensive physical contact between the infant(s) and the mother, in some cases because they spend much time together in a nest but usually because the mother carries her infant(s) around with her, clinging to her fur. Incidentally, the characteristic grasping foot of the primates also plays an important role in infant clinging during parental carriage. In many monogamous primate species, the father (sometimes along with other group members) also plays a part in infant carriage. This is seen most conspicuously in certain New World monkeys (marmosets, tamarins, Goeldi's monkey, and owl monkeys), but it is also seen in some monogamous lemurs.

Primates show all possible patterns of breeding over the annual cycle, ranging from year-round breeding with only mild fluctuations right through to strict seasonal breeding, with mating and births restricted to tightly constrained periods of the year. In a few cases, as with the Moholi bushbaby (*Galago moholi*), there are two mating periods and two birth periods during the year. Primate species living in rainforests with year-round rainfall generally show little seasonal restriction in mating and births, although there are some notable exceptions (e.g. squirrel monkeys, *Saimiri*). By contrast, primates living in forests characterized by a marked dry season tend to show some seasonal restriction of breeding. Unusually, almost all lemurs on Madagascar show strictly seasonal breeding patterns, regardless of whether they live in rainforests or in dry forests. The only two exceptions seem to be the aye-aye and the gentle lemurs.

Conservation

In contrast to certain other mammal groups (e.g., artiodactyls, bats), no known primate species has become extinct as yet, but it is probably only a question of time. Indeed, a score of lemur species documented only by subfossils died out about 2,000 years ago, following the initial human invasion of Madagascar, so this may have been the first major wave of human-induced primate extinction. As a rough approximation, it can be said that one third of extant primate species are subjected to some identifiable degree of threat. Close to 120 primate species (out of a total of 350) have been identified as critically endangered, endangered or vulnerable in the IUCN Red List of Threatened Species. The 19 species identified as critically endangered include species in South America, Africa, Madagascar, and Asia. They are the Sumatran orangutan (*Pongo abelii*), a gibbon (*Hylobates moloch*), a macaque (*Macaca pagensis*), a colobus monkey (*Procolobus rufomitratus*), a snub-nosed monkey (*Rhinopithecus avunculus*), two langurs (*Trachypithecus delacouri*, *T. poliocephalus*), two woolly spider monkeys (*Brachyteles arachnoides*, *B. hypoxanthus*), a woolly monkey (*Oreonax flavicauda*), two titi monkeys (*Callicebus barbarabrownae*, *C. coimbrai*), a capuchin monkey (*Cebus xanthosternos*), three lion tamarins (*Leontopithecus caissara*, *L. chrysopygus*, *L. rosalia*), two gentle lemurs (*Hapalemur aureus*, *H. simus*), and a sifaka (*Propithecus tattersalli*). Of the remaining 230 primate species, approximately half are probably threatened to some extent by reduction and fragmentation of habitat, while the other half can be provisionally regarded as relatively common.

Because primates are typically inhabitants of tropical and subtropical forests, the primary threat to natural populations comes from large-scale deforestation. Hunting is also a common threat to primates, although this is only a major menace where modern firearms have replaced traditional hunting methods. In tropical regions of South America, Africa, and Asia, large-scale hunting of primates to provide bushmeat has become an increasing problem. Trapping of certain species for biomedical use or for zoos has also posed a threat in the past, although this has been considerably reduced as a result of increasing awareness of conservation issues.

Recognition of the need for effective conservation measures is reflected by targeted programs in natural habitat areas and by breeding programs in captivity. The World Conservation Union (IUCN) plays a vital coordinating role through such programs as its Species Survival Commission (SSC), which has established a Specialist Group for primates. Extensive coordination of captive breeding has promoted the compilation of more than 30 international studbooks for primate species. In the wild, primates are protected to various extents through a network of national parks and reserves that are primarily designed to preserve tropical and subtropical forests, but effective protection remains an elusive goal in many cases.

Significance to humans

The most prominent use of non-human primates has been in biomedical research, where certain species (notably the rhesus monkey, the baboon, and the common marmoset) have become standard laboratory species. An emphasis on development of breeding programs has greatly reduced the impact of such usage on natural populations.

Some primates—notably macaques—are agricultural pests, raiding various crops (e.g., plantations of fruit trees and even stocks of maniok soaking in water) and occasionally causing major losses.

As a rule, primates are not directly dangerous to humans. Despite their reputation as fierce creatures, gorillas generally avoid contact with humans and their famous charges usually occur only when they feel threatened. Primates that are provisioned by humans, notably macaques, may inflict quite serious bites if they feel threatened. Primates can also represent a threat to humans because they harbor such pathogens as the Marburg and Ebola viruses.

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Robert D. Martin, PhD

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Lorises and pottos

(Lorisidae)

Class Mammalia

Order Primates

Family Lorisidae

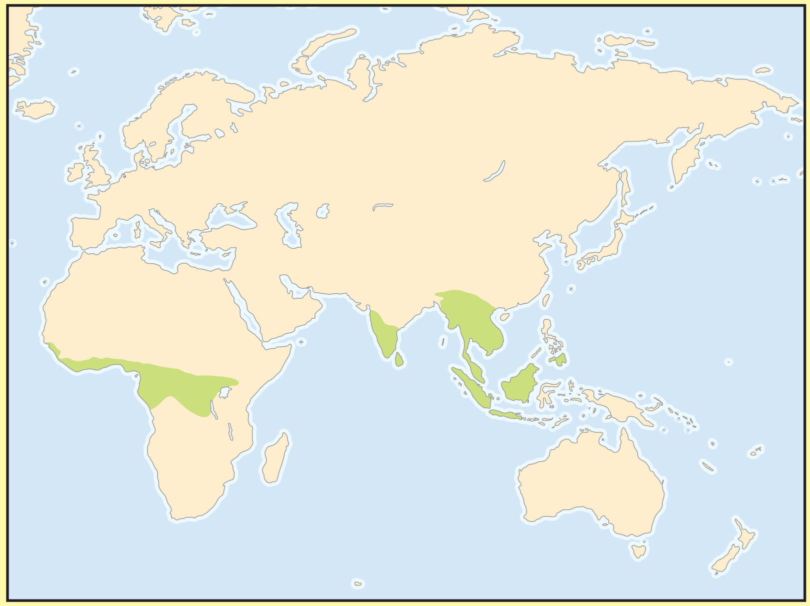
Thumbnail description
Relatively small, fully arboreal mammals inhabiting tropical and subtropical forests; their most prominent features are marked reduction of the tail and of the second digits of the hands and feet, in association with their slow, deliberate locomotion involving powerful grasping

Size
Relatively small body size, ranging from the gray slender loris (head and body length: 8.5 in, 21.5 cm); tail length: virtually zero; body mass 9 oz (255 g) to the potto (head and body length: 15 in, 37.5 cm); tail length: 2.5 in (6.5 cm); body mass 2 lb 11 oz (1,230 g)

Number of genera, species
5 genera; 9 species

Habitat
Lorisids occur in a range of tropical and subtropical forest habitats

Conservation status
Vulnerable: 2 species; Lower Risk/Near Threatened: 2 species; Data Deficient: 1 species



Distribution
Forested areas of Africa, Asia, and Southeast Asia

Evolution and systematics

Together with the bushbabies (family Galagidae), the lorises constitute the monophyletic infraorder Lorisiformes, which is the sister group of the Lemuriformes (Malagasy lemurs). The Lorisiformes and the Lemuriformes together form a monophyletic assemblage of strepsirrhine primates, which are characterized by retention of the rhinarium (a moist area of naked skin surrounding the nostrils), by non-invasive epitheliochorial placentation and by the derived, diagnostic feature of a toothcomb containing 4 incisors and 2 canines in the lower jaw. The two subfamilies of lorisids (Lorisinae and the Perodictinae) are probably monophyletic subgroups. However, both subfamilies contain slender, small-bodied species and stocky, large-bodied species that are superficially similar but probably developed convergently.

The fossil record for lorisids is very limited. A few isolated teeth of *Karanisia* indicate that members of the family may have been present in Egypt during the late Eocene. A skull of the early Miocene genus *Mioeuoticus* from Kenya provides the earliest well-preserved evidence for the existence of the family. Fragmentary remains of the late Miocene *Pronycticeboides* shows that the family was present in the Indian subcontinent at least by that stage. Given this sparse fossil record, it is not possible to infer a reliable date for the origin of the lorisids.

It has been proposed, on technical grounds of priority, that the family name "Lorisidae" should be changed to "Loridae." Because the customary name "Lorisidae" has been used so widely and for such a long period of time, the International Committee on Zoological Nomenclature has recently validated Lorisidae.

Physical characteristics

Body shape varies from slender (angwantibos and slender lorises) to stocky (pottos and slow lorises), but in all species the tail is markedly reduced to virtually absent (more so in the Asiatic species than in the African species). The head is short and broad at the back; the snout is also short. The eyes are quite large and oriented obliquely upwards rather than directly forwards. The ears are medium-sized and covered with hair. The arms and legs are approximately equal in length. As in sloths, the circulatory system of the limbs is organized into a network of fine blood vessels (rete mirabile) to permit prolonged contraction of the muscles without exhaustion. In the hands and feet, the first digits

A potto (*Perodicticus potto*) in the daytime, resting in a tree hole in Ituri Rainforest Reserve near Epulu, Democratic Republic of the Congo. (Photo by Bruce Davidson/Naturepl.com. Reproduced by permission.)

(thumb and the big toe) are strongly divergent, permitting powerful grasping, while the second finger and toe are very short to vestigial, enhancing the pincer action. All digits (fingers and toes) bear nails, although the nail on the second toe is elongated and angled obliquely upwards to form a "grooming claw."

Distribution

Slender lorises occur in Asia (India and Sri Lanka), slow lorises are widely distributed in South-East Asia, and pottos and angwantibos occur in tropical/subtropical regions of West and Central Africa.

Habitat

Lorisids occur in a range of forest habitats. They most commonly inhabit evergreen tropical rainforest, but also occur in dry, semi-deciduous forest, scrub forest, swamps, and montane forest up to middling altitudes.

A young pygmy slow loris (*Nycticebus pygmaeus*) forages at night. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

Behavior

All lorisids show cryptic behavior, moving slowly and deliberately through the trees while foraging. This seems to be their primary strategy for avoidance of predation. In fact, members of this family all have low basal metabolic rates, so

A potto (*Perodicticus potto*) in day nesting hole in Ituri Rainforest Reserve near Epulu, Democratic Republic of the Congo. (Photo by Animals Animals ©Bruce Davidson. Reproduced by permission.)

A slender loris (*Loris tardigradus*) with trumpet creeper flowers. (Photo by Animals Animals ©David Haring. Reproduced by permission.)

A potto (*Perodicticus potto*) in a tree in Ituri Rainforest Reservation near Epulu, Democratic Republic of the Congo. (Photo by Animals Animals ©Bruce Davidson. Reproduced by permission.)

The Sunda slow loris (*Nycticebus coucang*) is a relatively common species. (Photo by Animals Animals ©Mark Stouffer. Reproduced by permission.)

they are probably constrained to slow movement for energetic reasons. All species show scent marking. They have specialized marking glands in the genital region (scrotal and vulval glands) and some of them (e.g., slender loris) perform "urine washing" in which the palms of the hands and the soles of their feet are impregnated with urine before being applied to the substrate.

Feeding ecology and diet

Members of this family typically consume a mixed diet of fruit and arthropods (mainly insects), and they may also eat small vertebrates and birds' eggs. The proportions of fruit and arthropods vary between species, with small-bodied species tending to be more insectivorous and large-bodied species tending to be more frugivorous. There is a common tendency to feed on insect species that are generally regarded as unpalatable. Some species include plant exudates (gums) in their diets, and the pygmy slow loris (*Nycticebus pygmaeus*) may be a specialized gum-feeder.

The pygmy slow loris (*Nycticebus pygmaeus*) is found in China, Vietnam, and Laos. A juvenile is pictured here. (Photo by Rod Williams/Naturepl.com. Reproduced by permission.)

Reproductive biology

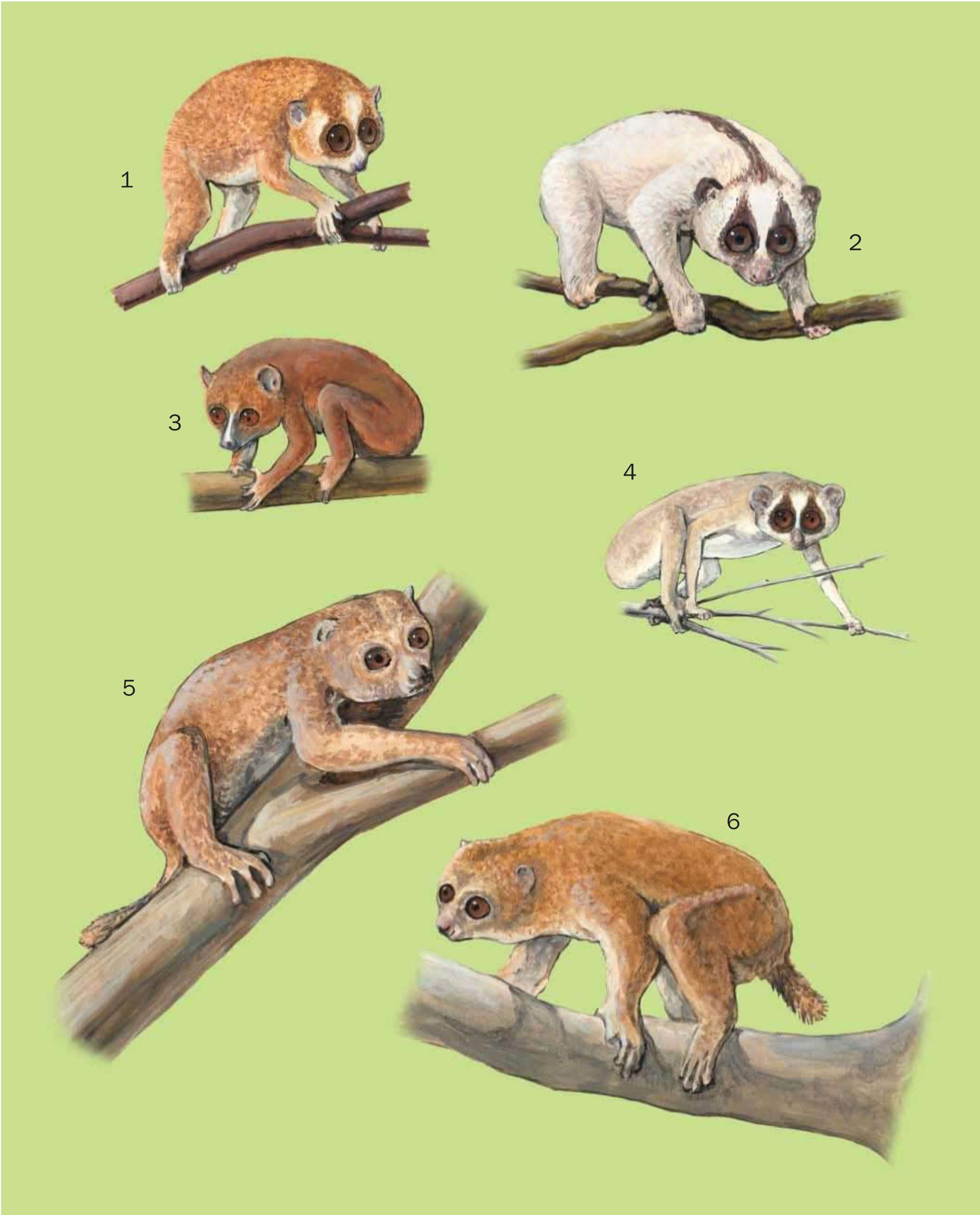
Most species typically have one offspring, but the pygmy slow loris often has twins. Prior to independence, the infant is typically carried around clinging to the mother's fur, and "parking" of the infant on a small branch while the mother is foraging seems to be characteristic of all species. Gestation periods are notably long relative to body size, ranging from 134 to 193 days according to species. All lorisids have non-invasive epithelichorial placentation, and are probably polygamous.

Conservation status

Four species are thought to be relatively common. No species are listed as endangered, but two are Vulnerable (*Loris tardigradus* and *Nycticebus pygmaeus*) and two are Near Threatened (*Arctocebus aureus* and *Arctocebus calabarensis*). One species, *Nycticebus bengalensis*, is listed as Data Deficient.

Significance to humans

Lorisids seem to be of no real significance to local human populations, although the larger-bodied species may occasionally be eaten.



1. Pygmy slow loris (*Nycticebus pygmaeus*); 2. Sunda slow loris (*Nycticebus coucang*); 3. Calabar angwantibo (*Arctocebus calabarensis*); 4. Gray slender loris (*Loris lydekkerianus*); 5. False potto (*Pseudopotto martini*); 6. Potto (*Perodicticus potto*). (Illustration by Brian Cressman)

Species accounts

Gray slender loris
Loris lydekkerianus

SUBFAMILY
Lorisinae

TAXONOMY
Loris tardigradus lydekkerianus Cabrera, 1908. *Loris tardigradus* was traditionally the only species recognized in this genus, but the far more widely distributed and larger-bodied gray slender loris is now regarded as a separate species (*L. lydekkerianus*) containing four subspecies.

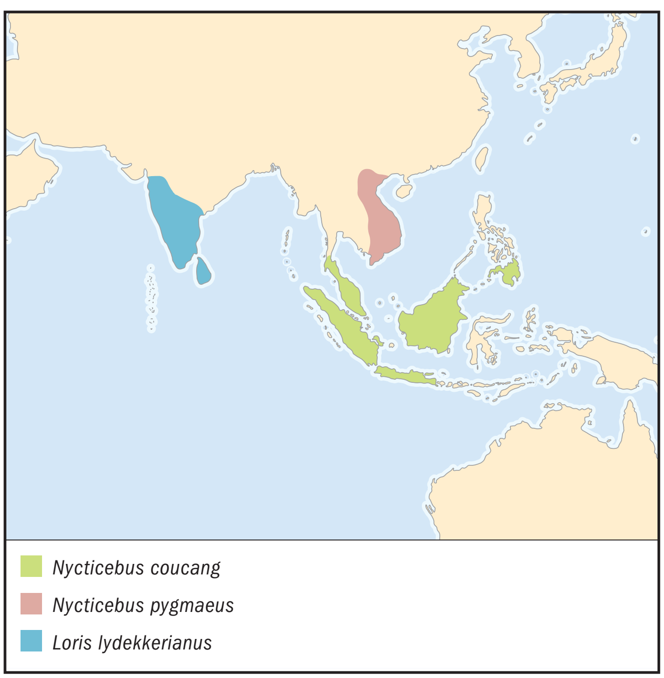
OTHER COMMON NAMES
French: Loris grèle; German: Grauer Schlanklori.

PHYSICAL CHARACTERISTICS
Relatively small, with a slender body and spindly limbs. Eyes are conspicuously large, while the snout is narrow. Fur reddish brown dorsally and grayish brown ventrally. Eyes surrounded by dark reddish brown rings. No dorsal stripe present. Head and body length: 8.5 in (21.5 cm); tail length: virtually zero. Body mass: males 9 oz (255 g); females 9 oz (255 g).

DISTRIBUTION
Southern India and Sri Lanka.

HABITAT
Deciduous forest zones.

BEHAVIOR
Nocturnal and fully arboreal. Forages solitarily at night, but individual males and females have social contacts within overlapping ranges. No nests are constructed; animals typically sleep clinging to a branch among dense foliage.



FEEDING ECOLOGY AND DIET
Diet consists primarily of arthropods (mainly insects) with a supplement of fruits along with occasional eggs and small vertebrates (e.g., geckos and other lizards).

REPRODUCTIVE BIOLOGY
Probably polygamous. Typically gives birth to a single offspring. Gestation period 168 days.

CONSERVATION STATUS
Because of its large geographical range, this species does not seem to be immediately threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Sunda slow loris
Nycticebus coucang

SUBFAMILY
Lorisinae

TAXONOMY
Nycticebus coucang (Boddaert, 1785), Malacca, Malaysia. For many years, this was the only species recognized in the genus *Nycticebus*. However, it became increasingly evident that a separate species should be recognized for the much smaller pygmy slow loris (*Nycticebus pygmaeus*), and it is also justifiable to give specific rank to the Bengal slow loris (*Nycticebus bengalensis*). After removal of these two species, the remaining species *Nycticebus coucang* contains 3 subspecies.

OTHER COMMON NAMES
French: Nyticèbe; German: Plumplori.

PHYSICAL CHARACTERISTICS
Medium-sized slow loris. Fur pale brown dorsally and buffy white ventrally. A wide brown midline stripe runs down the back. Head and body length: 12.5 in (31 cm); tail length: virtually zero. Body mass: males 1 lb 8 oz (680 g); females 1 lb 6 oz (625 g).

DISTRIBUTION
Malaysian Peninsula south of the Isthmus of Kra, Sumatra and nearby islands, Java, Borneo and neighboring islands.

HABITAT
Evergreen tropical rainforest, with a preference for forest edges.

BEHAVIOR
Nocturnal and fully arboreal.

FEEDING ECOLOGY AND DIET
Feeds primarily on fruit, with a complement of arthropods (mainly insects) and some gums. Also eats eggs and small vertebrates. Reportedly concentrates on insects with a repugnant taste and/or smell.

REPRODUCTIVE BIOLOGY
Believed to be polygamous. Typically gives birth to single offspring. Gestation period 191 days.

CONSERVATION STATUS
Relatively common and not immediately threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Pygmy slow loris
Nycticebus pygmaeus

SUBFAMILY
Lorisinae

TAXONOMY
Nycticebus pygmaeus Bonhote, 1907, Nhatrang, Vietnam. This dwarf form of the slow loris was traditionally included in the species *Nycticebus coucang*, but it is now recognized as a separate species. In fact, *Nycticebus pygmaeus* has a more limited geographical range, overlapping extensively with that of *Nycticebus coucang*.

OTHER COMMON NAMES
English: Pygmy loris; French: Nycticèbe nain; German: Zwergplumplori.

PHYSICAL CHARACTERISTICS
Small-bodied slow loris. Fur bright orange-brown dorsally and orange-tinted gray ventrally. Midline dorsal stripe is faint or completely lacking. Head and body length: 10 in (25.5 cm); tail length: virtually zero. Body mass: males 11 oz (310 g); females 11 oz (310 g).

DISTRIBUTION
East of the Mekong River in the southernmost part of China, Laos, eastern Cambodia, and Vietnam.

HABITAT
Evergreen tropical rainforests, with a preference for secondary growth.

BEHAVIOR
Nocturnal and fully arboreal. Forages solitarily at night. Does not use nests, but sleeps clinging to branches in dense foliage.

FEEDING ECOLOGY AND DIET
Combined diet of fruit, arthropods, and gum. A habit of gouging wood with the toothcomb that has been observed in captivity suggests that this species may be a specialized gum-feeder.

REPRODUCTIVE BIOLOGY
Gives birth to singletons or twins with approximately equal frequency. Gestation period 192 days. Mating system is not known.

CONSERVATION STATUS
Listed as Vulnerable.

SIGNIFICANCE TO HUMANS
None known. ◆

Calabar angwantibo
Arctocebus calabarensis

SUBFAMILY
Perodictinae

TAXONOMY
Arctocebus calabarensis (J. A. Smith, 1860), Old Calabar, Nigeria. Most classifications have recognized only a single species in the genus *Arctocebus*, but there are convincing reasons for raising the golden angwantibo to the rank of a separate species (*Arctocebus aureus*).

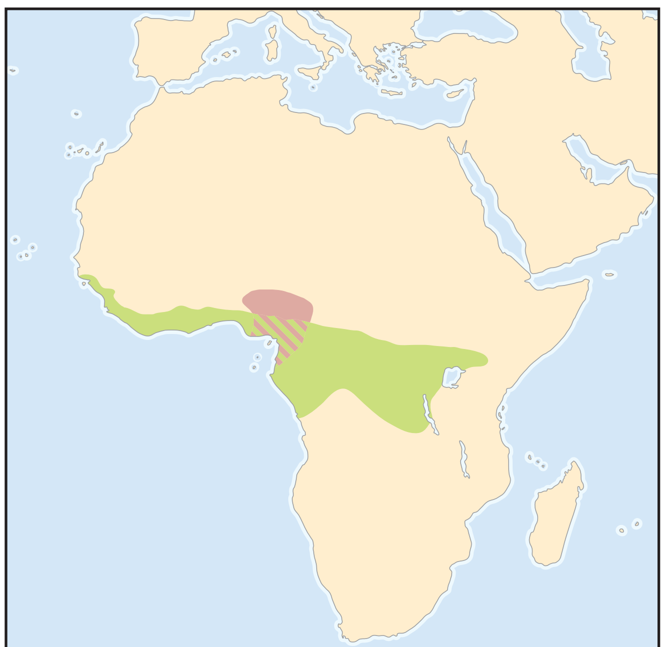
OTHER COMMON NAMES
English: Golden potto; French: Arctocèbe; German: Bärenmaki.

PHYSICAL CHARACTERISTICS
Relatively small, with a slender body. Second finger and toe even more reduced than in lorisines. Fur orange-brown dorsally and white or pale gray to buff ventrally. Head and body length: 9.5 in (24 cm); tail length: 3 in (8 cm). Body mass: males 11 oz (310 g); females 11 oz (315 g).

DISTRIBUTION
Cameroon and Nigeria, north of the Sanaga River and extending westward to the Niger River.

HABITAT
Evergreen tropical rainforests of equatorial Africa, including both primary and secondary forests.

BEHAVIOR
Nocturnal and fully arboreal. Typically moves around slowly and deliberately among fine branches, and is generally cryptic. Forages solitarily, but individual males and females have social contacts through overlapping home ranges.



Perodicticus potto
Arctocebus calabarensis

FEEDING ECOLOGY AND DIET
Feeds predominantly on arthropods (mainly insects) with a complement of fruit.

REPRODUCTIVE BIOLOGY
Typically gives birth to a single infant. Gestation period 134 days. Mating system is not known.

CONSERVATION STATUS
Listed as Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Potto
Perodicticus potto

SUBFAMILY
Perodictinae

TAXONOMY
Perodicticus potto (Müller, 1766), Elmina, Ghana. Three subspecies recognized. It is likely that there are several cryptic potto species that will be recognized once a thorough review has been conducted.

OTHER COMMON NAMES
French: Potto de Bosman; German: Potto.

PHYSICAL CHARACTERISTICS
Fur dark brown dorsally and paler brown ventrally. Second finger and toe even more reduced than in lorisines. There are long processes on most of the neck vertebrae and on the first two thoracic vertebrae. The shoulder region is covered by a protective scapular shield through which the vertebral spines protrude. Head and body length: 15 in (37.5 cm); tail length: 2.5 in (6.5 cm). Body mass: males 2 lb 12 oz (1,250 g); females 2 lb 11 oz (1,210 g).

DISTRIBUTION
Equatorial Africa, from Nigeria in the west to western regions of Uganda and Kenya in the east. Range includes Sierra Leone, Ghana, Cameroon, Equatorial Guinea, Congo-Brazzaville, and Democratic Republic of the Congo (Zaïre).

HABITAT
Evergreen tropical rainforests of equatorial Africa, both primary and secondary, and wooded savanna.

BEHAVIOR
Nocturnal and fully arboreal. Generally cryptic, with ponderous, slow-moving locomotion. Responds to predators by presenting its upper back region, which is protected by a scapular shield and long vertebral spines. Individuals forage solitarily, but an adult male may have social contact with one or more females through range overlap. No nests are constructed; individuals simply sleep in dense foliage.

FEEDING ECOLOGY AND DIET
Feeds primarily on fruits, but complements its diet with arthropods (mainly insects) and gums. Particularly consumes insects that are generally unpalatable, such as ants.

REPRODUCTIVE BIOLOGY
May be polygamous. Typically gives birth to a single infant. Gestation period 193 days.

CONSERVATION STATUS
Relatively common and not immediately threatened, although it is possible that there are several potto species, some of which may be threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

False potto
Pseudopotto martini

SUBFAMILY
Perodictinae

TAXONOMY
Pseudopotto martini Schwartz, 1996, West Africa. This new genus and species was first recognized in 1996 on the basis of a museum skeleton of uncertain origin.

OTHER COMMON NAMES
None (because of the recent discovery of this genus and species).

PHYSICAL CHARACTERISTICS
External appearance unknown. Head and body length: unknown; tail length: unknown, but the type skeleton indicates that it is certainly longer than in the potto. Body mass: unknown.

DISTRIBUTION
The type specimen reportedly came from an unknown locality in equatorial West Africa, while a second specimen came from Cameroon. (Specific distribution map not available.)

HABITAT
Evergreen tropical rainforest.

BEHAVIOR
Presumably nocturnal and fully arboreal.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Golden angwantibo *Arctocebus aureus* French: Arctocèbe doré; German: Goldener Barenmaki	Fur reddish brown dorsally and reddish buff ventrally. Head and body length: 10 in (24.5 cm); tail length: 0.5 in (1.5 cm). Body mass: males and females 7.5 oz (210 g).	Inhabits evergreen tropical rainforests of equatorial Africa, including both primary and secondary forests. Nocturnal and fully arboreal. Typically moves around slowly and deliberately among fine branches, and is generally cryptic. Forages solitarily, but individual males and females have social contacts through overlapping home ranges.	Cameroon, Congo, and Gabon.	Feeds predominantly on arthropods (mainly insects) with a complement of fruit.	Lower Risk/Near Threatened
Slender loris *Loris tardigradus* French: Lori grèe rouge; German: Roter Schlanklori	Fur reddish brown dorsally and reddish gray ventrally. Head and body length: 8 in (19.5 cm); tail length: virtually zero. Body mass: approximately 4.5 oz (125 g).	Lives in humid tropical forest. Nocturnal and fully arboreal. Forages solitarily at night, but individual males and females have social contacts within overlapping ranges. No nests are constructed; animals typically sleep clinging to a branch among dense foliage.	Southwestern Sri Lanka.	Diet consists primarily of arthropods (mainly insects) with a supplement of fruits and occasional small vertebrates.	Vulnerable
Bengal slow loris *Nycticebus bengalensis* French: Nycticèbe de Bengal; German: Bengalplumplori	Fur orange-buff dorsally and cream-gray ventrally; strong frosting on neck and limbs. Head and body length: 12.5 in (31 cm); tail length: virtually zero. Body mass: males 2.4 lb (1.1 kg); females 2.25 lb (1.0 kg).	Inhabits evergreen tropical rainforest. Nocturnal and fully arboreal.	Northeastern India, Bangladesh, China, and northern part of Thailand.	Feeds primarily on fruit, supplemented with arthropods (mainly insects) and perhaps some gum. Probably also eats eggs and small vertebrates.	Data Deficient

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Robert D. Martin, PhD

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Bushbabies

(Galagidae)

Class Mammalia
Order Primates
Family Galagidae

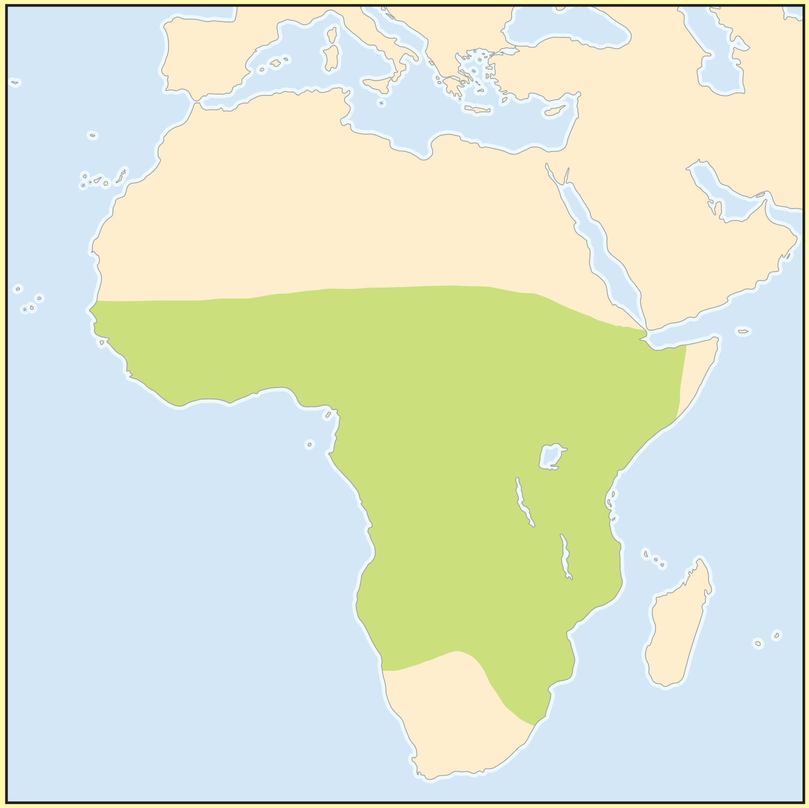
Thumbnail description
Relatively small mammals with a long, often bushy tail; fur coloration varies from gray to black dorsally and from white to orange-buff ventrally; eyes large and oriented obliquely forwards; ears membranous and moderate to large; hindlimbs markedly longer than forelimbs; all digits of the hand and foot bear nails

Size
Relatively small body size, ranging from Demidoff's bushbaby (head and body length: 5 in [13 cm]; tail length: 7 in [18 cm]); body mass: males 2.5 oz [65 g]; females 2 oz [55 g]) to the Brown greater bushbaby (head and body length: 12.5 in [31.5 cm]; tail length: 16.5 in [41 cm]; body mass: males 2 1b 10 oz [1,190 g]; females 2 1b 7 oz [1,110 g])

Number of genera, species
4 genera; 20 species

Habitat
Inhabit a wide spectrum of forest and woodland types, from dry, thorny scrub to evergreen tropical rainforest

Conservation status
Endangered: 1 species; Lower Risk/Near Threatened: 6 species; Data Deficient: 2 species



Distribution
Widespread occurrence throughout Africa

Evolution and systematics

For several decades, all bushbaby (or galago) species were generally allocated to the single genus *Galago*, but it was eventually recognized that there are major differences between the species and up to 4 different genera are now recognized (*Euoticus*, *Galago*, *Galagoides*, and *Otolemur*). Molecular evidence indicates that divergence between these four genera took place at a very early stage, although the relationships between them have not been clearly established.

Together with the lorises (subfamily Lorisinae) and pottos (subfamily Perodictinae) in the family Lorisidae, the bushbabies constitute the monophyletic infraorder Lorisiformes, which is the sister group of the Lemuriformes (Malagasy lemurs). The Lorisiformes and the Lemuriformes together form a monophyletic assemblage of strepsirrhine primates, which are characterized by retention of the rhinarium (a moist area of naked skin surrounding the nostrils), by non-invasive epitheliochorial placentation and by possession of a toothcomb containing four incisors and two canines in the lower jaw as a derived, diagnostic feature. The bushbabies (family Galagidae) almost certainly belong to a monophyletic assemblage, but the relationships between bushbabies, lorises and pottos remain unclear.

For many years, the fossil record for bushbabies was limited to two early Miocene genera from East Africa (*Komba* and *Progalago*). These Miocene forms have now been supplemented by isolated teeth from late Eocene deposits in Egypt, showing resemblances to modern bushbabies and allocated to the genus *Saharagalago*. Thus, fossil evidence indicates that the families Lorisidae and Galagidae have existed as separate lineages for at least 38 million years.

It was proposed, on technical grounds of priority, that the family name "Galagidae" be changed to "Galagonidae." Because the usual name "Galagidae" has been in widespread use for a very long time, however, the International Committee on Zoological Nomenclature retained the name officially.

Physical characteristics

Bushbabies are relatively small mammals. The tail, which is often bushy, is always long in comparison to the body and

A Demidoff's bushbaby (*Galagoides demidoff*) climbs in the trees of central Africa. (Photo by Animals Animals ©Mark Stouffer. Reproduced by permission.)

is actively used in locomotion. According to species, fur coloration ranges from gray to black dorsally and from white to orange-buff ventrally. The eyes are relatively large and oriented obliquely forwards. The ears, which are membranous and moderate to large in size, can be folded concertina-fashion. In the skull, there is a bony strut (postorbital bar) on the outer margin of the eye socket. The dental formula is (I2/2 C1/1 P3/3 M3/3) $\times$ 2 = 36 total teeth. In the lower jaw, the crowns of the four incisors (two on each side) and

The Senegal bushbaby (*Galago senegalensis*) has thick pads on the ends of its fingers to help with locomotion through the trees. (Photo by © Gallo Images/Corbis. Reproduced by permission.)

The brown greater bushbaby (*Otolemur crassicaudatus*). (Photo by John Shaw. Bruce Coleman, Inc. Reproduced by permission.)

the two canines (one on each side) are angled forwards to form a dental comb that is used both for feeding and for grooming the fur. The hindlimbs are markedly longer than the forelimbs. All digits of the hand and foot bear nails, although the second toe bears an elongated nail ("grooming claw") that is angled away from the dorsal surface. Mild sexual dimorphism in body size is present in some bushbabies but absent in others.

Distribution

Bushbabies occur exclusively in Africa, but have a very wide distribution on that continent.

Habitat

Bushbabies are found in a wide variety of habitats, ranging from dry, thorny scrub to evergreen tropical rainforests. There is a fairly clear separation between species that occur in evergreen rainforests and those that live in dry deciduous forests.

The northern greater bushbaby (*Otolemur garnettii*) is mainly frugivorous. (Photo by Tom & Pat Leeson/Photo Researchers, Inc. Reproduced by permission.)

A Senegal bushbaby (*Galago senegalensis*) leaps to a new branch. (Photo by Animals Animals ©Stephen Dalton. Reproduced by permission.)

A Demidoff's bushbaby (*Galago demidoff*) climbs a tree. (Photo by Bruce Davidson/Naturepl.com. Reproduced by permission.)

Behavior

All bushbabies are typically arboreal and nocturnal. They have a reflecting layer (tapetum lucidum) behind the retina. It has been shown for the thick-tailed bushbaby (*Otolemur crassicaudatus*) that flat crystals of riboflavin are responsible for the reflecting properties of the tapetum and the resulting golden yellow eyeshine. Although all bushbaby species have relatively long hindlimbs, with conspicuous elongation of the calcaneum and navicular in the ankle region, there is considerable variation in their patterns of locomotion. Most species are active leapers, but only some of them are specialized vertical-clingers and leapers that can jump several meters between supports and show bipedal hopping along broad horizontal branches and on the ground (e.g., *Galago alleni* and *Galago moholi*). Many species are primarily quadrupedal (e.g., *Galagoides demidoff* and *Otolemur garnettii*), and some (e.g., *Otolemur crassicaudatus*) leap relatively rarely. All species show scent marking of some kind and most if not all show the unusual pattern of "urine washing" in which the palms of the hands and the soles of the feet are impregnated with urine, such that urine traces are deposited on the substrate during locomotion. Although most of them are solitary foragers, all bushbabies live in social networks of some

A Senegal bushbaby (*Galago senegalensis*). (Photo by Peter Davey. Bruce Coleman, Inc. Reproduced by permission.)

kind, involving occasional encounters within overlapping ranges of adult males and females and sharing of nest sites during the daytime. Species differ in features such as the number of individuals in a social network, the amount of contact shown during nocturnal activity, the degree of tolerance among adults and subadults of the same sex, and the stability of nesting groups.

Feeding ecology and diet

The basic diet of most bushbaby species is a mixture of fruit and arthropods (mainly insects), although small vertebrates, eggs, gum and other items may also be eaten. The proportions of arthropods and fruits in the diet vary from species to species. Small-bodied species tend to be more insectivorous, while large-bodied species tend to be more frugivorous. Some bushbaby species include quite large amounts of gum in their diets, and the needle-clawed bushbabies (e.g., *Euoticus* species) are specialized gum-feeders, feeding predominantly on that resource.

Reproductive biology

Bushbabies are polygynous. Most species give birth to a single infant, but some regularly produce twins, and triplets can also occur. All species have non-invasive epitheliochorial placentation. Average gestation period lasts between 112 and 136 days according to species. All species show maternal carriage of the infant(s), usually in the mouth but in certain cases (e.g., *Otolemur crassicaudatus*) also clinging to the mother's fur.

Conservation status

Most species are thought to be relatively common. One species is endangered (*Galago rondoensis*) and six are Near Threatened (*Euoticus elegantulus*, *Euoticus pallidus*, *Galago alleni*, *Galago gallarum*, *Galago matschiei*, and *Galago zanzibaricus*). Two species are listed as Data Deficient (*Galago granti* and *Galago orinus*).

Significance to humans

Bushbabies seem to be of no real significance to local human populations, although the larger-bodied species may occasionally be eaten.

1. Demidoff's bushbaby (*Galagoides demidoff*); 2. Senegal bushbaby (*Galago senegalensis*); 3. Gabon Allen's bushbaby (*Galago gabonensis*); 4. Southern needle-clawed bushbaby (*Euoticus elegantulus*); 5. Moholi bushbaby (*Galago moholi*); 6. Zanzibar bushbaby (*Galagoides zanzibaricus*); 7. Brown greater bushbaby (*Otolemur crassicaudatus*); 8. Northern greater bushbaby (*Otolemur garnettii*). (Illustration by Brian Cressman)

Species accounts

Southern needle-clawed bushbaby
Euoticus elegantulus

SUBFAMILY
Galaginae

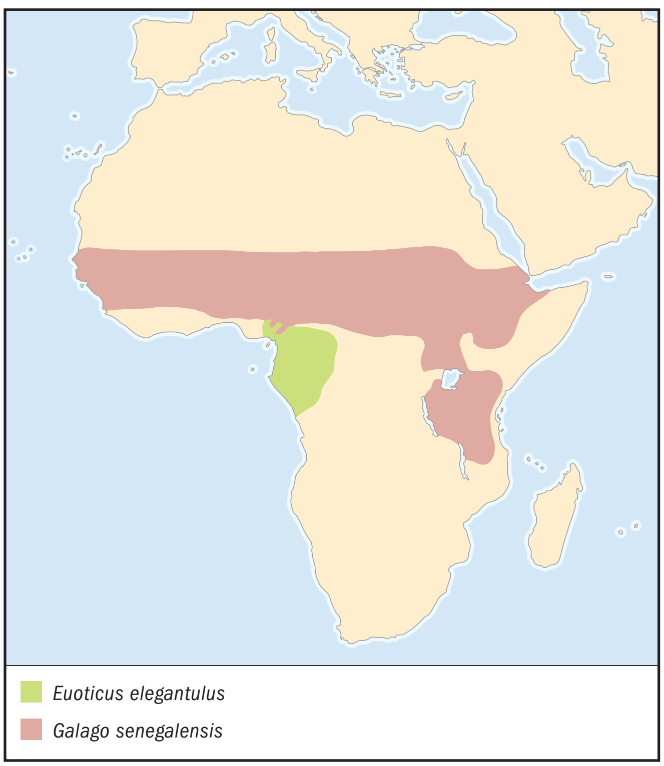
TAXONOMY
Euoticus elegantulus (Le Conte, 1857), West Africa. In many former classifications, this species included the northern needle-clawed bushbaby as a subspecies, but that form is now recognized as the separate species *Euoticus pallidus.*

OTHER COMMON NAMES
French: Galago élégant; German: Südlicher Kielnagelgalago; Spanish: Abolí, galago elegante.

PHYSICAL CHARACTERISTICS
Fur bright rufous brown dorsally and gray-white ventrally. Mandibular tooth comb notably elongated relative to other teeth. Nails on fingers and toes are strongly keeled and bear sharp tips ("needle-claws"). Head and body length: 8.6 in (21.5 cm); tail length: 12 in (29.5 cm). Body mass: males 10 oz (285 g); females 9 oz (260 g).

DISTRIBUTION
Equatorial West Africa: Gabon, Equatorial Guinea, Congo-Brazzaville, and Cameroon.

HABITAT
Primary and secondary evergreen tropical rainforest.



BEHAVIOR
Nocturnal and fully arboreal. A primarily quadrupedal active leaper.

FEEDING ECOLOGY AND DIET
This bushbaby is a specialized gum-feeder and its "needle claws" are typically used for clinging to broad trunk surfaces while collecting gum. In addition to gum, it eats a certain quantity of arthropods (mainly insects). Solitary foraging is the rule, but little is known about the social organization of this species.

REPRODUCTIVE BIOLOGY
Polygynous. Typically gives birth to a single infant. Infants are carried both on the mother's fur and in her mouth. Breeds throughout the year in Gabon. Gestation period unknown.

CONSERVATION STATUS
Listed as Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Gabon Allen's bushbaby
Galago gabonensis

SUBFAMILY
Galaginae

TAXONOMY
Galago gabonensis Gray, 1863. Originally included in the species *Galago alleni*, which is now restricted to the form found on Bioko Island.

OTHER COMMON NAMES
French: Galago d'Allen gabonais; German: Buschwaldgalago; Spanish: Gálago de Allen.

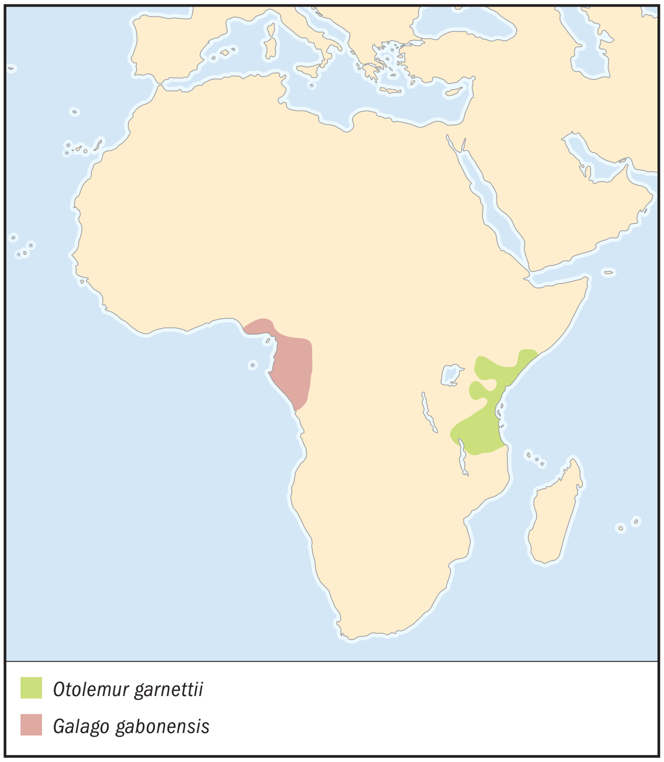
PHYSICAL CHARACTERISTICS
Fur gingery brown dorsally and pale gray with a yellow tone ventrally. Limbs bright orange. Overall light coloration is distinctive. Head and body length: 8.5 in (21.5 cm); tail length: 10 in (24.5 cm). Body mass: males 10 oz (280 g); females 9.5 oz (270 g).

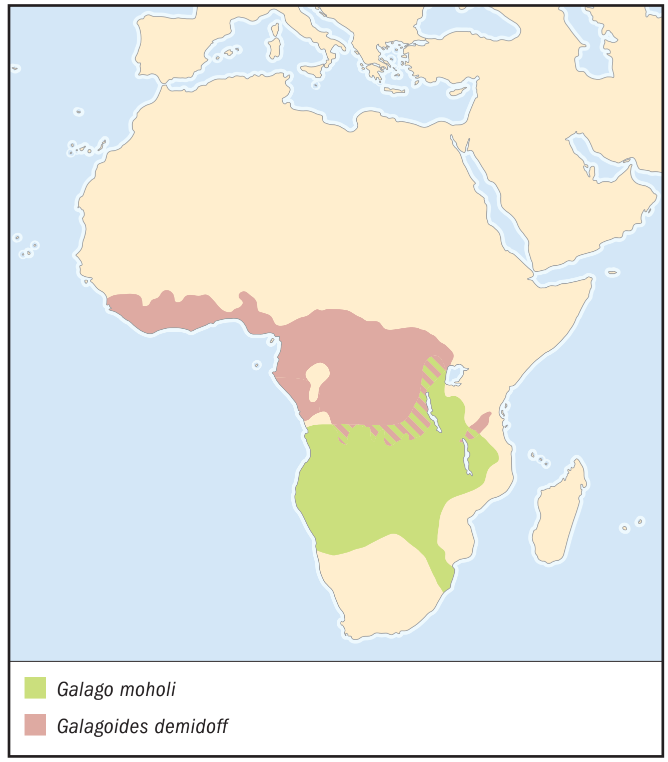
DISTRIBUTION
Cameroon, Río Muni, Gabon, and Congo Republic.

HABITAT
Evergreen tropical rainforests.

BEHAVIOR
Nocturnal and primarily arboreal, but preferentially occupies the forest understorey and frequently descends to ground to feed. Specialized vertical-clinger-and-leaper. Forages solitarily, but adult males and females form social networks through occasional contacts by night in overlapping ranges and sharing of nests by day. Adult males are notably aggressive in their interactions.

FEEDING ECOLOGY AND DIET
Feeds primarily on fallen fruit, with a complement of arthropods (mainly insects).





REPRODUCTIVE BIOLOGY
Polygynous. Typically gives birth to a single infant. Breeds throughout the year in Gabon. Gestation period 135 days.

CONSERVATION STATUS
Relatively common and not immediately threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Moholi bushbaby
Galago moholi

SUBFAMILY
Galaginae

TAXONOMY
Galago moholi A. Smith, 1836, Marico-Limpopo confluence, west Transvaal, South Africa. Originally included within the larger-bodied species *Galago senegalensis*, but now recognized as a distinct species.

OTHER COMMON NAMES
English: Southern lesser bushbaby; French: Galago de Moholi; German: Moholigalago.

PHYSICAL CHARACTERISTICS
Fur typically gray dorsally and white with a distinct yellowish tinge ventrally. Eyes surrounded by thick, dark eye-rings separated by a pale nasal stripe. Head and body length: 6 in (15 cm); tail length: 9 in (22.5 cm). Body mass: males 7.5 oz (210 g); females 6.5 oz (190 g).

DISTRIBUTION
Southern Africa in northern Namibia and Botswana, Angola, southwestern Tanzania, northern Mozambique and South Africa down to Kwazulu-Natal.

HABITAT
Deciduous woodland and wooded savanna, including thorny scrub vegetation.

BEHAVIOR
Nocturnal and essentially arboreal, occasionally descending to the ground while foraging. Specialized vertical-clinger-and-leaper. Hops along bipedally when on the ground. Foraging is typically solitary, but adult males and females form social networks based on occasional contacts in overlapping ranges during the night and variable sharing of nests during the daytime. Prime adult males are tolerant to other males and show extensive range overlap with them. This is reflected in the variable paternity of offspring born in a social network.

FEEDING ECOLOGY AND DIET
Feeds primarily on gum and arthropods (predominantly insects).

REPRODUCTIVE BIOLOGY
Polygynous. Typically gives birth to twins. Gestation period 124 days. Two clear birth peaks per year, separated by 4 months.

CONSERVATION STATUS
Relatively common and not immediately threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Senegal bushbaby
Galago senegalensis

SUBFAMILY
Galaginae

TAXONOMY
Galago senegalensis E. Geoffroy, 1796, Senegal. Originally included the Moholi bushbaby, which is now recognized as a separate species (*Galago moholi*).

OTHER COMMON NAMES
English: Northern lesser bushbaby; French: Galago du Sénégal; German: Senegalgalago.

PHYSICAL CHARACTERISTICS
Fur almost pure gray dorsally and yellowish white ventrally. Eyes surrounded by thick, dark eye-rings separated by a pale nasal stripe. Head and body length: 6.5 in (16.5 cm); tail length: 10.5 in (26 cm). Body mass: males 11 oz (315 g); females 9 oz (250 g).

DISTRIBUTION
Range extends from Senegal in the west across to northern Somalia in the east and southward in East Africa to the southern limit of Tanzania.

HABITAT
Deciduous woodland savanna and open woodlands.

BEHAVIOR
Nocturnal and essentially arboreal, occasionally descending to the ground while foraging. Specialized vertical-clinger-and-leaper. Little studied in the wild, so the social system is unknown.

FEEDING ECOLOGY AND DIET
Feeds primarily on gum and arthropods (mainly insects). May eat some fruit as well.

REPRODUCTIVE BIOLOGY
Polygynous. Single births are typical, although twins are born occasionally. Gestation period 142 days. Two clear birth peaks per year, separated by 4 months.

CONSERVATION STATUS
Relatively common and not immediately threatened.

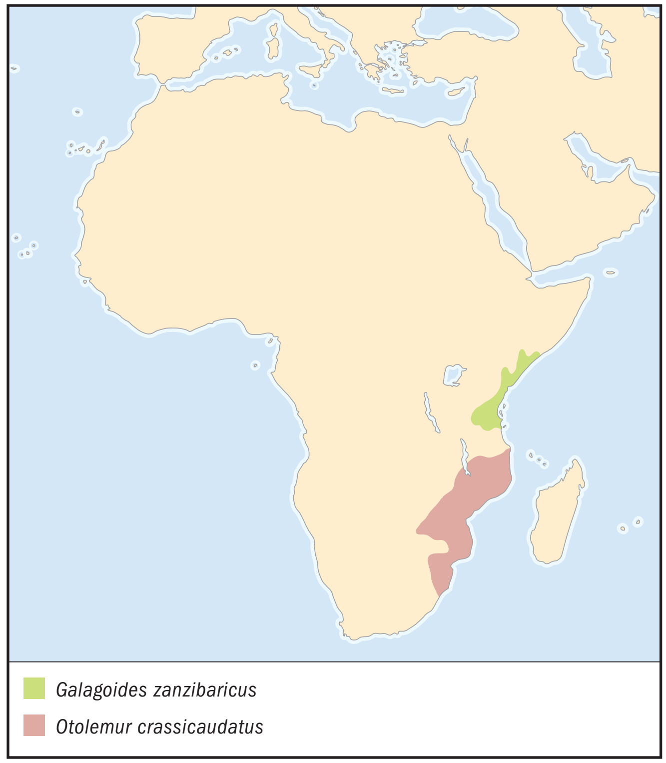
SIGNIFICANCE TO HUMANS
None known. ◆

Zanzibar bushbaby
Galagoides zanzibaricus

SUBFAMILY
Galaginae

TAXONOMY
Galago zanzibaricus, (Matschie, 1893), Yamhiani, Zanzibar, Tanzania. Long regarded as a subspecies of the considerably larger-bodied *Galago senegalensis* but now recognized as a distinct species. Two subspecies are recognized.

OTHER COMMON NAMES
French: Galago de Zanzibar; German: Zanzibargalago.



PHYSICAL CHARACTERISTICS
Fur brown dorsally and pale brown ventrally. Yellowish tinge on cheeks and throat. Thick black eye rings present and separated by a long, thick white stripe extending up the snout from the rhinarium to the forehead. Head and body length: 6 in (15 cm); tail length: 8.5 in (21 cm). Body mass: males 5.5 oz (150 g); females 5 oz (135 g).

DISTRIBUTION
Occurs in coastal and low-lying mountain-flank forests of East Africa, from southern Somalia to central Tanzania, and on the island of Zanzibar.

HABITAT
Evergreen tropical rainforests.

BEHAVIOR
Nocturnal and fully arboreal. Locomotion predominantly quadrupedal. Each adult male shares a range with one or two adult females, with which stable sleeping groups are formed.

FEEDING ECOLOGY AND DIET
Diet consists essentially of fruit and arthropods (mainly insects).

REPRODUCTIVE BIOLOGY
Polygynous. Predominantly single births, although twins also occur. Gestation period 124 days. Two clear birth peaks per year, separated by 5 months.

CONSERVATION STATUS
Listed as Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Demidoff's bushbaby
Galagoides demidoff

SUBFAMILY
Galaginae

TAXONOMY
Galagoides demidoff (G. Fischer, 1806), Senegal. *Galagoides demidoff* was long confused with the partially sympatric, larger-bodied *Galagoides thomasi*.

OTHER COMMON NAMES
English: Dwarf bushbaby; French: Galago de Demidoff; German: Zwerggalago.

PHYSICAL CHARACTERISTICS
This is the smallest bushbaby species. Fur rufous to reddish-brown dorsally and yellow ventrally. Head narrow; muzzle pointed and upturned. Prominent yellow nasal stripe present. Dark rings surrounding eyes only moderately to weakly apparent. Head and body length: 5 in (13 cm); tail length: 7 in (18 cm). Body mass: males 2.5 oz (65 g); females 2 oz (55 g).

DISTRIBUTION
Equatorial regions of West and Central Africa, extending into East Africa as far as the western shore of Lake Victoria in Uganda and the Uluguru Mountains in Tanzania.

HABITAT
Evergreen tropical forest, both primary and secondary, including marshy areas and riverine forest. Preferentially active in dense undergrowth below 16.4 ft (5 m).

BEHAVIOR
Nocturnal and fully arboreal. Locomotion predominantly quadrupedal. Adult males and females typically forage solitarily but form social networks based on occasional contact during the night in overlapping ranges and on sharing of nests during the daytime. Subordinate adult males and subadults are tolerated to some extent by prime adult males.

FEEDING ECOLOGY AND DIET
Feeds primarily on arthropods (mainly insects) and fruits, but also consumes some gum.

REPRODUCTIVE BIOLOGY
Polygynous. Typically gives birth to a single infant. Gestation period about 112 days.

CONSERVATION STATUS
Relatively common and not immediately threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Brown greater bushbaby
Otolemur crassicaudatus

SUBFAMILY
Galaginae

TAXONOMY
Otolemur crassicaudatus (É. Geoffroy, 1812), Quelimane, Mozambique. Greater bushbabies were formerly included in the genus *Galago* in many classifications, but the separate genus *Otolemur* has been recognized for these large-bodied forms. The Northern greater bushbaby was previously included as a subspecies of *Otolemur crassicaudatus*, but is now recognized as a separate species (*Otolemur garnettii*), as is the silvery greater bushbaby *Otolemur monteiri*. Two subspecies can be recognized for the brown greater bushbaby species remaining after these removals.

OTHER COMMON NAMES
English: Thick-tailed bushbaby; French: Galago à queue touffue; German: grosser Riesengalago.

PHYSICAL CHARACTERISTICS
Largest-bodied bushbaby species. Fur buffy gray to brown dorsaly and creamy white to creamy yellow ventrally. Head and body length: 12.5 in (31.5 cm); tail length: 16.5 in (41 cm). Body mass: males 2 1b 10 oz (1,190 g); females 2 1b 7 oz (1,110 g).

DISTRIBUTION
Occurs south of the Zaïre Basin in South Africa, Mozambique, Malawi and Zimbabwe.

HABITAT
Found in a wide range of habitats including tropical and subtropical forests, riverine and coastal forests and woodland/savanna.

BEHAVIOR
Nocturnal and fully arboreal. Locomotion predominantly quadrupedal running and climbing. Adult males and females typically feed alone but form social networks based on overlapping ranges and sharing of nests.

FEEDING ECOLOGY AND DIET
Feeds predominantly on fruits and arthropods (mainly insects), but also includes some gum in the diet.

REPRODUCTIVE BIOLOGY
Polygynous. Typically gives birth to twins or triplets. Gestation period 136 days. Infants are carried both on the mother's fur and in her mouth.

CONSERVATION STATUS
Relatively common and not immediately threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Northern greater bushbaby
Otolemur garnettii

SUBFAMILY
Galaginae

TAXONOMY
Otolemur garnettii (Ogilby, 1838), Zanzibar. Formerly included in the genus *Galago*, but now allocated to the separate genus *Otolemur*. Previously included as a subspecies of *Otolemur crassicaudatus*. Four subspecies can be recognized for *Otolemur garnettii*.

OTHER COMMON NAMES
English: Garnett's bushbaby; French: Galago de Garnett; German: Garnettgalago.

PHYSICAL CHARACTERISTICS
Fur reddish- to grayish brown dorsally and paler but of variable coloration ventrally. No facial markings present. Head and body length: 10.5 in (26.5 cm); tail length: 14.5 in (36.5 cm). Body mass: males 1 lb 12 oz (795 g); females 1 lb 10 oz (735 g).

DISTRIBUTION
Range extends down the coast region of East Africa from the Juba River in Somalia through Kenya to the Ruvuma River in Tanzania, probably extending westward into Mozambique. Also occurs on the islands of Pemba, Zanzibar and Mafia.

HABITAT
Confined to coastal, riverine and highland forests. Not found in woodland savanna.

BEHAVIOR
Nocturnal and fully arboreal. Locomotion predominantly quadrupedal running and climbing, but also includes bipedal hopping. Usually feed alone at night, but individual adult males and females live in social networks based on overlapping ranges and sharing of nests. Prime adult males tolerate subordinate males within their ranges.

FEEDING ECOLOGY AND DIET
Feeds primarily on fruits and arthropods (mainly insects).

REPRODUCTIVE BIOLOGY
Polygynous. Typically gives birth to singletons or twins. Gestation period 132 days. Infants are carried only in the mother's mouth.

CONSERVATION STATUS
Relatively common and not immediately threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Northern needle-clawed bushbaby *Euoticus pallidus*	Fur reddish brown to reddish gray dorsally and yellow-white to gray-white ventrally. Head and body length: 7 in (18 cm); tail length: 11.5 in (29 cm). Body mass unknown.	Little studied in the wild. Probably similar to *Euoticus elegantulus.*	Bioko Island, Nigeria, and Cameroon.	No field data available. Probably a specialized gum-feeder like *Euoticus elegantulus.*	Lower Risk/Near Threatened
Bioko Allen's bushbaby *Galago alleni* French: Galago de lîle Bioko	Fur very dark gray (possibly with a red tinge) dorsally and white or gray-white ventrally. Head and body length: 10 in (24 cm); tail length: 10 in (26 cm). Body mass unknown.	No field data available. Probably similar to *Galago gabonensis.*	Bioko Island.	No data available from the wild. Probably similar to *Galago gabonensis,* concentrating on fallen fruit, supplemented by arthropods.	Lower Risk/Near Threatened
Cross River Allen's bushbaby *Galago cameronensis*	Fur dark gray-brown dorsally and gray ventrally. Head and body length: 7 in (18 cm); tail length: 10 in (25 cm). Body mass unknown.	No field data available. Probably similar to *Galago gabonensis.*	Northwestern Cameroon and southeastern Nigeria.	No data available from the wild. Probably similar to *Galago gabonensis,* concentrating on fallen fruit, supplemented by arthropods.	Not threatened
Somali bushbaby *Galago gallarum* French: Galago de Somalie; German: Somaligalago	Fur buff to sandy brown dorsally and white to light gray ventrally. Head and body length: 7 in (17 cm); tail length: 10 in (25 cm). Body mass recorded for a single male: 7 oz (200 g).	Inhabits semi-arid deciduous woodland. Exhibits vertical clinging and leaping in the trees and bipedal hopping on the ground.	Range lies between the Ethiopian Rift Valley and the Webi Shebeyli River to the north and the Tana River and the Somali coastal zone to the south.	Limited data indicate a mixed diet of fruit and arthropods.	Lower Risk/Near Threatened
Grant's bushbaby *Galago granti* French: Galago de Grant; German: Grantgalago	Fur gray with reddish tinge dorsally and yellowish white ventrally. Head and body length: 6 in (15 cm); tail length: 9 in (23 cm). Body mass unknown.	No field data available.	From southern Tanzania to southern Mozambique.	No field data available.	Data Deficient
Dusky bushbaby *Galago matschiei* English: Matschie's bushbaby, spectacled bushbaby; French: Galago de Matschie; German: Matschiegalago	Fur dark brown dorsally and yellowish brown ventrally. Head and body length: 6.5 in (16.5 cm); tail length: 10 in (25.5 cm). Conspicuous dark rings around eyes. Nails keeled and pointed. Body mass: males and females 7.5 oz (205 g).	Inhabits evergreen tropical rainforest. Little studied in the wild.	Kivu region of eastern Zaire and western Uganda.	Mixed diet of fruit, arthropods (mainly insects), and gum. Pointed nails suggest that this species may be a specialized gum-feeder.	Lower Risk/Near Threatened
Malawi bushbaby *Galago nyasae* French: Galago de Malawi; German: Malawigalago	Fur brownish gray dorsally and gray-white ventrally. No information available for bodily dimensions or body mass.	No field data available.	Malawi and Mozambique.	No field data available.	Not threatened
Uluguru bushbaby *Galago orinus*	Fur reddish gray dorsally and yellow ventrally. Head and body length: 5 in (12.5 cm); tail length: 7 in (17 cm). Body mass unknown.	No field data available.	Montane areas of Tanzania.	No field data available.	Data Deficient

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Rondo bushbaby *Galago rondoensis* French: Galago de Rondo; German: Rondogalago	Fur medium brown dorsally and pale yellow ventrally. This is a very small bushbaby with a relatively long tail, but no information is available for bodily dimensions or body mass.	No field data available.	Lowland forests in southeastern Tanzania.	No field data available.	Endangered
Uzungwa bushbaby *Galago udzungwensis* French: Galago de Uzungwa; German: Uzungwagalago	Fur gray-brown dorsally and yellowish buff ventrally. No information is available for bodily dimensions or body mass.	No field data available.	Lowland forests in southern Tanzania.	No field data available.	Not threatened
Thomas's bushbaby *Galagoides thomasi* French: Galago de Thomas	Fur ashy gray-brown dorsally and pale gray ventrally. Dark rings around eyes. Head and body length: 6 in (14.5 cm); tail length: 10.5 in (26 cm). Body mass: males 3 oz (80 g); females 2.5 oz (70 g).	Primary evergreen rainforest. No field data on behavior available.	Disjunct distribution in montane and highland regions of Gabon, Cameroon, Angola, Zaire, and southwestern Uganda.	No field data available.	Not threatened
Silvery greater bushbaby *Otolemur monteiri* French: Galago argenté	Fur pale silvery gray-white dorsally and creamy yellow ventrally. No data available for bodily dimensions or body mass.	No field data available. Probably comparable to *Otolemur crassicaudatus*.	Trans-African woodland zone from Angola in the west to Kenya and Tanzania in the east.	No data available from the wild. Probably resembles *Otolemur crassicaudatus* in eating mainly fruits supplemented by arthropods.	Not threatened

Resources

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Robert D. Martin, PhD

Dwarf lemurs and mouse lemurs

(Cheirogaleidae)

Class Mammalia

Order Primates

Suborder Prosimii

Family Cheirogaleidae

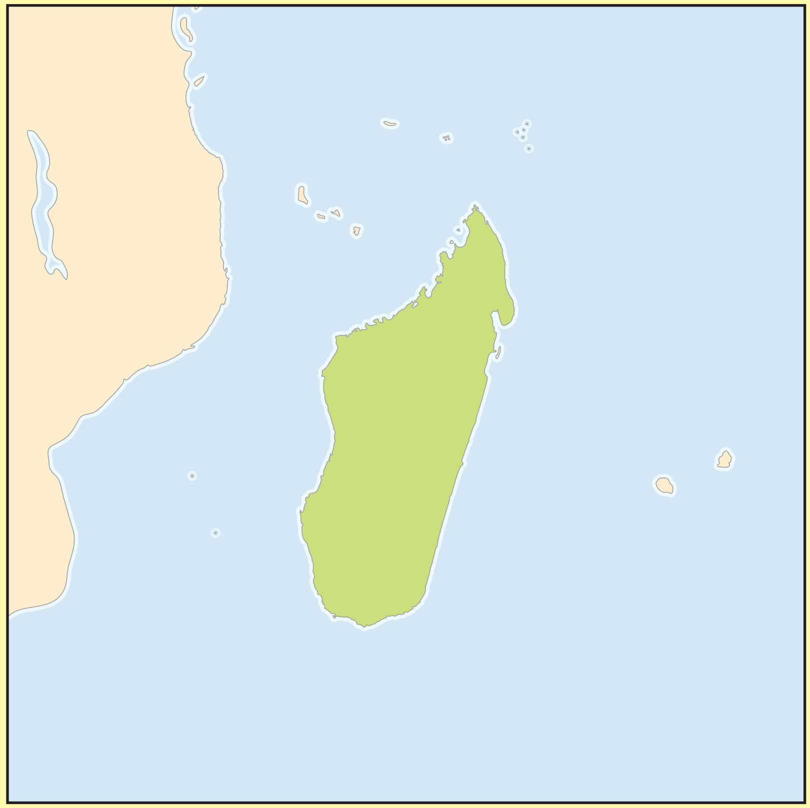
Thumbnail description
Dwarf and mouse lemurs are the smallest of the Madagascar lemurs, with colors ranging from gray to dark brown dorsally and cream to yellowish brown ventrally; some have conspicuous facial markings (e.g., dark rings around the eyes; pale nose stripe)

Size
Head and body length, 5–11 in (12–27 cm); weight 1–16.5 oz (30–460 g)

Number of genera, species
5 genera, 17 species

Habitat
Members of this family are found throughout Madagascar in all forest types; all species are nocturnal and essentially arboreal

Conservation status
Endangered: 3 species; Vulnerable: 1 species; Lower Risk/Near Threatened: 1 species



Distribution
Restricted to forested regions of Madagascar

Evolution and systematics

There is no fossil record in Madagascar for any lemurs, although mouse lemur skulls have been reported among subfossils from sites just a few thousand years old. An Eocene primate from Pakistan, *Bugtilemur*, shows some similarities to modern dwarf lemurs (*Cheirogaleus*) in molar tooth morphology and was therefore allocated to the family Cheirogaleidae by its discoverers.

Chromosomal and molecular evidence overwhelmingly indicates that lemurs are a monophyletic group (i.e., all derived from a specific common ancestor), thus resolving a conflict in interpretation of morphological characters. At one time, numerous authors suggested that the dwarf and mouse lemurs (Cheirogaleidae) are closer to the loris group (Lorisiformes) than to other lemurs, but this has now been effectively discounted. Within the adaptive radiation of the Madagascar lemurs, it is equally clear that dwarf and mouse lemurs belong to a monophyletic subgroup, derived from a later common ancestor retaining many primitive features from the earliest lemurs. While chromosomal and molecular evidence indicates that the aye-aye (*Daubentonia*) branched away first during diversification of the lemurs, relationships between the remaining four families (Cheirogaleidae, Lemuridae, Lepilemuridae, Indriidae) remain unresolved, probably because they separated from one another relatively quickly.

Physical characteristics

These are the smallest lemurs, ranging in size from 1 oz (30 g) for the pygmy mouse lemur (*Microcebus berthae*) to 16.5 oz (460 g) for the fork-crowned lemur (*Phaner furcifer*). All species are nocturnal, with correspondingly large eyes, and essentially arboreal, with relatively long tails. The tarsal bones in the heel region of the foot are mildly elongated. The fur is dense and woolly in all species. As a general rule, species inhabiting the eastern rainforest tend to be rufous (reddish brown) in dorsal coloration, while those living in the dryer forests in the west are grayer. In all species, the ventral fur is considerably lighter and varies from white through cream to yellowish brown. The external ears (pinnae) are relatively large and, in some species, very conspicuous.

The red mouse lemur (*Microcebus rufus*) is nocturnal. (Photo by Wolfgang Kaehler/Cobris. Reproduced by permission.)

A greater dwarf lemur (*Cheirogaleus major*) feeding on ravenala. (Photo by Harald Schütz. Reproduced by permission.)

Distribution

Species of the genera *Cheirogaleus* and *Microcebus* occur throughout the forested regions of Madagascar, while the hairy-eared mouse lemur (*Allocebus*), Coquerel's lemur (*Mirza*), and fork-crowned lemurs (*Phaner*) have more restricted ranges.

Habitat

All species are essentially arboreal and use nests of some kind. Mouse lemurs (*Microcebus* and *Mirza*) construct globular leaf-nests but can also use tree hollows, whereas dwarf lemurs (*Cheirogaleus*), hairy-eared mouse lemurs, and fork-crowned lemurs typically use tree hollows.

Dwarf and mouse lemurs are found in every kind of forested habitat in Madagascar, including evergreen rainforest in the east, deciduous forest in the northwest and west, and semiarid forest in the southwest and south. Mouse lemurs (*Microcebus* species) also occur in small patches of scrub vegetation and even in gardens in settled areas.

Behavior

Although they typically forage alone at night, all species in the family Cheirogaleidae live in social networks involving overlapping ranges, occasional contacts during the night, and nest sharing during the day. However, the degree of tolerance between same-sex adults varies, such that some species (e.g., mouse lemurs) live in dispersed multi-male/multi-female groups, while others (e.g., dwarf lemurs) live in dispersed monogamous groups.

Because all species are typically solitary while foraging, social communication during the night is mainly based on vocalizations and scent marking. Due to their small body sizes,

The pygmy mouse lemur (*Microcebus berthae*) is the smallest primate in the world. (Photo by Harald Schütz. Reproduced by permission.)

A Coquerel's mouse lemur (*Mirza coquereli*) on a branch. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

most vocalizations are relatively high-pitched and the small-

contact, alarm, threat, and range defense. According to species, scent marking can involve deposition of urine, feces, or secretions of special skin glands.

All species show some degree of home-range defense between adults of each sex, but only those that are clearly monogamous (*Cheirogaleus*) or that show a tendency to monogamy (*Mirza* and *Phaner*) defend an exclusive territory.

All dwarf and mouse lemurs are exclusively nocturnal. Smaller species show incomplete control of body temperature, which declines during daytime sleep, and varying degrees of torpor, ranging from facultative to obligatory. Fat may be stored in the tail during the rainy season as a reserve for torpor during the dry season.

Feeding ecology and diet

Fruits and insects are the staple diet for most dwarf and mouse lemurs, but each species shows a particular specialty, sometimes involving plant exudates (gums). Whereas dwarf lemurs feed mainly on fruits, mouse lemurs tend to eat a relatively balanced diet of fruits and insects. However, Coquerel's mouse lemur also consumes secretions produced by insects as part of its diet. Gum-feeding occurs to a limited extent in both

A western fat-tailed dwarf lemur (*Cheirogaleus medius*) feeds on gum. (Photo by Harald Schütz. Reproduced by permission.)

The gray mouse lemur (*Microcebus murinus*) is native to Madagascar. (Photo by Animals Animals ©Mark Stouffer. Reproduced by permission.)

Cheirogaleus and *Microcebus* species, but fork-crowned lemurs are heavily specialized on this food source as the main dietary intake. Some species also feed on nectar from flowers (e.g., *Cheirogaleus* and *Phaner*).

Most species tend to concentrate foraging activity for fruits and insects in the fine branches of trees and bushes, but fork-crowned lemurs spend much time on tree trunks searching for gums.

A red mouse lemur (*Microcebus rufus*) marking its territory. (Photo by Harald Schütz. Reproduced by permission.)

As an adaptation to gum-feeding, fork-crowned lemurs have a particularly well-developed tooth comb in the lower jaw. They also have sharply pointed tips (needle-claws) on the nails of all digits, except the big toe, for clinging to broad trunk surfaces while feeding on gums. The caecum (located at the extreme of the colon) is enlarged in *Phaner* as an adaptation for digestion of gum assisted by symbiotic bacteria. The presence of needle-claws in the hairy-eared mouse lemur suggests that this species also feeds regularly on gums.

Reproductive biology

In all dwarf and mouse lemurs, females show a clear-cut brief period of estrus. In the smaller species, a membrane seals the vulva most of the time. Estrus is marked by the swelling and opening of the vulva, and in some species a vaginal plug is formed after mating. Males actively pursue estrous females in the trees, and in most or all species the male emits a specific mating call. In species with a multi-male/multi-female social system (e.g., *Microcebus* species), several males can mate with a female during estrus, and genetic tests have shown that different fathers may sire offspring in the same litter. The gestation period, lasting between two and three months according to species, is relatively short compared to other primates. All species typically rear their offspring in a nest. The smaller dwarf and mouse lemurs have multiple litters commonly containing two to three offspring, whereas the larger species usually have a single offspring. Suckling occurs relatively frequently during the night, so mothers must reduce their activity away from the nest for some weeks after birth. Strictly seasonal breeding is found in all species. Births typically take place during the wet season (October–March).

Conservation status

At one time all lemurs were classified as Endangered and as a result all are included in Appendix I of the CITES legislation. However, some mouse lemurs (e.g., *Microcebus murinus*, *M. rufus*) are in fact very widespread in Madagascar, occurring in all kinds of habitats, including domestic gardens. However, two mouse lemur species with very restricted ranges are listed as Endangered (*M. berthae* and *M. ravlobensis*). Most dwarf lemurs are also quite widespread, although less common than *M. murinus* and *M. rufus* species. Species in the remaining genera (*Allocebus*, *Mirza*, and *Phaner*) all have much more restricted geographical distributions. *Allocebus trichotis* is listed as Endangered, *Mirza coquereli* as Vulnerable, and *Phaner furcifer* as Near Threatened.

Significance to humans

Dwarf and mouse lemurs are all too small to be of much significance to humans. They may occasionally be eaten, but the amount of meat obtained is generally too limited to make targeted hunting worthwhile, with the possible exception of fork-crowned lemurs.

1. Red mouse lemur (*Microcebus rufus*); 2. Greater dwarf lemur (*Cheirogaleus major*); 3. Western fat-tailed dwarf lemur (*Cheirogaleus medius*); 4. Gray mouse lemur (*Microcebus murinus*); 5. Masoala fork-crowned lemur (*Phaner furcifer*); 6. Coquerel's mouse lemur (*Mirza coquereli*); 7. Hairy-eared mouse lemur (*Allocebus trichotis*). (Illustration by Patricia Ferrer)

Species accounts

Hairy-eared mouse lemur
Allocebus trichotis

SUBFAMILY
Cheirogaleinae

TAXONOMY
Cheirogaleus trichotis (Günther, 1875), Madagarcar, between Tamatave and Morondava.

OTHER COMMON NAMES
French: Allocèbe; German: Büschelohrmaki; Spanish: Lemur orejipeludo.

PHYSICAL CHARACTERISTICS
Conspicuous tufts of hair on relatively small, rounded ears. Dorsal fur is brownish gray with darker midline stripe down back; ventral fur light gray. Tail hair darkens towards tip. Narrow, dark rings surround eyes. Nails are small with sharp tips on all digits except the big toe. Length 5.6 in (14 cm), tail 6.8 in (17 cm); 3 oz (85 g).

DISTRIBUTION
Northeastern Madadascar, inland from Mananara just south of the Bay of Antongil; near Mananara in the Zahamena Reserve and in the Vohidrazana forest; *Allocebus* may occur north of Mananara on the Masoala peninsula.

HABITAT
Canopy of evergreen rainforest.

BEHAVIOR
Individuals are solitary when active, but nesting groups have been recorded.

FEEDING ECOLOGY AND DIET
Basic diet of fruit and insects; some gum-feeding.

REPRODUCTIVE BIOLOGY
Largely unknown. Birth season thought to be January–February.

CONSERVATION STATUS
May be locally abundant in small areas, but listed as Endangered.

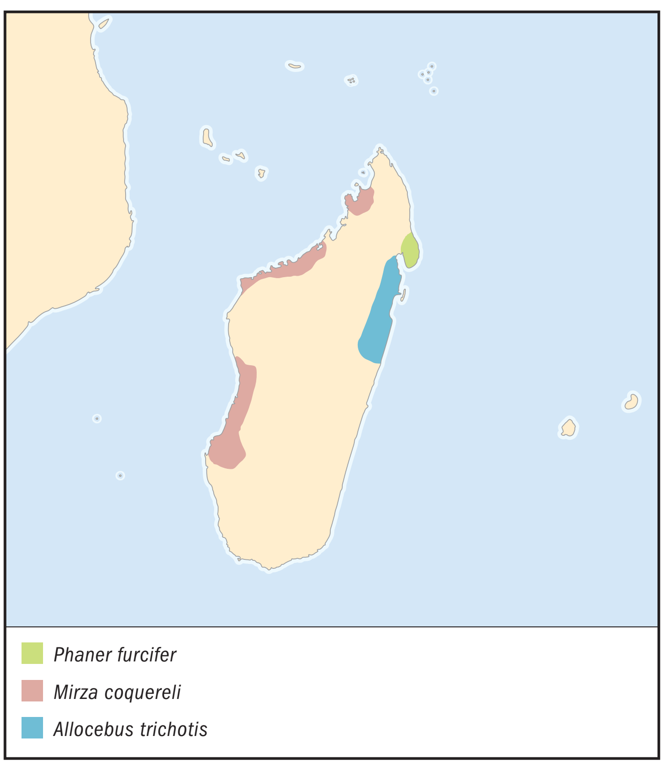
SIGNIFICANCE TO HUMANS
None known. ◆

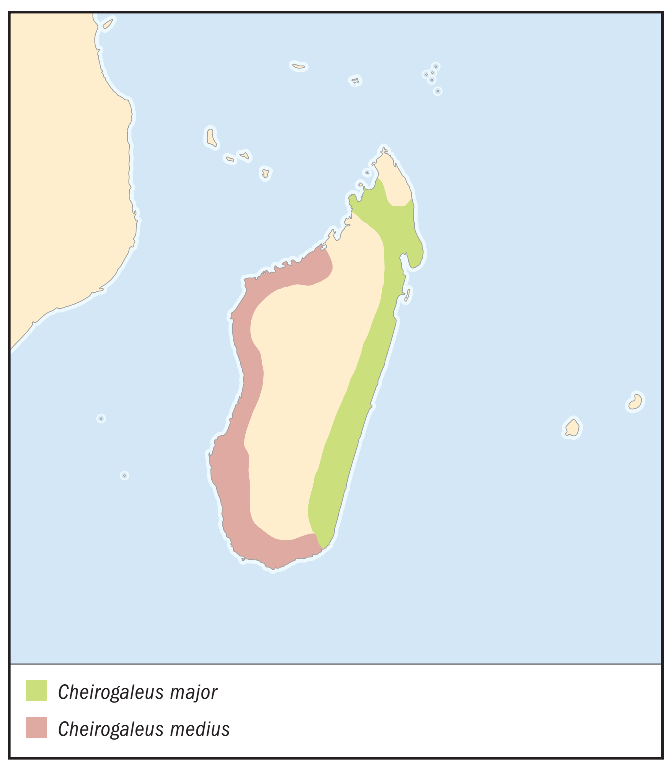
Greater dwarf lemur
Cheirogaleus major

SUBFAMILY
Cheirogaleinae

TAXONOMY
Cheirogaleus major É. Geoffroy, 1812, Fort Dauphin, Madagascar.

OTHER COMMON NAMES
French: Grand cheirogale; German: Grosser Katzenmaki.





PHYSICAL CHARACTERISTICS
Dorsal fur medium brown to deep reddish brown; ventral fur creamy white or yellowish white. Eyes surrounded by dark rings and separated by a pale stripe. Ears medium-sized and naked, but partially hidden by surrounding fur. Length 9.6 in (24 cm), tail 11.2 in (28 cm); 16 oz (438 g) for males, 13 oz (362 g) for females.

DISTRIBUTION
Occurs throughout the eastern rainforest of Madagascar, from the extreme north to the far south.

HABITAT
Evergreen rainforest.

BEHAVIOR
Generally solitary when active at night, but share nests. Undergo a period of genuine obligatory torpor during the austral winter (dry season), accumulating fat stores in the tail prior to becoming inactive.

FEEDING ECOLOGY AND DIET
Feed mainly on fruit, supplemented with insects and possibly some plant exudates.

REPRODUCTIVE BIOLOGY
Monogamous. Strictly seasonal breeding, with births and rearing of offspring during the wet season (October–March). Gestation period of about 70 days. Usually two offspring.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Sometimes eaten by humans, but otherwise of little significance. ◆

Western fat-tailed dwarf lemur
Cheirogaleus medius

SUBFAMILY
Cheirogaleinae

TAXONOMY
Cheirogaleus medius É. Geoffroy, 1812, Fort Dauphin, Madagascar.

OTHER COMMON NAMES
French: Petit cheirogale; German: Fettschwanz-Katzenmaki.

PHYSICAL CHARACTERISTICS
Fur soft and dense; dorsal fur pale silvery gray (sometimes tinged with pale brown); ventral fur creamy white or yellowish white. Eyes surrounded by dark rings and separated by a pale nose stripe. Ears medium-sized and naked, but partially hidden by surrounding fur. Length 7.6 in (19 cm), tail 7.6 in (19 cm); 7 oz (188 g) for males, 6 oz (172 g) for females.

DISTRIBUTION
Occurs throughout the western region of Madagascar, in most forested areas of the south, west, and northwest.

HABITAT
Deciduous and semiarid forests.

BEHAVIOR
Undergoes a period of genuine obligatory torpor during the austral winter, accumulating conspicuous fat stores in the tail prior to entering torpor. Generally solitary when active at night, but adults form monogamous pairs with shared nests and home ranges.

FEEDING ECOLOGY AND DIET
Feeds mainly on fruit, supplemented with insects and plant exudates.

REPRODUCTIVE BIOLOGY
Monogamous. Strictly seasonal breeding, with births and rearing of offspring during the wet season (October–March). Ovarian cycle length approximately 20 days. Gestation period about 62 days. Usually two offspring, but sometimes three or even four.

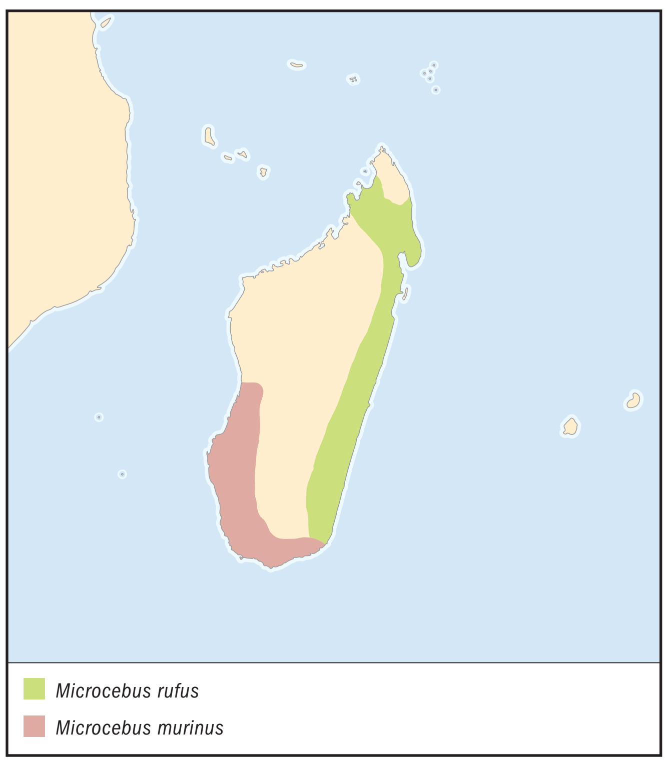
CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Sometimes eaten by humans, but otherwise of little significance. ◆

Gray mouse lemur
Microcebus murinus

SUBFAMILY
Cheirogaleinae

TAXONOMY
Lemur murinus (J. F. Miller, 1777), Madagascar.



OTHER COMMON NAMES
French: Microcèbe gris; German: Grauer Mausmaki.

PHYSICAL CHARACTERISTICS
Dorsal fur gray or gray-brown; ventral fur white or yellowish white. Dark midline stripe down the back. Pale nose stripe between the eyes, extending almost to the tip of the snout. Ears large, rounded, membranous, and mobile. Length 5.0 in (12.5 cm), tail 5.4 in (13.5 cm); 2 oz (60 g) for both sexes when most active.

DISTRIBUTION
Occurs throughout forested areas of west and south Madagascar.

HABITAT
Deciduous and semiarid forests, including scrub vegetation.

BEHAVIOR
Individuals (particularly females) can exhibit intermittent, facultative torpor during the dry season, relying on fat stores accumulated in the tail during the wet season. Commonly described as "solitary," but nevertheless have well-developed social networks with overlapping ranges and shared nests. Daytime sleeping groups containing up to l5 individuals have been reported.

FEEDING ECOLOGY AND DIET
Rely mainly on fruits and insects, although they also eat other animal prey (e.g., small frogs and chameleons) and plant exudates.

REPRODUCTIVE BIOLOGY
Polygynous. Strictly seasonal breeding, with births and rearing of offspring during the wet season (October–March), possibly with two successive litters. Ovarian cycle length approximately 50 days. Gestation period about 60 days. Usually two offspring, but occasionally one or three.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Sometimes eaten by humans, but otherwise of little significance. ◆

Red mouse lemur
Microcebus rufus

SUBFAMILY
Cheirogaleinae

TAXONOMY
Microcebus rufus É. Geoffroy, 1834, Madagascar.

OTHER COMMON NAMES
English: Brown mouse lemur; French: Microcèbe roux; German: Roter Mausmaki.

PHYSICAL CHARACTERISTICS
Dorsal fur dark rufous brown; ventral fur white or yellowish white. Pale stripe between the eyes, extending almost to the tip of the snout. Ears medium-sized, rounded, membranous, and mobile. Length 5 in (12.5 cm), tail 5.6 in (14 cm); 1.5 oz (43 g) for both sexes.

DISTRIBUTION
Occurs throughout the eastern rainforest of Madagascar, from the extreme north to the far south. Extends westward onto the central plateau as well.

HABITAT
Evergreen rainforest.

BEHAVIOR
Generally solitary when active at night, but have well-developed social networks involving overlapping ranges and shared nests. Accumulate fat in the tail during the period of high rainfall and use this reserve when less active during the dry season.

FEEDING ECOLOGY AND DIET
Feed mainly on fruits and insects (notably beetles), but also eat other animal prey (e.g., small frogs and chameleons) and possibly plant exudates.

REPRODUCTIVE BIOLOGY
Mating system unknown. Strictly seasonal breeding, with births and rearing of offspring during the wet season (October–March), possibly with two successive litters. Ovarian cycle length approximately 50 days. Gestation period about 57 days. Usually two offspring, but occasionally one or three.

CONSERVATION STATUS
Not listed by the IUCN, but listed on CITES Appendix I and as endangered by the U.S. Endangered Species Act.

SIGNIFICANCE TO HUMANS
None known. ◆

Coquerel's mouse lemur
Mirza coquereli

SUBFAMILY
Cheirogaleinae

TAXONOMY
Cheirogaleus coquereli (A. Grandidier, 1867), Morondava, Madagascar.

OTHER COMMON NAMES
French: Microcèbe de Coquerel; German: Coquerels-Zwergmaki.

PHYSICAL CHARACTERISTICS
Dense fur, dorsally light brown to grayish brown, ventrally yellowish gray. Tail darkens along its length, becoming dark brown or black at the tip. Large, naked ears. Nails keeled and sharply pointed. Length 8.5 in (21 cm), tail 13 in (33 cm); 11 oz (304 g) for males, 11.5 oz (326 g) for females.

DISTRIBUTION
Patchy distribution in deciduous forests of Madagascar, occurring in three separate areas of dry forest in the western region.

HABITAT
Deciduous forests.

BEHAVIOR
Usually solitary when active at night, but individuals are linked in social networks on the basis of overlapping ranges and shared nests.

FEEDING ECOLOGY AND DIET
Feed mainly on fruits and insects, but have also been reported to consume sugary secretions produced by bugs of the family Flattidae.

REPRODUCTIVE BIOLOGY
Polygynous. Strictly seasonal breeding, with birth and rearing of offspring during the wet season (October–March). Gestation period about 89 days. Usually one offspring.

CONSERVATION STATUS
Vulnerable.

SIGNIFICANCE TO HUMANS
Sometimes eaten by humans, but otherwise of little significance. ◆

Masoala fork-crowned lemur
Phaner furcifer

SUBFAMILY
Phanerinae

TAXONOMY
Lemur furcifer (Blainville, 1839), Morondava, Madagascar.

OTHER COMMON NAMES
French: Phaner; German: Gabelstreifenmaki; Spanish: Maki ardilla.

PHYSICAL CHARACTERISTICS
Dorsal fur dark brown; ventral fur creamy. A dark, well-defined stripe runs up most of the back and divides just behind the head into two stripes passing across the otherwise paler crown, becoming continuous with dark eye rings. The face is blunt and the anterior premolars in the upper jaw are enlarged, giving the impression that there are two canine teeth on each side. Ears are large, rounded, and membranous. Tail very bushy; first half similar in color to dorsal fur and other half very dark. Nails on fingers and toes (except big toe) are strongly keeled with pointed tips. Length 9.4 in (23.5 cm), tail 14.2 in (35.5 cm); 16.5 oz (460 g).

DISTRIBUTION
Restricted to the Masoala Peninsula in northeastern Madagascar.

HABITAT
Evergreen rainforest.

BEHAVIOR
Usually solitary when active at night, but individuals are linked in social networks through overlapping ranges. Members of a pair maintain vocal contact during the night and typically sleep in the same nest during the day.

FEEDING ECOLOGY AND DIET
Specialized for gum-feeding from trunks of trees, but insect galleries may also be opened. Main diet is complemented with insects, fruits, and flowers (may be licked rather than ingested).

REPRODUCTIVE BIOLOGY
There is a tendency towards monogamy, with one adult male and one adult female often occupying a joint territory, but a male may associate with more than one female. Births occur in November–January. Ovarian cycle length about 15 days. Typically gives birth to a single infant. Gestation period unknown.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Sometimes eaten by humans, but otherwise of little significance. ◆

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Robert D. Martin, PhD

Lemurs
(Lemuridae)

Class Mammalia

Order Primates or Primata

Family Lemuridae

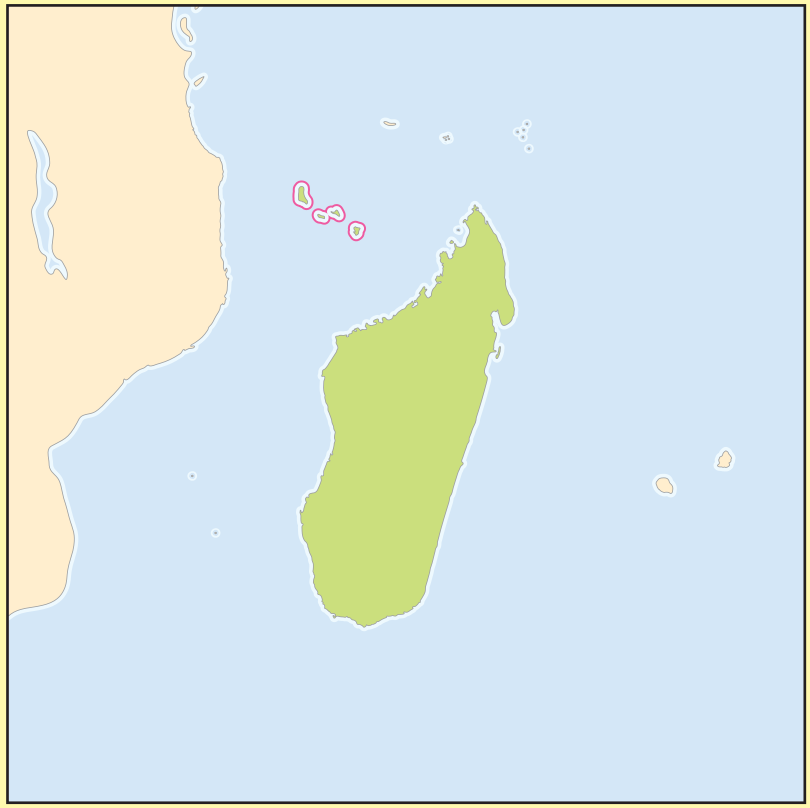
Thumbnail description
Arboreal primates with monkeylike bodies and foxlike heads

Size
Approximately that of a house cat; adult head-and-body length 11–22 in (28–56 cm), tail length 11–24 in (28–60 cm), adult weight 4.4–10 lb (2–4.5 kg)

Number of genera, species
2 genera; 9 species

Habitat
Tropical and subtropical forests

Conservation status
Critically Endangered: 2 species; Endangered: 1 species; Vulnerable: 5 species



Distribution
The island of Madagascar and the Comoro Islands

Evolution and systematics

The evolutionary history of the Malagasy prosimians has been, until recently, one of the knottiest in the life sciences. As of 2000, cladistic analyses, genetic and mitochondrial DNA studies, and morphological comparisons support a monophyletic (single species) origin of all Malgasy prosimians from a founder species that rafted on vegetation from Africa to Madagascar in the early Eocene epoch (55 to 34 million years ago).

There are at least 60 known species of Malagasy prosimians, living and recently extinct, all generally lumped under the umbrella name "lemurs." The total includes 15 large-bodied species, most with unique adaptations, that became extinct within the last 200–300 years. "Lemuridae" is used here as referring to the so-called true lemurs, house cat-sized with fairly long, fox-like muzzles.

Lemurs are prosimians (suborder Prosimii), the term "prosimian" is loosely translated as "pre-monkey" and covers several lines of primate evolution diverging from those of the anthropoids (suborder Anthropoidea: monkeys, apes, and hominids). Living prosimian species include the prosimians of Madagascar (superfamily Lemuroidea), the lorisoids, and the tarsiers. The lorisoids (superfamily Lorisoidea) include the galagos (bushbabies) and pottos of the African mainland and the lorises of Southeast Asia. There are only three living species of tarsiers (infraorder Tarsiiformes, superfamily Tarsiodea), small, headlight-eyed, goblinesque arboreal primates found on some of the Southeast Asian islands.

The eye socket of the skull is open in prosimians but closed in anthropoids. Prosimians have mostly nails on their digits, except for the second digit of the hind foot, which carries a claw or clawlike nail used for self-grooming; anthropoids have only nails on all digits (with the distant exception of the neotropical marmosets and tamarins). Prosimians' lower canines and incisors are modified into a comblike structure used as a grooming tool; anthropoids have no such structure.

Suborder Strepsirrhini ("wet nose") covers lemurs and lorisoids, since those species keep the generalized mammalian condition of noses wet by self-licking to facilitate the olfactory sense, obvious in animals like dogs and cats. In strepsirrhines, the upper lip is divided, again as in dogs and cats, to

Greater bamboo lemur (*Hapalemur simus*) mother and baby live in the trees of Madagascar. (Photo by Harald Schütz. Reproduced by permission.)

make way for the frequent nose-lapping tongue. Tarsiers, monkeys, apes, and hominids are placed in suborder Haplorrhini ("dry nose"), since they have discarded the split lip and the wet nose, coming to rely more on vision and less on olfaction.

Ringtailed lemur (*Lemur catta*) baby clings to its mother's back. (Photo by John Giustina. Bruce Coleman, Inc. Reproduced by permission.)

A mongoose lemur (*Lemur mongoz*) drinks out of a tree trunk. (Photo by Harald Schütz. Reproduced by permission.)

There are several differing classifications of lemur species, all in fluctuation as the latest studies in morphology and DNA comparison studies of lemurs reveal new interrelationships among species. The other families of living Malagasy prosimians, not covered in this entry, are Cheirogaleidae, the dwarf and mouse lemurs; Lepilemuridae, the weasel or sportive lemurs; Indriidae, covering the indris, sifakas, and avahis; and Daubentoniidae, the specialized, enigmatic aye-aye.

Physical characteristics

Lemuridae are arboreal primates, the size of house cats, with bodies, limbs, hands and feet much like those of monkeys, somewhat foxlike heads with long muzzles, and large, brightly hued, round, owl-like eyes. Adult Lemuridae head-and-body length ranges 11–22 in (28–56 cm) and tail length 11–25.5 in (28–65 cm). The tail length in most species is longer than the head-and-body length. Adult weights run 4.4–10 lb (2–4.5 kg). Bodies and limbs are gracile, the hind limbs longer than the forelimbs. The pelage is dense, soft, woolly or cottony, and rather long. Species may carry face or neck ruffs of long fur. Coat colors and patterns vary considerably among species. Some species are sexually dichromatic.

The eyes are set close for binocular vision, and in most species are brilliantly colored. Olfactory communication being important, lemuridae are equipped with scent glands in various parts of their bodies, the exact number and location

Scent-marking in *Lemur catta*. 1. The lemur scent marks a sapling with his brachial gland; 2. The lemur runs his tail between his brachial glands to saturate it with scent; 3. The lemur flicks scent toward a rival lemur band with his tail in a "stink fight." (Illustration by Gillian Harris)

varying throughout genera and species. The animals rub exhudations from the glands on various spots and objects to mark territory.

All lemuridae (and all prosimians) carry grooming combs, modified lower incisors and canines that form a comblike structure that the animals use for grooming themselves and others of their group. Mutual grooming is a social glue, maintaining and reinforcing bonds among the members of a group.

The ears are partially furred and not especially prominent, except in *Lemur catta*, where they are large and triangular, resembling the ears of housecats.

The hands and feet are more or less monkeylike. The pollex (thumb) and hallux (big toe) are set off more or less at right angles to the other digits and are opposable, ensuring firm holds on tree branches. The palms and soles are deeply ridged for a firm grip. A claw or clawlike nail, used for self-grooming, is present on the second toe of each hind foot.

Distribution

Madagascar and the Comoro Islands.

Habitat

Lemur species have adapted to several varied habitats within their range, including humid lowland and montane

A black lemur (*Lemur macaco*) in northwest Madagascar. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

Gray gentle lemurs (*Hapalemur griseus griseus*) eat primarily bamboo shoots, leaves, and stems. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

tropical forests, dry scrub, dense gallery forest, dry tropical deciduous forest, sparse rocky areas, and occasionally grassland.

Behavior

All Lemuridae species are arboreal, although most spend some minimum time on the ground. The ringtailed lemurs are notable for spending about half their foraging time on the ground and can live in treeless areas.

In the trees, Lemuridae walk and run quadrupedally along the tops of tree limbs and leap between trees. At rest, they sit upright or lay down. The tail is about as long as the body, thickly furred, and used for balance and for steering during jumps.

The Lemuridae are for the most part diurnal foragers, with some exceptions. *Lemur mongoz* alternates between diurnal and nocturnal activity in response to season and food availability.

All the Lemuridae species are social, but the exact formalities vary among species. The number of individuals within a group may range anywhere from two to 20. There may be large groups that break up into smaller foraging groups during the day, then reconglomerate at nightfall into the original, single, large group. There may be small family groups of permanently bonded males and females and their offspring.

Groups maintain their cohesion by means of the frequent and all-important activity of mutual grooming with the "grooming comb" derived from the lower incisor and canine teeth.

Lemuridae societies are female-dominant. Females have priority in choosing mating partners and helping themselves to larger amounts of food. A single female leads a typical group of females and males in foraging and sheltering. Either sex has its own dominance hierarchy.

Lemuridae are territorial. Abutting same-species territories may or may not overlap. When neighboring foraging troops meet at territory boundaries, both react by staging hyperactive bouts of alarm calls and branch-shaking.

The Lemuridae have an almost musical range of vocalizations for various needs. There are calls for greeting, territorial assertions, contact and threats between in-group or out-group individuals, and alarm calls that vary according to the type of threat.

Red-fronted lemurs (*Lemur fulvus rufus*) touching noses; the female is on the left. (Photo by Animals Animals ©David Haring. Reproduced by permission.)

Feeding ecology and diet

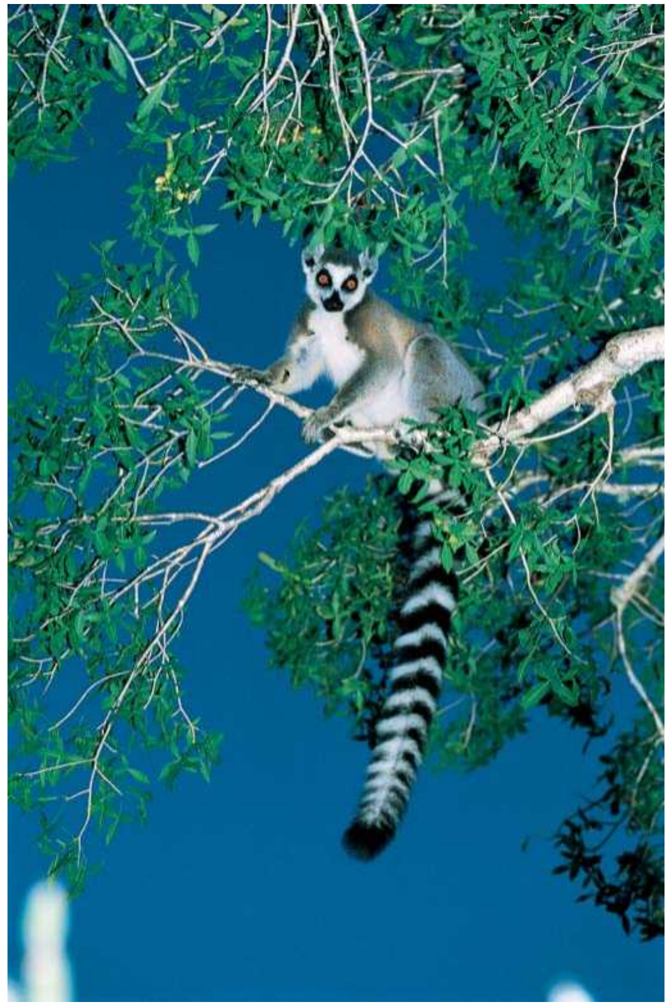
Diet is herbivorous overall, with some omnivory. Plant foods include flowers, pollen, nectar, fruits, leaves, seeds, and seed pods. Less often on the menu are insects and other invertebrates, small vertebrates, and birds' eggs.

Reproductive biology

All species of Lemuridae mate from April through June, the females have a gestation period of about 4.5 months and give birth from August through October, generally coinciding with the beginning of the monsoon season. When plant growth resumes, animals wake from torpor and new food becomes available.

The females of all the Lemuridae genera except *Varecia* have but one pair of mammae, while *Varecia* carries six pairs. A female reaches sexual maturity at two years old and usually starts bearing young, annually, in her third year. There are generally one or two young per birth, although *Varecia* may have up to six young (and six mammae to feed them all).

Two female crowned lemurs (*Lemur coronatus*) feed on bark. (Photo by Harald Schütz. Reproduced by permission.)



A ringtailed lemur (*Lemur catta*) feeding on baobab. (Photo by Harald Schütz. Reproduced by permission.)

For the first four weeks of life a newborn young rides beneath the mother's body, gripping the ventral fur and hugging the torso. After the fourth week, the youngster switches to riding on the mother's back. At about one month of age it starts wandering and exploring on its own. In two months, it begins sampling solid food, and until weaning—at about five to six months—will gradually replace its milk diet with solid food. The exact timing of these different stages of development may vary among species.

Lemurs in the wild can live perhaps 20 years. The record for longevity in captivity among Lemuridae is 39 years for a hybrid of *Lemur macaco* and *Lemur fulvus*.

Conservation status

Since the Lemuridae are primarily arboreal, rampant destruction of Madagascar's remaining forests for the purpose of agriculture and grazing puts all the lemuridae species at risk.

Taking a lesser but significant toll is the hunting and trapping of lemurs for both food and for the illicit market in exotic pets.

Significance to humans

Lemuridae species are hunted and trapped for food. Some are kept as pets or shipped abroad for the exotic pet trade. A few species are blamed for raiding crops and are consequently hunted and trapped.

On the brighter side, ecotourism has taken off in Madagascar, and lemurs in the wild and their habitats have become a substantial tourist draw, bringing in valuable foreign exchange to Madagascar, one of the world's poorest countries. Through the scientific study of lemurs we can learn more about adaptive evolution and speciation. Lemurs have become rallying symbols for conservation because they are beautiful, charming, and fascinating animals.

1. Female and infant ringtailed lemurs (*Lemur catta*); 2. Female mongoose lemur (*Lemur mongoz*); 3. Male mongoose lemur; 4. Male variegated lemur (*Varecia variegata*); 5. Male black lemur (*Lemur macaco*); 6. Female black lemur. (Illustration by Gillian Harris)

1. Male red-bellied lemur (*Lemur rubriventer*); 2. Female red-bellied lemur; 3. Male brown lemur (*Lemur fulvus*); 4. Female crowned lemur (*Lemur coronatus*); 5. Male crowned lemur. (Illustration by Gillian Harris)

Species accounts

Ringtailed lemur
Lemur catta

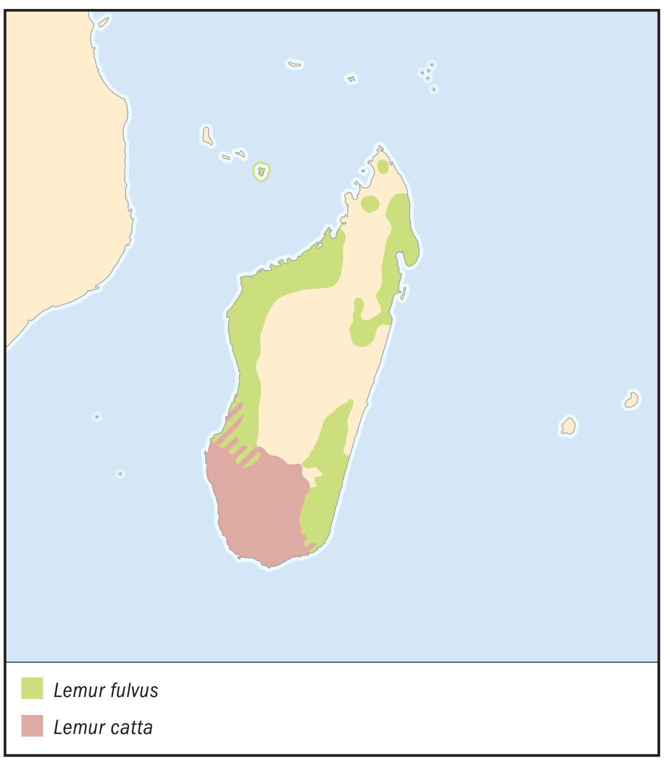
TAXONOMY
Lemur catta Linnaeus, 1758, Madagascar.

OTHER COMMON NAMES
French: Maque, maki mococo, maki; German: Katta; Spanish: Lemur colianillado.

PHYSICAL CHARACTERISTICS
Adult head-and-body length of 15–18 in (39–46 cm), tail length of 22–24 in (56–62 cm), and adult body weight of 6.5–7.75 lb (3–3.5 kg). People without foreknowledge of lemurs, on seeing ringtailed lemurs in zoos or pictures, may regard them as some sort of aberrant raccoon, suggested by the overall shape and especially by the bandit-masked faces and vividly striped tails.

The pelage is dense and soft. The main body color is light gray to gray-brown on the flanks, rump, and limbs, light reddish-brown along the back, and dark gray on the crown and back of the neck. The head is the least monkey-like feature, with its long, foxlike muzzle. The triangular ears are covered with white fur. The forehead, bridge of the snout and proximal half of the muzzle and face are white. The distal half of the muzzle is dark gray or black. The eyes, each encircled by a prominent black ring, are bright red-brown or orange, with less of the "dead fish" stare common among lemur species. The most arresting feature is the tail, as long as the head and torso, and emphatically striped bright white and jet-black, with 13 or 14 black rings. Hindlimbs considerably longer than the forelimbs, giving the animals a somewhat hunched, leaning-forward look as they stand on all fours or locomote.

Individuals are equipped with scent glands on wrists (carpal or antebrachial glands), arms (brachial glands), and chests with which they mark territory and foraging routes with exhudations. Males' wrist glands are further gifted with small, horny, thornlike outcrops with which the males gouge scars into tree trunks and branches to add a visual component to their scent markings.



DISTRIBUTION
Ringtailed lemurs live throughout southern Madagascar, from Tôlanaro (Fort-Dauphin) on the east coast and as far north as Morandava on the west coast, with a separate population in Andringita Natioanl Park in south-central Madagascar.

HABITAT
Ringtails are comfortable in several types of indigenous forest, from dry scrub forest to dense, closed-canopy gallery (riverside) forest. They also reside in (or at least take excursions into) indigenous, dry-adapted *spiny forests*, which are extensive in the south of Madagascar. A separate population has taken to living in dry, rocky, treeless areas in Andringitra National Park in south-central Madagascar, perfectly at home on rocky outcrops and vertical cliffs. These ringtails differ from the general run in having darker pelts and fewer rings on their tails. They have created and colonized their own unique ecological niche and are the only living lemur species to have adapted to a treeless environment in the wild.

BEHAVIOR
Lemur catta is among the most adaptable lemur species and the one that spends the most time on the ground, although they are just as comfortable in the trees. Ringtails live in groups of 5–25 individuals, an average being 14. Larger groups form a core group of adult females and infants, juveniles, and one or more high-ranking males. Females dominate males, thereby getting first pick of food and mating partners, but there is not always a single, individual leader for the entire group. A female remains within the group in which she was born, while males tend to wander among groups.

A ringtailed lemur group forages in a range of 15–22 acres (6–9 ha) in densely forested areas and up to 57 acres (23 ha) in scrub. Ringtailed lemur territories border on one another without overlap.

Ringtailed lemurs are diurnal, starting the day with a "sun-worship" posture, sitting upright on the ground, arms held out from the sides and resting on the knees, palms open. This gesture is seen in other lemur species and serves to soak up sunlight and thus warm the body in the cool mornings. As the day warms, the troop goes searching for food and forages until noon, when the group naps in trees or on the ground during the hottest part of the day. In the afternoon, they rouse and forage again before nightfall, at which time they take to the trees for sleeping.

In-group disputes are common and may culminate in "stink-fights" between rival males. One male positions his wrist glands close together and drags his tail between them, coating the tail fur with his scent. Then he flicks and waves the tail at the rival, who may respond in kind or back off.

Ringtailed lemurs have a range of identification and alarm calls. The most often-heard sounds are a very cat-like meow for group cohesion, though the sound is a little more high-pitched and songlike. The animals also make rapid, high-pitched yapping or barking sounds for threat or alarm.

Although arboreal animals, ringtail lemurs walk and run quite comfortably and efficiently on the ground. When a ringtail troop travels on the ground, the members keep their tails raised straight into the air, like flags, for group cohesion.

FEEDING ECOLOGY AND DIET
The ringtailed lemur diet is varied but primarily vegetable, including fruit, leaves, flowers, herbs, tree sap, bark, and other plant parts, although they may at times supplement their diets with insects and small vertebrates. A favorite fruit, when in season, are the seed pods of the tamarind tree (*Tamarindus indica*). The only edible parts are the sticky, sweet-tart arils, or coatings on the seeds.

REPRODUCTIVE BIOLOGY
Females reach sexual maturity at two years of age, birth their first young at three years and follow with annual births. Males reach sexual maturity at two and a half years old, but must contend with older, dominant males who may curtail any mating moves on the part of young males.

Mating begins in mid-April. During the mating season, females enter estrous for only a few hours of a single day, although all the females of a group will enter estrous within two weeks of one another. The males, driven by hormones, fight madly among themselves for mating privileges during that narrow time window. Females typically mate with more than one male, often with one of the males being from another troop. The young are born in August and September. One or sometimes two are born, depending on food abundance.

The newborn at first clings to the fur of its mother's underside, but in three days it begins moving about on its mother's body, still grasping the pelt. By two weeks of age, the youngster is riding stomach-down on the mother's back. By two and a half months it leaves the mother to play with other young, explore and sample solid foods, though it is still carried by the mother whenever the group moves. The youngster spends more time per day on its own, eating more solid food and taking less milk until final weaning at 5–6 months of age.

Females in a group with newborns show considerable "aunt behavior," handing infants about, even nursing other females' infants, and attending groups of young as they play.

CONSERVATION STATUS
Vulnerable. Multiple threats include deforestation and hunting for food and the illegal pet trade.

SIGNIFICANCE TO HUMANS
Ringtailed lemurs are readily visible in several protected areas in southern Madagascar and have thereby become a banner species for ecotourism. In Berenty Reserve, near Fort Dauphin, at least one troop of ringtails has become so tame that visitors can follow the group about its business throughout the day. Ringtailed lemurs have become reliable ecotourism magnets and thereby bring visitors, cash, and business into Madagascar. ◆

Mongoose lemur
Lemur mongoz

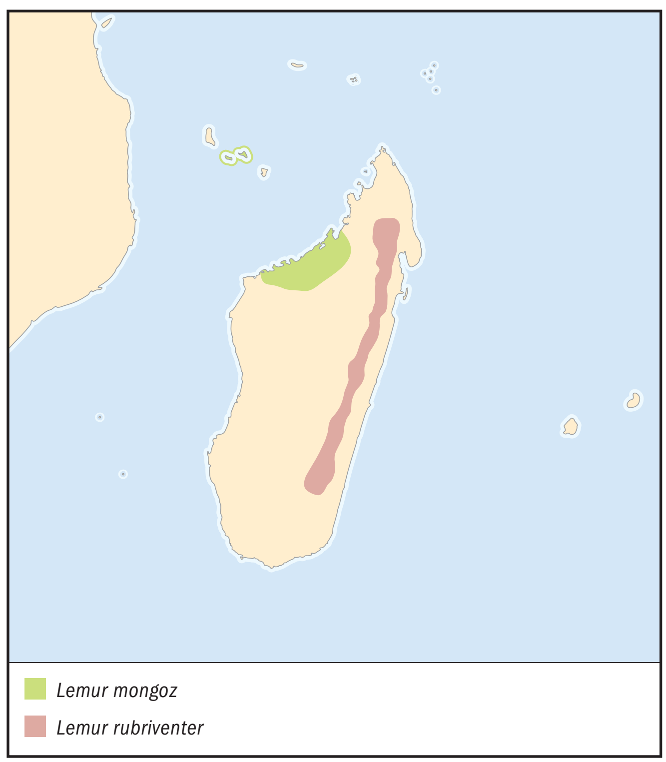
TAXONOMY
Lemur mongoz Linnaeus, 1766, Anjouan Island, Comoros.

OTHER COMMON NAMES
French: Lémur mongoz; German: Mongozmaki; Spanish: Lemur mangosta.

PHYSICAL CHARACTERISTICS
Adults have an average head-and-body length of 14 in (35 cm), tail length of 19 in (48 cm), and adult body weight of 4.5 lb (2 kg). Pelages are colored gray on the heads, forelimbs, and shoulders, dark grey on the back, accentuated by a reddish brown beard. Often the muzzle is white. The eyes are a lustrous red-brown.

DISTRIBUTION
Mongoose lemurs are found in forests in northwestern Madagascar and on the islands of Moili (Moheli) and Ndzouani (Anjouan) of the Comoros. In northwestern Madagascar, the range of mongoose lemurs extends from the Bay of Narinda in the north to as far south as the Betsiboka River.

The Comoros are a volcanic-origin island group in the Mozambique Channel, northwest of Madagascar, midway between Madagascar and mainland Africa. The mongoose lemur is one of only two lemur species living naturally outside of mainland Madagascar, the other being the brown lemur (*L. fulvus*), also living on the comoro. Both species are probably feral descendants of individuals brought by man from Madagascar to the islands.



HABITAT
Mongoose lemurs live in tropical dry deciduous forests on Madagascar and in humid lowland and montane tropical forests on Moheli and Anjouan.

BEHAVIOR
Mongoose lemurs live in groups of three or four individuals, a female-male pair and their pre-weaned young, the adult female dominant to the adult male. Territories of neighboring groups often overlap. Groups encountering each other at the edges or overlap zones of abutting territories respond with elaborate, noisy intimidation displays. Yet, groups of mongoose lemur and brown lemur may forage alongside one another, or even intermingle as they forage.

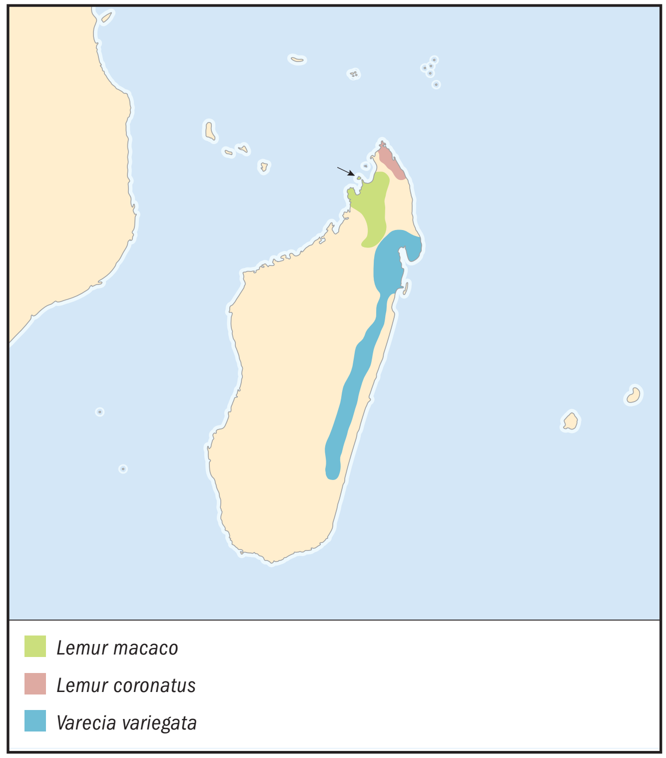
Mongoose lemurs on mainland Madagascar forage diurnally or nocturnally, depending on the season, a prime changeover time from day to night activity taking place at the beginning of the dry season, when food becomes scarce. Nocturnal feeding reduces competition from other species.

FEEDING ECOLOGY AND DIET
Mongoose lemurs help themselves to flowers, nectar, pollen, fruits, and leaves.

REPRODUCTIVE BIOLOGY
Monogamous. Young are born in mid-October, usually one per litter, with annual births. Male mongoose lemurs are born with white beards that change to reddish-brown at five to six weeks of age. Newborn young cling to their mothers' undersides for the first three weeks. At five weeks, youngsters begin to walk independently and sample solid food. Nursing continues, with the mother's milk gradually replaced by solid food, until weaning at 5–6 months of age. Young mongoose lemurs reach sexual maturity by two or three years, at which time male and female young are driven from the parental group. Intergroup encounters are rare, however, and often result in agitation, vocalizations, and scent marking.

CONSERVATION STATUS
Vulnerable. Mongoose lemurs exist in only a few limited populations threatened by deforestation. The species is hunted for food and for the illegal pet trade.

SIGNIFICANCE TO HUMANS
Mongoose lemurs are hunted for food. ◆



Black lemur
Lemur macaco

TAXONOMY
Lemur macaco Linnaeus, 1766, Madagascar.

OTHER COMMON NAMES
English: Blue-eyed lemur, Sclater's lemur; French: Lémur macaco, maki dimorphisme; German: Mohrenmaki; Spanish: Lemur negro.

PHYSICAL CHARACTERISTICS
There are two subspecies, black lemurs or *Lemur macaco macaco* and blue-eyed lemurs or Sclater's lemurs, *Lemur macaco flavifrons*. Blue-eyed lemurs are the only primates besides humanity to bear blue eyes. The trait is probably due to the genetics of an isolated population that enabled recessive genes to express. Matings of black and blue-eyed lemurs produce only brown-eyed young.

The two subspecies are nearly identical in shape, size, and behavior, but they live in different habitats and show different colors in pelage and eyes. An adult individual of either subspecies has an average adult head-and-body length of 16 in (41 cm), tail length of 22 in (55 cm), and an adult body weight of 5 lb (2.4 kg).

Both subspecies are sexually dichromatic. *Lemur macaco macaco* males have jet-black fur with brown highlights from nose tip to tail tip, while female pelages sport mixtures of brown, reddish brown, and gray on their backs, with off-white undersides and black faces. Both sexes bear somewhat ragged-looking ruffs of fur framing the sides of their faces, black in males and off-white in females. Males' eyes are dark brown; females' are golden to orange. *Lemur macaco flavifrons* males are completely black but with blue eyes. Females have a light reddish brown coat with a white brow-bar above the blue eyes.

DISTRIBUTION
Lemur macaco macaco are found in the northwest humid tropical forests of Madagascar, including those on the islands of Nosy Be and Nosy Komba off the northwest coast. On Nossi Komba, black lemurs have become part of the tourist circuit, semi-tame individuals obligingly cadging bananas from visitors and locals, and lounging about on rooftops. *Lemur macaco flavifrons* are found in northwestern Madagascar in a range south and separate from that of *L. m. macaco*, from the Andranomalaza River further southward to the Sandrakota River.

HABITAT
Black lemurs are at home in humid and dry primary and secondary tropical forest, and humanity-altered land such as tim-

ber plantations and combinations of partially cleared forests and plantings of coffee, citrus, and cashew.

BEHAVIOR
Black lemurs are diurnal and social, groups being made up of 2–15 individuals, often with more males than females. Small groups may forage within their own territories during the day, but several such groups may bunch together for the night.

FEEDING ECOLOGY AND DIET
Ripe fruit, leaves, flowers, and insects.

REPRODUCTIVE BIOLOGY
Polygamous. Black lemurs reach sexual maturity at two years. Mating in both subspecies takes place from June through July. Mothers give birth to one or two young after a gestation period of about 126 days.

CONSERVATION STATUS
Vulnerable. Deforestation and hunting are the primary threats.

SIGNIFICANCE TO HUMANS
Because of the large amounts of fruit in their diet, black lemurs may indirectly benefit man by being important dispersers of fruit seeds in forests, thus contributing to the overall health of those forests. ◆

Variegated lemur
Varecia variegata

TAXONOMY
Lemur variegata Kerr, 1792, Madagascar.

OTHER COMMON NAMES
English: Ruffed lemur.

PHYSICAL CHARACTERISTICS
Varecia variegata is the largest in body size of the living Lemuridae species. The adult head-and-body length is 20–22 in (51–56 cm), tail length is 22–25.5 in (56–65 cm), and adult body weight is 7–10 lb (3.2–4.5 kg). Females are larger than males. The ruffed lemur carries a scent gland on its neck, and females have six mammae.

There are two subspecies: black and white ruffed lemurs, *Varecia variegata variegata* and red ruffed lemurs, *Varecia variegata rubra*. Black and white ruffed lemurs have a black tail, a body patched black and white in varied arrangements, and a white ruff around a black face. The fur is rather long, with a soft, cottony texture. The eyes are light gray or gray-green. Red ruffed lemurs have a black tail, face and hands, a reddish-brown body, and a white patch on the back of the neck and across the shoulders. The undersides and inner limbs are black. The eyes are golden and look almost self-luminous contrasted with the dark face. The ruff is like that on *V. v. variegata* but colored off-white.

DISTRIBUTION
Lowland and montane rainforest belt paralleling the east coast of Madagascar, including the forests of the Masoala Peninsula in northeastern Madagascar.

HABITAT
Black and white ruffed lemurs live throughout the montane rainforests paralleling the east coast of Madagascar, and on the small island of Nosy Mangabe in the Bay of Antongil. Red ruffed lemurs live only in the forests of the Masoala Peninsula, which forms the Bay of Antongil in northeastern Madagascar. The Masoala forests include some of the few large remnants of Malagasy east coast lowland tropical rainforest. Part of the forested peninsula is now Masoala National Park.

BEHAVIOR
Black and white ruffed lemurs live in small groups averaging five individuals, a bonded female-male pair and offspring. Females are dominant to males. Larger, female-led groups form during the rainy season, when food is more abundant, and fall apart into smaller groups or lone individuals during the food-scarce dry season.

Ruffed lemurs are the most committedly arboreal of the living Lemuridae species, spending their days in the upper levels of their rainforest homes. An individual moves through this area by walking or running on all fours on larger branches and jumping between trees, but more slowly and carefully than smaller species of the Lemuridae. Ruffed lemurs are crepuscular, being most active during morning and evening twilight.

Ruffed lemurs sound off with an impressively varied repertoire of loud, strange calls, including roaring alarm calls. They can produce up to a dozen differing alarm calls at the sight of boas, raptors, and the fossa (*Cryptoprocta ferox*), a small but aggressive predatory mammal endemic to Madagascar.

FEEDING ECOLOGY AND DIET
Completely herbivorous and consists almost entirely of fruit, sometimes varied with leaves, nectar, and seeds.

REPRODUCTIVE BIOLOGY
Polygamous. Females may bear litters of up to six young, something of an oddity among primates. They carry six mammae although the most common count is three young per litter. The gestation period lasts 90–102 days, shorter than is common for the Lemuridae.

The young do not hold onto or ride the mother as in other Lemuridae species; instead, the mother carries them about, one at a time, in her mouth, and builds a nest of leaves for holding them while she goes off seeking food on her own. The mother blankets the nest with her own fur, which she pulls from her pelt.

The young mature rapidly. They begin leaving the nest tentatively and temporarily at only three weeks of age. They are able to climb expertly in trees at five weeks and are as active and agile as their mother at seven weeks. Full weaning comes about at around five and a half months. At six months the young have nearly reached adult size.

CONSERVATION STATUS
Endangered. Prospects for the future of ruffed lemurs is a mix of unfavorable and favorable. Black-and-white ruffed lemurs are severely threatened by the loss of rainforest habitat along the east coast of Madagascar, in the lowlands and in the mountains paralleling the coast. Nearly all the original eastern lowland rainforest is gone, converted into farmland, and the mountain rainforests are shrinking yearly as they are cleared. The Malagasy hunt and trap the animals for food. They also fall victim to a lively worldwide black market in exotic pets. Red-ruffed lemurs are somewhat better off in the partially protected forests of Masoala Peninsula, but deforestation and hunting continue to decrease their numbers.

SIGNIFICANCE TO HUMANS
Variegated lemurs are hunted for food and captured for the illegal exotic pet trade. However, captive-born ruffed lemurs have been reintroduced to the wild and serve as educational aids in Madagascar. ◆

Brown lemur
Lemur fulvus

TAXONOMY
Lemur fulvus Geoffroy, 1796, Madagascar.

OTHER COMMON NAMES
English: Fulvous lemur; French: Lémur brun; German: Brauenmaki.

PHYSICAL CHARACTERISTICS
There are seven subspecies of brown lemur. The subspecies are similar in body size and behavior, but pelage color and markings vary among them, and all subspecies show sexual dichromatism. An adult brown lemur of any subspecies has a head-and-body length of 15–20 in (38–50 cm), tail length 18–24 in (47–60 cm). Adult body weight runs 4.5–9 lb (2.1–4.2 kg).

DISTRIBUTION
Brown lemurs are found throughout all of Madgascar's remaining dry western and central forests. In the west, they live all through the belt of forest starting north of the Betsiboka River, to the northwest corner of Madagascar. Subspecies *Lemur fulvus mayottensis* lives on the island of Mayotte in the Comores. Along with mongoose lemurs (*L. mongoz*), brown lemurs are the only lemurs living naturally outside of Madagascar.

Of the seven subspecies, the exact distributions of the six on mainland Madgascar have not been determined. Only *L. f. mayottensis*, in its limited range on Mayotte Island, has a confirmed distribution.

HABITAT
Brown lemurs live in tropical deciduous forest along the west coast of Madagascar, in scattered forest fragments on Madagascar's high plateau, and in lowland and montane rainforest on Mayotte Island. Brown lemurs have adapted rather well to degraded and secondary forests.

BEHAVIOR
Brown lemurs live in social groups of between three and 12 individuals, and up to 29 on Mayotte Island. The Mayotte groups are unstable, individuals freely circulating throughout groups every day. Brown lemur groups are unusually peaceful internally, with little or no dominance hierarchy and little dominance of females toward males. Even though abutting territories show a great deal of overlap, groups of neighboring territories make efforts to avoid each other. A brown lemur group holds a territory that can range from 17–50 acres (7–20 ha). Groups often break up into subgroups during the day, re-forming the original large group by nightfall.

FEEDING ECOLOGY AND DIET
Brown lemur diet consists mostly of fruit, young leaves, and flowers. Diet varies depending on local habitat. Brown lemurs in the southwest make the leaves of the tamarind tree (*Tamarindus indica*) their staple, while browns on Mayotte eat mostly fruit.

REPRODUCTIVE BIOLOGY
Polygamous. Reproduction in brown lemurs and development of the young follows the standard Lemuridae pattern. Adults mate April through June and young are born from September through November after a gestation period of about 120 days. A mother usually gives birth to only a single young per season, becoming pregnant annually. Young are weaned in five and a half months and reach sexual maturity at 1.5–2 years of age.

CONSERVATION STATUS
Four subspecies, *L. f. albocollaris*, *L. f. collaris*, *L. f. mayottensis*, and *L. f. sanfordi* are considered Vulnerable. Forest destruction and hunting are the main threats to brown lemurs.

SIGNIFICANCE TO HUMANS
Brown lemurs are hunted and trapped for food. ◆

Crowned lemur
Lemur coronatus

TAXONOMY
Lemur coronatus Gray, 1842, Madagascar.

OTHER COMMON NAMES
French: Lémur couronné; German: Kronenmaki; Spanish: Lemur coronado.

PHYSICAL CHARACTERISTICS
Head-and-body length averages 13.4 in (34 cm), tail length 17.7 in (45 cm). Adult body weight averages 4.5 lb (2 kg). The species is sexually dichromatic. Males are gray-brown, females are more gray. The male wears a triangular patch of black fur between his ears, and the female keeps a bright red-orange V-shaped patch leading from the brows back and along the bases of the ears; these are the "crowns" of the common name. Crowned lemurs have scent glands for marking territory on their hands, arms, face, genitals, and anus.

DISTRIBUTION
Crowned lemurs live from near the very northern tip of Madagascar, westward to the Ankarana Massif, and eastward to the east to the Fanambana River south of Vohimarina, in all the coastal zones and at low altitude. Their range includes the slopes of Montagne d'Ambre and the dry forests of the Cap d'Ambre.

HABITAT
Crowned lemurs have adapted quite well to humid tropical rainforest, dry tropical forests, and forested land in various stages of degradation. The primary humid forest that is home to crowned lemurs is on and around Montagne d'Ambre outside of Antsiranana (Diego Suarez). That forest abuts on the drier forest of the Cap d'Ambre, which is also home to crowned lemurs. The species also lives in remaining areas of lowland dry forest in northern Madagascar. They have adapted well to degraded forest and even grassland studded with isolated trees, the lemurs hiking overland between trees, which they use as refuges.

BEHAVIOR
Crowned lemur group size runs from two to 11. A typical group has five or six individuals, two adult pairs and one or two younger sub-adults.

Times of activity vary throughout the range. Generally, groups rouse near dawn and forage until nightfall with a four-hour rest in the middle of the day, although some groups will continue to forage for a few hours after night sets in.

FEEDING ECOLOGY AND DIET
The crowned lemur's menu includes flowers, fruits, and leaves, exact proportions varying with seasons. Fruit is the major food type and may make up almost all of the diet at the end of the dry season, while leaves become important in the rainy season. Crowned lemurs visit water sources during the dry season, even hiking to sources in caves.

REPRODUCTIVE BIOLOGY
Polygamous. Mating, gestation, birth, and development of the young follow the standard Lemuridae pattern. Births begin in mid-September, earlier for crowned lemur females in humid tropical rainforest, later for females in dryer forests.

CONSERVATION STATUS
Vulnerable. Pressure on the species are brought about by deforestation and hunting.

SIGNIFICANCE TO HUMANS
Crowned lemurs are hunted for food and as pests, since they sometimes help themselves to crops. ◆

Red-bellied lemur

Lemur rubriventer

TAXONOMY
Lemur rubriventer Geoffroy, 1850, Tamatave, Madagascar.

OTHER COMMON NAMES
French: Lémur à ventre rouge, German: Rotbauchlemur, Rotbauchmaki; Spanish: Lemur de vientre rojo.

PHYSICAL CHARACTERISTICS
Average adult head-and-body length is 15 in (40 cm), with a tail length of 20 in (50 cm) and an adult body weight of 4.5 lb (2 kg). There is some sexual dichromatism. Both sexes have dark brown pelages and black tails, but males have reddish brown undersides (hence the common name) while females differ with cream-white undersides. Males have prominent white teardrop-shaped marks under the eyes, which females do not have. Males keep a scent gland on the tops of their heads.

DISTRIBUTION
Eastern Madagascar.

HABITAT
Red-bellies live throughout the belt of middle to high-altitude rainforests that runs north-south in eastern Madagascar.

BEHAVIOR
Red-bellied lemurs live in family groups of up to five individuals, each led by a bonded monogamous pair, though females are still dominant and lead foraging trips. A typical group keeps a territory of 30–37 acres (12–15 ha). Red-bellied lemurs only rarely show territorial behavior. In most cases, groups of neighboring territories, on meeting, scarcely acknowledge each other and almost never fuss.

FEEDING ECOLOGY AND DIET
Red-bellied lemurs forage for the fruit, flowers, and leaves of at least 30 species of tropical forest plants.

REPRODUCTIVE BIOLOGY
Monogamous. Individuals reach sexual maturity at two years of age. Pairs mate during May through June and young are born after a 120-day gestation. Mothers bear one young per season. Raising the young in red-bellied lemurs departs from the standard Lemuridae model: the young at first cling to their mother's undersides, switching to riding on her back in two weeks. From then until five weeks, the young will take clinging rides on both parents, sharing time between the two equally. After the fifth week, females start refusing to carry the young, handing them over to the father to carry constantly, until the young are about 100 days old.

CONSERVATION STATUS
Vulnerable. The main threat to red-bellied lemurs is the ongoing destruction of Madagascar's eastern rainforests.

SIGNIFICANCE TO HUMANS
Red-bellied lemurs are hunted and trapped for food. ◆

Resources

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Yoder, A. D., M. Cartmill, M. Ruvolo, K. Smith, and R. Vilgalys. “Ancient Single Origin for Malagasy Primates.” *Proceedings of the National Academy of Sciences* 93 (1996): 5122–5126.

Organizations

Duke University Primate Center. 3705 Erwin Road, Durham, NC 27705 United States. Phone: (919) 489-3364. Fax: (919) 490-5394. E-mail: primate@duke.edu Web site: <http://www.duke.edu/web/primate>

Madagascar Fauna Group, San Francisco Zoo. 1 Zoo Road, San Francisco, CA 94132 United States. E-mail: mfg@sfzoo.org Web site: <http://www.selu.com/bio/mfg/text/conservation.html>

Other

2002 IUCN Red List of Threatened Species (International Union for the Conservation of Nature and Natural Resources). <http://www.redlist.org>

Yoder Lab Page. <http://www.basic.nwu.edu/yoder/yoder.html>

Kevin F. Fitzgerald, BS

Avahis, sifakas, and indris
(Indriidae)

Class Mammalia
Order Primates
Family Indriidae

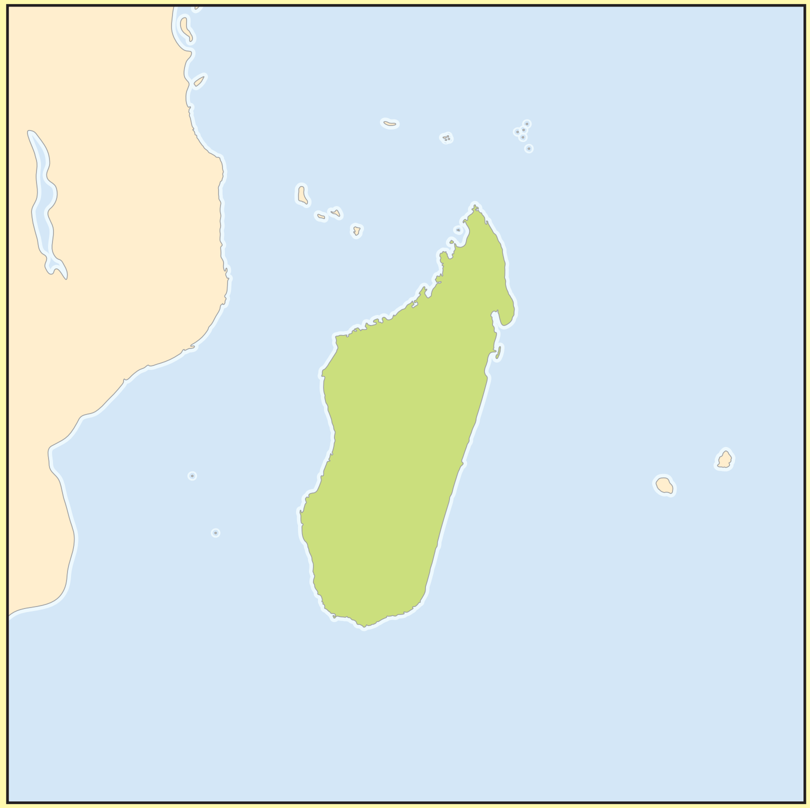
Thumbnail description
Medium- to large-sized primates with powerful hind limbs and short snouts

Size
Weight: 2.2–16.1 lb (1.0–7.3 kg); head and body length: 10.4–20.5 in (264–520 mm)

Number of genera, species
Extinct: 6 genera, 10 species; Extant: 3 genera, 8–10 species

Habitat
Subtropical spiny desert and its gallery forest, humid moist tropical forest, tropical dry forest

Conservation status
Extinct: 10 species; Critically Endangered: 3 species; Endangered: 5–7 species



Distribution
Throughout remaining forests in Madagascar

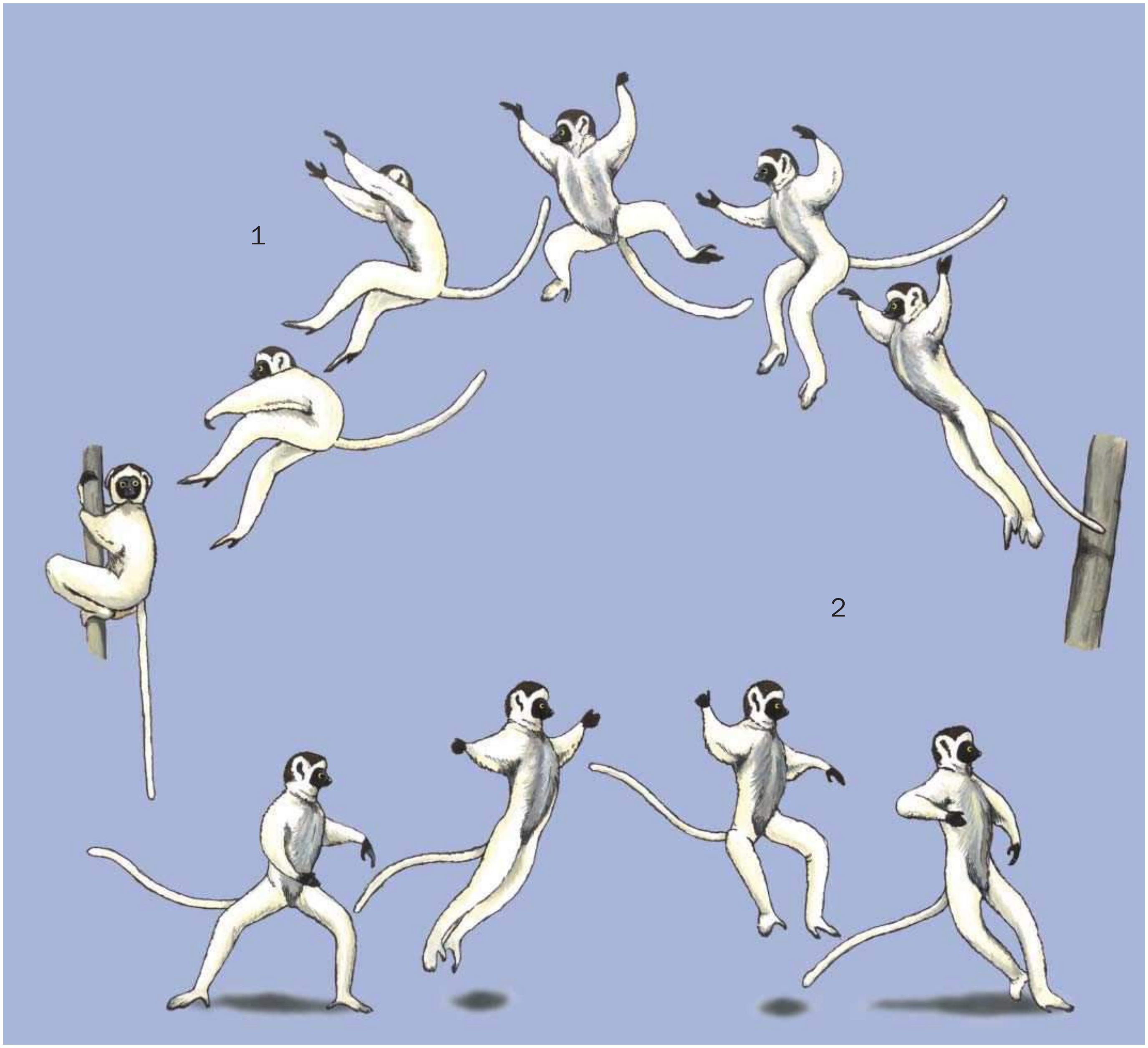
Evolution and systematics

There are five families of primates on the island of Madagascar, all lemurs. The family Indriidae has lost three-fifths of its species in the past 1,000 years. The extinct indriids consisted of the subfamilies: the Paleopropithecinae, the sloth lemurs, and the Archaeolemurinae, the baboon lemurs. The extinct lemurs were all larger than the extant lemurs, with body weights ranging from 27–441 lb (12–200 kg). The sloth lemurs (4 genera, 7 species) and baboon lemurs (2 genera, 3 species) were found throughout the north, west, and south of Madagascar. With long forelimbs and curved finger bones, the sloth lemurs climbed slowly and hung from tree branches to feed on leaves and tough vegetation. Body weight ranges are estimated at 22–441 lb (10–200 kg). The baboon lemurs were arboreal and terrestrial quadrupeds, feeding on leaves, tough seeds, and husked fruits. Body weights are estimated at 38–62 lb (17–28 kg).

The living Indriidae is comprised of three genera, including 8–10 species (depending on the authority). The medium-sized (15.4–17.6 lb [7–8 kg]), tailless indri consists of one species *Indri indri*. Woolly lemurs have been divided into a widespread eastern rainforest species (*Avahi laniger*) and a western species *A. occidentalis*. Originally divided into two species, *Propithecus verreauxi* (a smaller-bodied species in spiny desert and dry tropical forests in western Madagascar) and *P. diadema* (larger-bodied, eastern rainforest), a third species *P. tattersalli*, the golden crowned sifaka, was described in 1988. Recent molecular and morphometric evidence suggests that the diademed sifaka group, previously allopatric subspecies, consists of four species (*P. perrieri*, *P. candidus*, *P. diadema*, *P. edwardsi*). *P. tattersalli* is found in both wet and dry tropical forest in a limited area near Daraina, in northeastern Madagascar. Based on molecular evidence, it has come under recent controversy as to whether it should remain a distinct species. *Paleaopropithecus* has been found in limestone caves of the Manamby Plateau, north of Tulear. Forest destruction and human hunting may be partially responsible for the contraction of the range of the extant species and the extinction of *Paleopropithecus*, *Archeolemur*, *Archaoindris*, *Babakotia*, *Hadropithecus*, and *Mesopropithecus*.

Physical characteristics

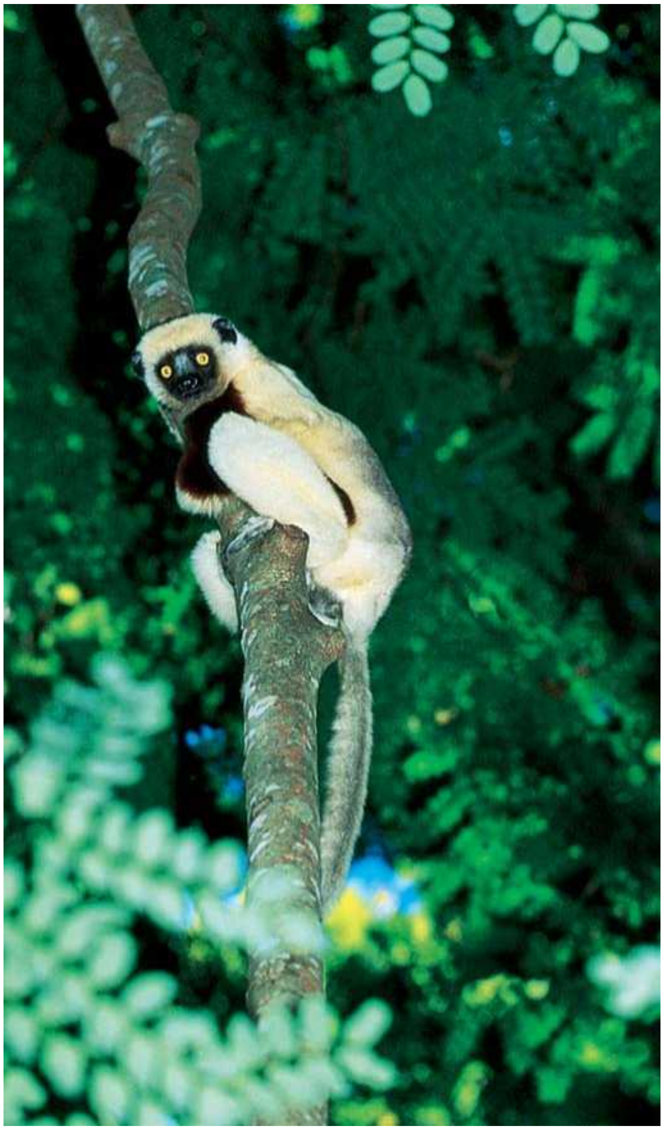
Indriids are medium- to large-sized prosimians. The extinct species *Archeoindris fontoynonti* weighed up to 400 lb (181 kg), while the smallest species in the family, the eastern woolly



Locomotion in Indriidae. Shown here (1) arboreal vertical leaping, and (2) sideways leaping on the ground. (Illustration by Gillian Harris)

lemur *Avahi laniger*, weighs about 2.3 lb (1 kg). Most indriids have tails shorter than their bodies, with the tail of the indri reduced to a few inches (about 5 cm). The extant indriids are magnificent leapers, with hind limbs longer than their forelimbs. Ears are small, bare or tufted, and rounded. The skin of the face is bare, and the snout is foreshortened. The eye color is often brown in woolly lemurs, orange or amber in sifakas, and yellow-green in indris. The fur is short, dense, and of various colors including brown, beige, white, orange, and black; often with head crowns, head ruffs, saddle backs, and eyebrows contrasting colors from the rest of the body. Indriids have five fingers on each of its two forefeet and five toes on each of its two hind feet; all with bare nails, except for the grooming claw on the second digit of their feet. Males have central chest scent glands, and females have anal scent glands.

Indriids have a dental tooth comb and small upper incisors with a reduced dental formula of only two premolars and four, rather than six, teeth in their tooth comb. Indriids retain the primitive primate features of a simple postorbital bar, relatively small brain case, and a well-developed rhinarium. All species of indriid, whether nocturnal or diurnal, have reflective eyes (tapetum lucidum) to increase perception in low light levels. Indriids are uniform in their cranial morphology and have a tympanic ring that lies free in the bulla and a large



A Coquerel's sifaka (*Propithecus verreauxi coquereli*) prepares to jump. (Photo by Harald Schütz. Reproduced by permission.)

stapedial artery. The digestive tract has an enlarged caecum and a large intestine for digesting vegetation.

Distribution

The family is a widespread successful group confined to Madagascar.

Habitat

Indriids are primarily arboreal, and are found in a wide range of ecotypes including primary forests, disturbed forest fragments, spiny desert, and gallery forests.

Behavior

Indriids have various social systems, with woolly lemurs and indris living in monogamous pairs, and sifakas living in

The eastern woolly lemur (*Avahi laniger*) has very thick and woolly fur. (Photo by © Wolfgang Kaehier/Corbis. Reproduced by permission.)

various social configurations including multi-male and multi-female. Predator attacks have been observed on woolly lemurs, indris, and sifakas. Periodic killing of both adult and infant sifakas by the carnivore fossa (*Cryptoprocta ferox*) has been observed with respect to rainforest sifakas. Hensti's

An indri (*Indri indri*) carries her babies in the trees of Madagascar. (Photo by Harald Schütz. Reproduced by permission.)

goshawk, a large raptor, has stalked and pursued woolly lemurs during the day, and remains have been found in the goshawk nest.

Indriids are primarily arboreal, although the Verraux's sifakas from the spiny desert occasionally travel on their hind legs in a bouncy gait for several meters. Woolly lemur families sleep together on low, shaded branches. Sifakas and indris sometimes sleep in pairs high in the trees. Indriids communicate with a variety of vocalizations from long distance piercing whistles (woolly lemurs) to loud clarinet-like duets (indris) to dog-like barking, honking, and sneezing (sifakas). All species communicate through scent marking. Chemicals from chest (males) and anal (females) glands may constitute individual signatures and indicate reproductive condition, sex, or dominance rank in sifakas. Avahis and indris do not have chest glands, but do use perianal glands in scent marking. Sexual dimorphism does not occur in body size or canine length in any indrid, and females are dominant over males in sifakas and indris. Dominance interactions have not been studied in woolly lemurs.

The indri (*Indri indri*) is one of the largest and loudest extant lemur species. (Photo by John Glustina. Bruce Coleman, Inc. Reproduced by permission.)

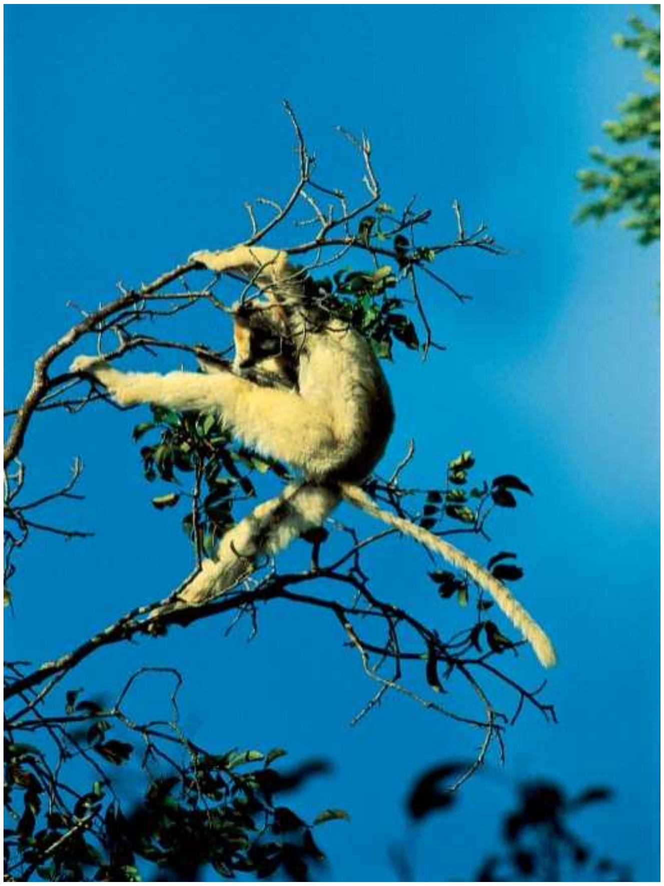
Diademed sifaka (*Propithecus diadema diadema*) mother carrying her baby. (Photo by Harald Schütz. Reproduced by permission.)

Feeding ecology and diet

Indriids are vegetarians, feeding on young and mature leaves of trees. In addition, rainforest sifakas feed on lianas, parasites, hemiparasites, herbs, and ferns. Sifakas eat three times as many different plant species as sympatric indris. Seeds are an important diet item for sifakas and fat intake is five times higher for sifakas than indris. Woolly lemurs eat leaves that are high in tannins, and are often found at higher densities in disturbed or edge forests. Flowers are a diet item of sifakas. Both sifakas and indris eat soil, often red clay on a weekly basis. It is unknown if woolly lemurs eat soil. Indris occasionally eat bark.

Reproductive biology

Sexual maturity is generally achieved between 3–5 years of age in indris and sifakas. Data concerning sexual maturity of woolly lemurs does not exist. Both males and females emigrate from natal groups after sexual maturity in indris, woolly lemurs, and sifakas. Male and female sifakas may change groups more than once, or occasionally remain in



A golden-crowned sifaka (*Propithecus tattersalli*) feeds in the trees of Madagascar. (Photo by Harald Schütz. Reproduced by permission.)

their natal group for a lifetime. Sifakas are seasonal breeders, mating in December or January. Male testicles begin to increase in size three months before the mating season (when the females come into estrus). Female sifakas have a 10–36 hour interval when they are in estrus, and they may come into estrus 1–3 times each year. In the wild they usually are pregnant after one breeding season. Females have swollen, bright pink vulvas when in estrus. Sifaka mating occurs when a male clasps a female around the waist and thrusts 10–50 times. Indris mate face-to-face, while hanging from a branch. Indris gestate for about six months. The smaller verraux's sifaka has a gestation of five months, while the larger diademed sifaka gestate for six months. A single infant is born fully furred and able to cling. Weights at birth are small, less than 0.2% of the mother's weight. Weaning occurs at about six months of age.

Conservation status

IUCN conservation status is Endangered for all living indriid species except for the Critically Endangered forms of *Propithecus perrieri*, *Propithecus diadema*, and *Propithecus candidus*.

Significance to humans

Sifakas and indris are often protected from traditional hunting by "fadys" (taboos). Malagasies recognize the human qualities of their hands and faces and therefore do not kill them as they are considered spirits of the ancestors.

1. Female and infant indris (*Indri indri*); 2. Milne-Edwards's sifaka (*Propithecus edwardsi*); 3. Baboon lemur (*Archeolemur edwardsi*); 4. Eastern woolly lemur (*Avahi laniger*); 5. Greater sloth lemur (*Palaeopropithecus ingens*). (Illustration by Gillian Harris)

Species accounts

Eastern woolly lemur
Avahi laniger

SUBFAMILY
Indriinae

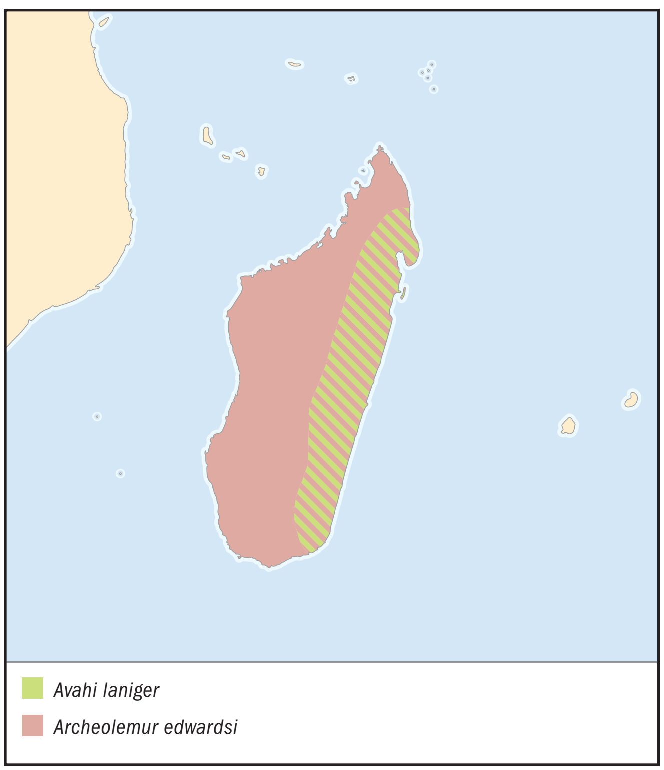
TAXONOMY
Avahi laniger Jourdan, 1834, Madagscar.

OTHER COMMON NAMES
Malagasy: Avahy, ampongy, fotsifaka, fotsife.

PHYSICAL CHARACTERISTICS
Woolly lemurs are small, nocturnal lemurs, well camouflaged in beige, brown, and gray fur. Their ears are small and furred. Their noses are broad, black, and wet. Nocturnal, medium-small lemurs adopt a vertical posture. The fur is woolly and dense. The muzzle is short and dark and the head rounded with large brown eyes, accented with beige eyebrows. The fur on the thighs is bright white—like splotches of sunlight or moonlight. The head and body length is 9.8–11.6 in (250–295 mm); tail length is 12.4–14.6 in (315–370 mm), and weight is 2.0–2.9 lb (0.9–1.3 kg).

DISTRIBUTION
The eastern woolly lemur is found throughout the eastern rainforest, from the Marojejy Massif in the north to the Andohahela Massif in the south. A remnant population occurs in the central forest of Ambohitantely Special Reserve.

HABITAT
Primary and secondary forests.



BEHAVIOR
Nocturnal. The animal lives in monogamous pairs and offspring with a group size of 3–5. The family group sleeps throughout the day, huddled on a horizontal branch, usually near a tree trunk about 3–8 ft (0.9–2.4 m) from the ground. Activity begins just after dusk with the family group foraging within 80 ft (25 m) of one another. During the night the family spends 40% of the night in close contact, grooming or resting over 60% of the time. Feeding occupies about 22% of their time, with traveling about 14%. Woolly lemurs communicate to one another with a long, high-pitched whistle, especially during the bright moon, and a neighboring group will respond with an answering whistle. Alarm screams are heard when an individual is chased by a raptor, but woolly lemurs are silent and still when approached, and do not mob. Woolly lemurs do not have obvious glands that secrete scent, which is unusual for a nocturnal primate. They may use anogenital glands to communicate, but this has not been documented to date. Grooming of family members occurs at dawn and dusk. The family returns to its sleep tree just before dawn.

FEEDING ECOLOGY AND DIET
Magnificent leapers, the woolly lemurs vertically cling and leap from trunk to trunk, then climb up to the canopy of trees to eat young leaves. Obligate leaf-eaters, the woolly lemurs are known to eat over 20 species of leaves but prefer the leaves of Dombeya and Harungana, both abundant tree species found in the edge or second growth forests. Leaves containing tannins are preferred diet items. They also have been seen to eat flowers.

REPRODUCTIVE BIOLOGY
A pair occupies a home range of between 2.5–4.9 acres (1–2 hectares). Woolly lemurs live in monogamous pairs with one infant born each year. Breeding is seasonal with infants born in August and September. The gestation period is unknown, although it may be 4–5 months. The infant clings ventrally to the mother for the first week and then rides on her back up to three months after birth. In one instance, a father has been seen to carry a two-month old infant on his back. The infant develops quickly. By three months of age the infant weighs 45% of adult weight, and has a full set of adult teeth.

CONSERVATION STATUS
Endangered.

SIGNIFICANCE TO HUMANS
Humans threaten to destroy their habitat. ◆

Milne-Edwards's sifaka
Propithecus edwardsi

SUBFAMILY
Indriinae

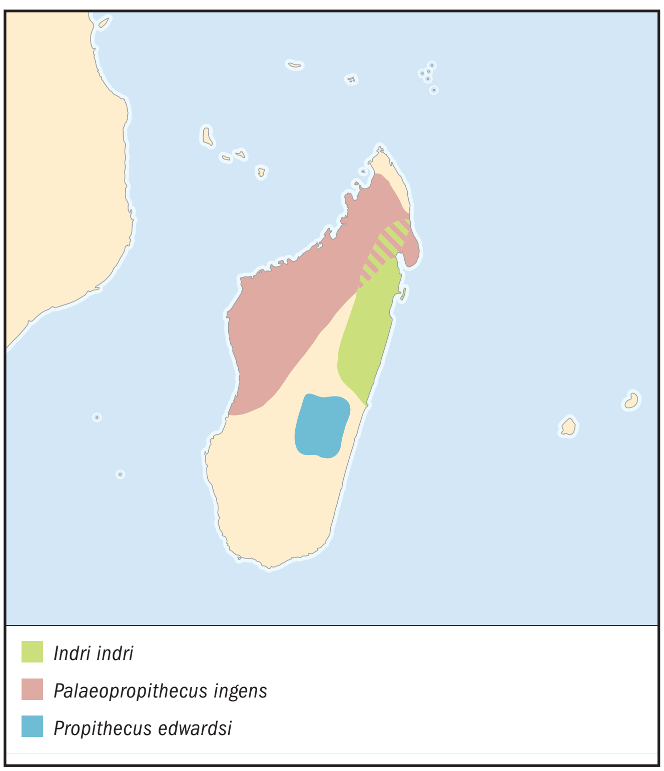
TAXONOMY
Propithecus edwardsi (A. Grandidier, 1871), Madagascar.

OTHER COMMON NAMES
Malagasy: Simpona, simpony.

PHYSICAL CHARACTERISTICS
The face is reduced and the muzzle is shortened. Adult females and males do not show differences in weight, canine size, or coloration. Long legs, broad hands and feet, and a vertical clinging and leaping locomotion characterize sifakas. The tail is about the same length as the body. The tooth comb is used for grooming fur by both males and females. Milne-Edwards's sifakas are black with a whitish beige back saddle patch. Sifaka noses are broad, black, and not furred. Sifaka eye color ranges from amber to orange to brown. The tail is the same length and color as the body.

DISTRIBUTION
Milne-Edwards's sifakas are found in southeastern mountain rainforests in Madagascar from Pic Ivohibe in the south until Kiriasy, south of the Onive River. This species is not seen on the coast or in elevations less than 1,310 ft (400 m). Although abundant in Ranomafana National Park, it is rare at Andingitra National Park and very rare in forests north of Ranomafana National Park.

HABITAT
Primary and secondary moist, humid forests in elevations higher than 1,310 ft (400 m).



BEHAVIOR
Diurnal. It lives in groups of 3–9, composed of multi-male, multi-female, one-male, or one-female. Females are dominant to males in both feeding and social situations. The group sleep huddled together on a broad horizontal branch about 49–82 ft (15–25 m) high off the ground. If the group is large, paired individuals sleep in nearby trees. The same sleep trees are used over time, but usually not on consecutive nights. During the day the family spends over 45% of the day in close contact, grooming or resting. Feeding occupies about one-third of their time, with 15% of time traveling. In contrast to indris, sifakas do not give daily long calls. Milne-Edwards's sifakas have over seven discrete calls. Lost individuals give long, warbling whistles that are answered by group members. Quieter contact moos are given among group members to indicate position and propose group movement. Alarm calls alerting for aerial predators are loud, raucous barking by all group members. Often males first sight a hawk or eagle, give the alarm bark, and the females and infants drop to the ground for protection. In contrast, a short staccato "zusss" call warns the group of proximity of terrestrial predators. Sifaka males have chest glands that secrete scent, and are used to scent mark over the anogenital marks that females rub on vertical tree trunks. He also urinates over her mark. Scent marking by both males and females occurs year round, and may indicate territorial marking. Frenzied scent marking bouts indicate that the breeding season is near.

FEEDING ECOLOGY AND DIET
Milne-Edwards's sifakas primarily eat vegetation including young leaves from trees and vines and seeds from fleshy fruits. Flowers, fruit pulp, mature leaves, and soil are also consumed regularly. Homopteran insects are consumed by Milne-Edwards's sifakas in December. Sifaka individuals often eat 25–30 plant species per day, and over 150 plant species within a year.

REPRODUCTIVE BIOLOGY
Milne-Edwards's sifakas live in monogamous pairs, harems, multi-male, multi-female groups and in polyandrous groups. Breeding is seasonal, and males' testicles begin to expand three months before the mating in December to January. During estrus the female's vulva becomes swollen and pink. Milne-Edwards' sifakas mate 3–4 times within a 10-hour period with the male mounting the female from the back. Females may mate with one or more males in the group. The gestation period is six months, and infants are born in May or June. One infant is born per mother on average every second year. Newborn infants weigh about 4.4 oz (125 g) and are 0.2% of the weight of the mother. The infant clings ventrally to the mother for the first four weeks and then rides on her back for five months. Males help transport older infants about 10% of the time, and defend the group against attacks by large raptors. Females are dominant in feeding and social situations. Infant mortality is high (over 50%).

CONSERVATION STATUS
Endangered.

SIGNIFICANCE TO HUMANS
In the Ranomafana region it is fady (taboo) to eat sifakas because they resemble humans. ◆

Indri
Indri indri

SUBFAMILY
Indriinae

TAXONOMY
Indri indri E. Geoffroy and G. Cuvier, 1796, Madagascar.

OTHER COMMON NAMES
Malagasy: Amboanala, babakoto, endrina.

PHYSICAL CHARACTERISTICS
Body length is about 23.6 in (600 mm), tail length is about 2.0 in (50 mm), and weight is 13.2–16.5 lb (6.0–7.5 kg).

DISTRIBUTION
The indri occurs from forests north of the Mangoro River to near Sambava, but excluding the Masoala peninsula.

HABITAT
Primary and secondary lowland and mid-altitude humid moist forests.

BEHAVIOR
Strictly diurnal. Group size varies from 2–6 and is normally comprised of adult pair and offspring. Females are dominant over males in feeding and social situations. The pair gives morning clarinet-like calls that can be heard up to 2 mi (3 km). The number of calls increases prior to and during the mating season. Home ranges are 20–74 acres (8–30 hectares), with the daily path length from 980–2,300 ft (300–700 m). Indris leap through the forest with spectacular bounds of up to 33 ft (10 m) between vertical trunks. Indris have no scent glands located on the chest, head, or arms. Salivary scent marks transmitted by mouth rubbing has been observed. Anogenital glands are used for scent marking during the mating season. Indris rest frequently and daily activity ranges from 4–11 hours depending on the time of the year.

FEEDING ECOLOGY AND DIET
The annual diet of Indri consists of 70–82% immature leaves from trees, 10–22% fruit, 6% flowers, and the remainder from mature leaves, bark, galls, and soil. Seventy-nine plant species are consumed during the year at mid-elevation forest, less than half of the number of species consumed by sympatric diademed sifakas. In low-elevation forest the indri feed on over 42 plant species. The indri has a long small intestine and enlarged caecum for digestion of vegetation. Females spend significantly more time feeding than males, although the number of feeding bouts per day is equal for males and females. Foliage from the Laurel family is the most frequently eaten by indri populations both in mid-altitude montane and low-altitude coastal rainforests.

REPRODUCTIVE BIOLOGY
Monogamous. Indris do not reach sexual maturity until 7–9 years of age, and females give birth every 2–3 years. Mating occurs between December and March with a single offspring born between April and August. Indri mate face-to-face, hanging from a branch. The gestation is between 120–150 days. The infant is born furred, able to cling, but very small in size. The infant rides on the ventrum of the mother until four months when it transfers to the mother's back. The offspring is capable of moving independently at eight months.

CONSERVATION STATUS
Endangered.

SIGNIFICANCE TO HUMANS
Local taboo restricts harming or hurting the indri. Local legend says an indri howls at dawn to mourn the loss of its tail stolen by black and white ruffed lemurs. ◆

Greater sloth lemur
Palaeopropithecus ingens

SUBFAMILY
Palaeopropithecinae

TAXONOMY
Palaeopropithecus ingens Grandidier, 1899, Madagascar.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Its estimated body weight is 121 lb (55 kg). It is dentally similar to the extant sifakas with long, narrow molars, and well-developed shearing crests. It has small, vertical lower incisors with no tooth comb. The skull is similar to living indriids, but more robustly built, with a longer snout, and a heavily buttressed nasal region suggesting prehensile lips. The forelimbs are considerably longer than the hind limbs, and it has very long, curved phalanges and very mobile joints. Extremely suspensory, its locomotor abilities have been compared to sloths or orangutans.

DISTRIBUTION
Sloth lemurs went extinct within the last few thousand years, but before that were widely distributed throughout Madagascar. Paleaopropithecus, the most sloth-like of the sloth lemurs was widespread throughout all Madagascar, with this species found in Andranomena, Analabe in the west, and Ankarana massif in the north. Paleaopropithecus have been found in limestone caves of the Manamby Plateau, north of Tulear.

HABITAT
Primary and secondary forests.

BEHAVIOR
From the morphology, it is predicted that they were slow moving, commonly climbing and suspending themselves in trees.

FEEDING ECOLOGY AND DIET
Highly folivorous.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Extinct.

SIGNIFICANCE TO HUMANS
Scientists have indications from cut marks on bones that early humans hunted subfossil lemurs. Climate changes suggest humans and perhaps wildfires destroyed their habitat. ◆

Baboon lemur

Archeolemur edwardsi

SUBFAMILY
Palaeopropithecinae

TAXONOMY
Archaeolemur edwardsi Filhol, 1895, Madagascar.

OTHER COMMON NAMES
Malagasy: Kadoky.

PHYSICAL CHARACTERISTICS
Its estimated body weight is 49 lb (22 kg). Males and females had the same body size. Tooth eruption patterns, including rapid eruption of adult dentition, are reminiscent of the living indris, sifakas, and woolly lemurs. The anterior premolar is caniniform, and the entire premolar row formed a long cutting edge. The broad molars had low, rounded cusps arranged in a bilophodont pattern similar to Old World monkeys. Cranially it is similar to living indrids. Short limbs relative to trunk length are reminiscent of both terrestrial and arboreal quadrapeds.

DISTRIBUTION
From north to south to west subfossil sites throughout Madagascar. This was the most widespread species of subfossil lemurs.

HABITAT
Primary and secondary forests and woodlands throughout Madagascar.

BEHAVIOR
From the morphology, it is predicted that the baboon lemurs fed on leaves and hard fruits, and traveled both on the ground and in the trees.

FEEDING ECOLOGY AND DIET
Projecting from morphology, baboon lemurs had a diverse diet including fruit, seeds, and invertebrates. The teeth of Archaeolemur appear specialized for processing foods requiring considerable preparation previous to processing, such as fruits with tough outer coverings or the seeds within them. It has been suggested that it ate seeds of baobab trees, which facilitated seed dispersal. High foliage consumption is supported by data on molar microwear.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Extinct.

SIGNIFICANCE TO HUMANS
Scientists have indications from cut marks on bones that early humans hunted them. Climate changes suggest humans and perhaps wildfires destroyed their habitat. ◆

Resources

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Organizations

Duke University Primate Center, Division of Fossil Primates. 1013 Broad Street, Durham, NC 27705 United States. Phone: (919) 416-8420. Fax: (919) 416-8584. Web site: <http://www.fossils.duke.edu/>.

Institute for the Conservation of Tropical Environments. N-543 SBS Bldg., SUNY at Stony Brook, Stony Brook, NY 11794-4364 United States. Phone: (631) 632-9440. Fax: (631) 632-7692. E-mail: icte@notes.cc.sunysb.edu Web site: <http://naples.cc.sunysb.edu/CAS/icteweb.nsf>.

Patricia Wright, PhD

Sportive lemurs

(Lepilemuridae)

Class Mammalia

Order Primates

Family Lepilemuridae

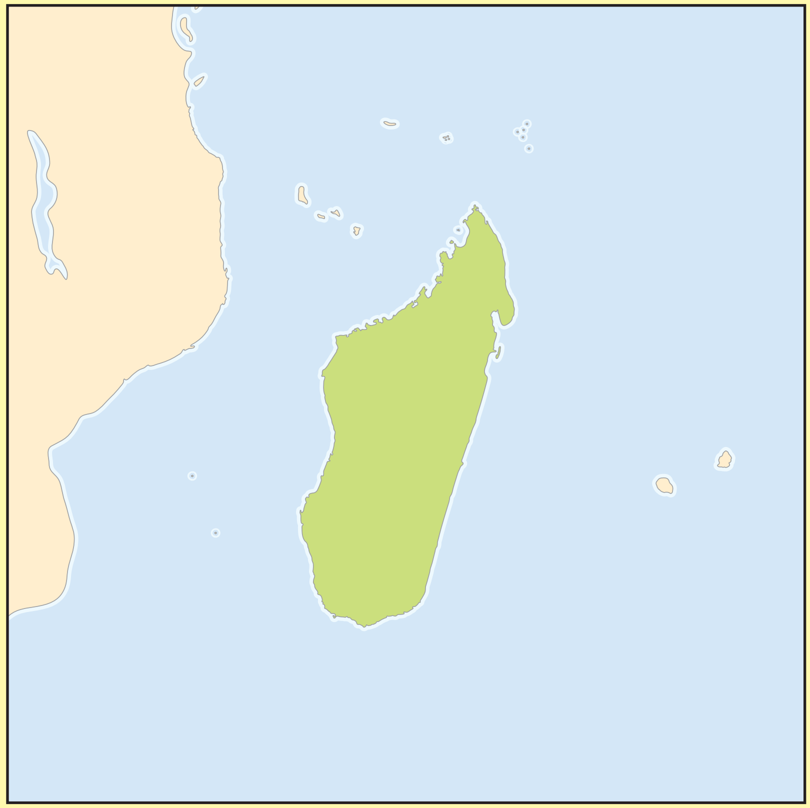
Thumbnail description
Often raises its hands when threatened by a transgressor, like a boxer who is in defense against an opponent's attack; nocturnal, arboreal, and medium-sized for lemurs; and possess long tails and binocular vision and they are distinguished amongst themselves in large part due to each species' unique chromosomes that were scientifically identified through cytogenetic (chromosome) studies

Size
Head and body length: 9.8–13.8 in (25.0–35.0 cm); tail length: 9.8–12.0 in (25.0–30.5 cm); weight 1.1–2.2 lb (0.5–1.0 kg)

Number of genera, species
Extinct: 1 genus, 3 species; Extant: 1 genus; 7 species

Habitat
Dry deciduous and tropical rainforests

Conservation status
Vulnerable: 2 species; Lower Risk/Near Threatened: 5 species



Distribution
Restricted to the island of Madagascar

Evolution and systematics

There is one extinct genus *Megaladapis*, or koala lemur, within the family Lepilemuridae, and within that extinct genus there are three extinct species *Megaladapis madagascariensis*, *M. edwardsi*, and *M. grandidieri*. *Megaladapis grandidieri* was known to exist (from subfossil material) from Ampasambazimba in central Madagascar, while *M. madagascariensis* and *M. edwardsi* were known to exist from southwestern and southern Madagascar.

Koala lemurs were very impressive during their time because, according to fossil skulls that have been found, their skulls were as large as that of the skull of an ass; and with a deduced head and body weight of 88–176 lb (40–80 kg). Such subfossil remains have been found during the last quarter of the twentieth century at sites in Madagascar, and date back (with radiocarbon dating procedures) about 600–3,000 years ago. Humans began to populate Madagascar during this period, moving in with domestic livestock. This put environmental pressure on the koala lemurs with respect to reduced natural forest habitat and a very aggressive human predator (they were earlier evolving without predators). In addition, drought was believed to have increased pressures during this time with respect to them. Koala lemurs probably became extinct sometime prior to the arrival of Europeans during the 1500s. In 1982 Tattersall indicated a similarity between the koala lemur and the prosimian ("primitive ape") family Adapidae of the Eocene Epoch (55–38 million years ago) of Europe.

From cranial and postcranial morphology, the locomotion and lifestyle of koala lemurs were similar to that of *Phascolarctos*, the living koalas of Australia. The skull was very large in relation to the short, bulky postcranial skeleton; and relatively narrow, greatly elongated, and resembling the skull of a pig. Cranial length of *Megaladapis grandidieri* was 10.8–11.8 in (27.3–30.0 cm), while the length of *M. madagascariensis* was 9.3–9.6 in (23.5–24.4 cm). Both species' postcranial specializations suggested that they had a greater flexibility of their limbs and most likely a more distinct arboreal (tree climbing) adaptation than *M. edwardsi*. Hind limb suspension was in all likelihood an important behavior of both animals. Cranial length

A white-footed sportive lemur (*Lepilemur leucopus*) in a tree in Berenty, Madagascar. (Photo by Nigel J. Dennis/Photo Researchers, Inc. Reproduced by permission.)

The white-footed sportive lemur (*Lepilemur leucopus*) is able to leap a distance of 16 ft (5 m). (Photo by © Gallo Images/Corbis. Reproduced by permission.)

of *M. edwardsi* was 10.9–12.5 in (27.7–31.7 cm); it possessed one of the largest sized cranial lengths of known prosimians.

The facial area of koala lemurs was long, the orbits divergent, the auditory bullae flat, and the braincase very small. The long nasal bones projected well past the anterior end of the palate; this feature tends to indicate to researchers that they had a moveable snout when alive. The zygomatic arches (the bone bar that connects the cheekbone with the temporal bone on the side of the skull) were massive, and there were strong nuchal (with respect to the nape of the neck) and sagittal (with respect to the suture at the top of the skull) crests. The foramen magnum (the opening at the base of the skull) was rotated back onto the posterior surface of the skull so that it faced forward when the species stood on all four feet. The occipital condyles (the knobs on each side of the foramen magnum) were oriented perpendicularly to the cranial base. Adults had no upper incisor teeth, instead had bony ridges that suggested a horny pad (similar to some ungulate herbivores). The large molars were complex cusps and increased in size from the front to the rear.

Hands and feet were extraordinarily long, but the legs were relatively short. The forelimbs were longer than the hind limbs, and all four powerful legs were somewhat curved, shaped for grasping. They clung to tree trunks and branches with all forelimbs, and moved upward with a series of short hops. Koala lemurs crossed to neighboring trees with short leaps. They fed by cropping leaves pulled by its forelimbs that were within easy reach of the mouth.

The living genus *Lepilemur* had for a long time been placed in the family Lemuridae. However, according to Rumpler (1975), Rumpler and Albignac (1975), and Petter and Petter-Rousseaux (1979), systematic investigations, which included cytogenetics (the scientific study of chromosomes), showed

A red-tailed sportive lemur (*Lepilemur ruficaudatus*) in front of its tree nest. (Photo by Harald Schütz. Reproduced by permission.)

that it represented a separate family and, therefore, took the family name Lepilemuridae. Later research by Buettner-Janusch and Tattersall (1985) and Tattersall (1982 and 1986) indicated that *Lepilemur* belonged in the same family as the extinct *Megaladapis* and, therefore, the family name was indicated to be Megaladapidae. Several studies in the late 1980s and early 1990s conflicted as to which family (Lemuridae, Lepilemuridae, or Megaladapidae) *Lepilemur* should be placed. (It is the contention of the experts collaborating on this publication that the extinct genus *Megaladapis* and the extant genus *Lepilemur* will be placed in the family Lepilemuridae.)

Physical characteristics

Sportive lemurs, sometimes also called weasel lemurs, have a head and body length of 9.8–13.8 in (25.0–35.0 cm), with a tail length of 9.8–12.0 in (25.0–30.5 cm) and a body weight of 1.1–2.2 lb (0.5–1.0 kg). Tails are longer than the head and body in some species, but shorter in other species. The seven species of sportive lemurs are outwardly quite similar to each other, but because of different chromosome patterns they are each considered distinctive species.

Each species possess woolly, dense fur that is usually colored in shades of red and mixed with gray and/or brown. The upper (dorsal) parts are rufous (reddish brown), gray, or brown, while the under (ventral) parts are yellowish white or pale gray. Some of the species have a long spinal stripe from the head to the base of the tail. The hind limbs are considerably longer than the forelimbs, adapted specifically to meet their mode of locomotion of vertically leaping and hopping. The feet are only slightly elongated, with the fourth and fifth toes being the longest. They have a prehensile thumb, which is semi-opposable; being able to, for example, strongly grip onto vertical branches. The large nails of the toes are flat; except for the nails of the great toes, which are ridged. The short head is conical (pointed) and the ears are large, round, and membranous. In the skull there is a median vertical articular (jointed) area and a transverse articular surface of the mandible. Adults lose their upper incisor teeth at a very early age, so during adulthood they normally have 32 teeth. The premolars widen out from front to rear, and as reported by researchers: "the upper molars display buccal cingula and parastyles, lingual buttressing of the paracones and metacones, and distal displacement of their lingual moieties." Sportive lemurs have a dental comb in which their lower front teeth are fused and tilted forward, providing a tool that helps to groom their fur.

Distribution

Sportive lemurs are confined to the island of Madagascar, which is off the east coast of Africa.

Habitat

Most habitation occurs in forest lands from the evergreen forests on the east coast of Madagascar to the hot, dry forests of the southwestern part of the country. They are basically solitary while in their habitat, but their population densities can be quite high. Males have larger territories than females, and the territory of a male usually overlaps that of several females. Members of the same sex defend territories against one another by using vocalizations, chases, and fights to drive out trespassers and transgressors.

A red-tailed sportive lemur (*Lepilemur ruficaudatus*) in the tree canopy. (Photo by Harald Schütz. Reproduced by permission.)

Behavior

They are strictly nocturnal and arboreal forest dwellers; often gathering from their individual hiding places in sometimes large groups during the hours of twilight and darkness in order to proceed to their separate feeding places. Daytime is usually spent curled up in a ball asleep in a hollow tree, thick foliage, vines, or other similar hiding places. Their sleeping hole or nest may be used for years. In the afternoon, they often stick their heads out of their hiding place, and sit dozing for hours. An exception to this occurs on Nosy Be where the species *Lepilemur dorsalis* (gray-backed sportive lemur) often sleeps out in the open because of a lack of predators. Socially, each species of sportive lemurs live basically solitary lives in their single territories except for mothers with their infants. Some marking of territories occur with urine and the secretion from glands in the circumanal (posterior) region. Males inhabit and vigorously defend territories (from other sportive lemur neighbors of the same sex) of about

A white-footed sportive lemur (*Lepilemur leucopus*) forages. (Photo by Harald Schütz. Reproduced by permission.)

30,000 sq ft (3,000 sq m), but which can go up to 107,000 sq ft (10,000 sq m). These territories are in the immediate overlapping vicinity to one or more females who roam territories of about 20,000 sq ft (2,000 sq m).

Their primary means of communication is a relatively large vocal repertoire. Locomotion is by vertical clinging and leaping, quickly moving among vertical tree trunks and boughs with occasional bipedal hops (similar to the movement used by kangaroos) on the ground. They are able to leap with the powerful extension of their hind limbs. They are also able to run on all four limbs, or hop on their two hind limbs, either along the branches of a tree or on the ground. The tail is not important for balancing.

Feeding ecology and diet

Sportive lemurs are folivorous (that is, feeding mostly on leaves) but also eating flowers, bark, and fruit. They are distinctive from other lemurs in being able to process difficult to digest foods, having developed special organic adaptations for the processing of these types of foods. They will also infrequently eat hard leaves of the cactus-like plant *Alluaudia*, which is partially digested in the cecum, and then eliminated and re-ingested (which is called cecotrophy).

Reproductive biology

Mating season for these animals is May-July. Calls of mating animals are often heard as they chase each other. An offspring of one is born in September-October, and is quite well developed and fairly active immediately after birthing. Mothers have been observed carrying their young in their mouths as they leap from tree to tree. After about one month the young will begin to forage for themselves, and by about two and one-half months they will no longer be directly dependent on their mothers for protection and food. However, the young will continue to stay with their mothers until the next generation of babies are born.

Conservation status

All seven species are listed in CITES Appendix I; the U.S. Endangered Species Act classifies all seven species as endangered; the IUCN classifies two species as Vulnerable and five as Lower Risk/Near Threatened; and the U.S. Department of the Interior lists all species as endangered.

All of these animals are threatened by loss of forest habitat by the continuing use of what is called "slash-and-burn" agriculture, which encourages the burning of forests for the clearing of settlements and for the use in farming. As a result, the growth of pastures and the overgrazing by cattle and goats continue to place increasing pressures on the habitat of all sportive lemurs in various degrees. Most, if not all, species are also hunted for food.

A Milne-Edwards's sportive lemur (*Lepilemur edwardsi*) with baby. (Photo by Harald Schütz. Reproduced by permission.)

Significance to humans

There has been little success in raising them in zoos. They have lived for less than one year at the Jardin des Plantes Zoo in Paris, France, and at the Philadelphia Zoo in Pennsylvania (United States). A breeding program has been set up at the Tananarive Zoo, now the Antananarivo Zoo, in Madagascar, but even it has not been successful at keeping them over long periods of time. The meat of the sportive lemur is sometimes eaten by locals, who like its taste (probably because of the animal's vegetable diet).

1. Small-toothed sportive lemur (*Lepilemur microdon*); 2. White-footed sportive lemur (*Lepilemur leucopus*); 3. Northern sportive lemur (*Lepilemur septentrionalis*); 4. Gray-backed sportive lemur (*Lepilemur dorsalis*); 5. Red-tailed sportive lemur (*Lepilemur ruficaudatus*); 6. Weasel sportive lemur (*Lepilemur mustelinus*); 7. Milne-Edwards's sportive lemur (*Lepilemur edwardsi*). (Illustration by Gillian Harris)

Species accounts

Gray-backed sportive lemur
Lepilemur dorsalis

SUBFAMILY
Lepilemurinae

TAXONOMY
Lepilemur dorsalis Gray, 1870, northwestern Madagascar.

OTHER COMMON NAMES
Spanish: Lémur juguetón de lomo gris.

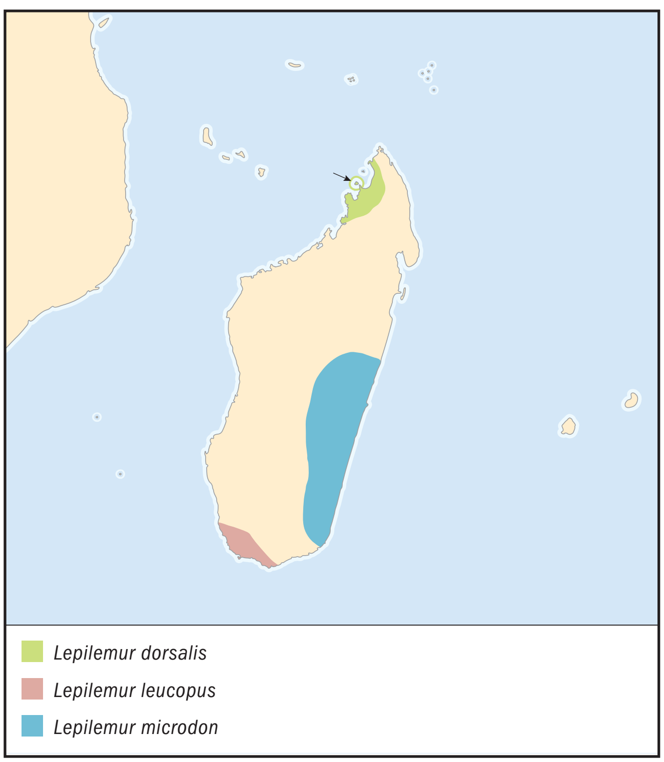
PHYSICAL CHARACTERISTICS
Gray-backed sportive lemurs have a head and body length of 9.8–10.2 in (25.0–26.0 cm), with a tail length of 10.2–10.6 in (26.0–27.0 cm) and an average body weight of 1.1 lb (0.5 kg). They have binocular vision, and hands and feet containing large digital pads that are used for clinging. The upper (dorsal) parts of the animal are colored medium to dark brown and its lower (ventral) parts are colored a more pale brown.

DISTRIBUTION
The extreme northwestern part of Madagascar, especially on Nosy Be Island and in the region of Sambirano.

HABITAT
Evergreen rainforests and moist deciduous forest.

BEHAVIOR
The gray-backed sportive lemur is arboreal and nocturnal. They often sleep in tropical vines, foliage, and hollow trees, and sometimes even out in the open. They move through the forest by vertical clinging and leaping. The social system is based around mothers and their offspring. Males live solitarily, and have home ranges that overlap one or more females. Mothers will leave their young on branches while they go off to forage for food. All animals are highly territorial, with males sometimes defending their territory with violent means.

Communication comes with various sounds, but with three primary calls. The "loud" calls are used most often as male territorial calls, to mark off a male's territory and to advise other males that an area is already occupied. The sounds start out as a series of harsh "hein" calls, then is often followed by high-pitched "hee" calls. Both calls can be also sounded individually. Mothers often use a "contact" call, which sounds similar to a loud kiss, in order to keep in contact with their infants that are placed on tree branches as they forage for food. The "contact-rejection" call often occurs when an individual approaches another one. It consists of a series of resonant hissing calls, which is followed by a two-phase vocalization.



FEEDING ECOLOGY AND DIET
The species is primarily folivorous (leaf-eating), but also eats fruit and bark in order to supplement their diet. They are cecotrophy, meaning the species re-ingests their feces in order to further break down the cellulose in leaves.

REPRODUCTIVE BIOLOGY
The species has a polygynous mating system, where one male will visit various females during the breeding season. Female gray-backed sportive lemurs give birth to a single offspring each year. The babies are usually born between August and November.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN. Also listed on CITES Appendix I and as endangered by the U.S. Endangered Species Act (ESA). Total populations are estimated to number 10,000–100,000.

SIGNIFICANCE TO HUMANS
None known. ◆

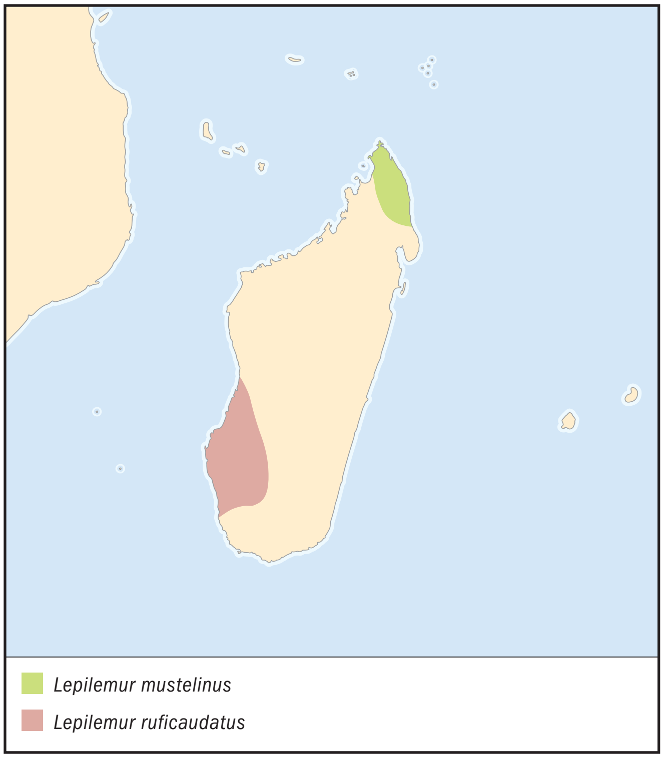
Red-tailed sportive lemur
Lepilemur ruficaudatus

SUBFAMILY
Lepilemurinae

TAXONOMY
Lepilemur ruficaudatus A. Grandidier, 1867, Morondara, Madagascar.

OTHER COMMON NAMES
French: Petit lépilémur; Spanish: Lémur juguetón de cola roja.

PHYSICAL CHARACTERISTICS
Red-tailed sportive lemurs have a head and body length of about 11.0 (28.0 cm), with a tail length of 9.8–10.2 in (25.0–26.0 cm) and a fluctuating weight of 1.3–2.0 lb (0.6–0.9 kg). They are arboreal and nocturnal, and possess binocular



vision, a large cecum, and large digital pads on its hands and feet that are used for clinging. Its dorsal side is light gray-brown in coloration with red-brown color on its front (anterior) side and light gray or white on its under parts. It travels through the forest by vertical clinging and leaping.

DISTRIBUTION
Southwestern Madagascar, in the region of Morondava and ending at its southern border along the Onilahy river.

HABITAT
They live in dry forests. The population density of the species is 180–350 animals per 0.4 sq mi (1.0 sq km).

BEHAVIOR
The social structure of the species is based around mothers and their young. Males live alone and have home ranges that overlap one or more females. Mothers often will leave their young on branches, while they go off to forage for food. For the first few weeks of life, mothers will transport the young by picking them up in their mouths. All animals are highly territorial, with the males sometimes defending their territory with violent means.

Communication comes with various sounds, but with two primary calls. The “loud” calls are used frequently as male territorial calls, to demarcate a male’s territory and to advise other males that an area is already taken. The call sounds like “boako-boako,” and is sometimes preceded by grunts. The “contact-rejection” call often occurs when an individual approaches another one. It consists of a series of resonant hissing calls, which is followed by a two-phase vocalization.

FEEDING ECOLOGY AND DIET
Red-tailed sportive lemurs are primarily folivorous animals (eating mostly tender leaves), but they also eat fruits. During summers the fruits from the *Diospyros* spp. are often eaten. The species is also a cecotroph, re-digesting their feces in order to break down the cellulose in the already eaten leaves.

REPRODUCTIVE BIOLOGY
The mating system is polygynous, where a male will visit one or more females during the mating season. The mating season begins around May. Females give birth to a single offspring each year, with the young normally born between September and November. The young become independent of their mothers at around one year of age.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN. Also listed on CITES Appendix I and as endangered by the U.S. ESA. Total populations are estimated to number 10,000–100,000, and the species is threatened with destruction of its habitat.

SIGNIFICANCE TO HUMANS
Hunted for food. ◆

Milne-Edwards’s sportive lemur
Lepilemur edwardsi

SUBFAMILY
Lepilemurinae

TAXONOMY
Lepilemur edwardsi (Forbes, 1894), Betsaka, Madagascar, 12 mi (19.3 km) inland from Majunga.

OTHER COMMON NAMES
Spanish: Lémur juguetón de Milne-Edwards.

PHYSICAL CHARACTERISTICS
Milne-Edwards’s sportive lemurs have a head and body length of 10.6–11.4 in (27.0–29.0 cm), with a tail length of 10.6–11.4 in (27.0–29.0 cm) and an approximate weight of 2.2 lb (1.0 kg). They are arboreal and nocturnal, and possess binocular vision, a large cecum, and their hands and feet contain large digital pads that are used for clinging. The species has a pelage color that is gray-brown on the dorsal side with a reddish brown wash and gray ventrally speckled with cream colorations.

DISTRIBUTION
West-central Madagascar.

HABITAT
They live in dry forests. The population density of the species is about 57 animals per 0.4 sq mi (1.0 sq km). Their home ranges are relatively small.

BEHAVIOR
The social structure of the species is based around mothers and their young. Males live alone and have home ranges that overlap one or more females. Mothers often will leave their young on branches, while they forage for food. Mothers will transport their several week old young by picking them up in their mouths. All animals are highly territorial, with the males sometimes defending their territory in violent means. Two or three individuals may sleep together in a tree hole by day, but will roam separately by night. They move through the forest by vertical clinging and leaping, tending to leap between tree limbs with sloping and horizontal supports. They are able to leap distances of 13 ft (4 m) or more.

Communication comes with various sounds, but with three primary calls. The “loud” calls are used more often as male territorial calls, to demarcate a male's territory and to caution other males that an area is taken. The call sounds similar to a crow, starting out like "oooai," and then followed by a rapid series of "oui oui oui" sounds. Mothers often use the "contact" call in order to keep in contact with their infants that are set on tree branches as they forage for food. The call sounds like "tchen". The "contact-rejection" call often occurs when an individual approaches another one. It consists of a series of resonant hissing calls, which is followed by a two-phase vocalization.

FEEDING ECOLOGY AND DIET
Milne-Edwards's sportive lemurs are primarily a folivorous (leaf eating) species. It also eats a small amount of fruits and flowers in order to supplement its diet. It will also eat older leaves and even dead or dying leaves of *Tabemaemontana modesta*. The animals forage for various types of foods that are found relatively close together. The leaves that they consume are relatively low in available sugars, which mean it has a low energy diet. This diet contributes to a small home range because of its reduced thermoregulation levels. It is also a cecotroph, re-digesting their feces in order to further break down the cellulose in the leaves.

REPRODUCTIVE BIOLOGY
The mating system is polygynous, where a male will visit one or more females during the mating season. Females give birth to a single young.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN. Also listed on CITES Appendix I and as endangered by the U.S. ESA. Total populations are estimated to number more than 100,000, and the species is threatened with destruction of its habitat.

SIGNIFICANCE TO HUMANS
Hunted for food. ◆

White-footed sportive lemur
Lepilemur leucopus

SUBFAMILY
Lepilemurinae

TAXONOMY
Lepilemur leucopus Major, 1894, Fort Dauphin (Bevilany), Madagascar.

OTHER COMMON NAMES
English: White-footed weasel lemur; Spanish: Lémur Juguetón de patas blancas.

PHYSICAL CHARACTERISTICS
White-footed sportive lemurs have a head and body length of about 9.8 in (25.0 cm), with a tail length of about 9.8 in (25.0 cm) and weight of 19.2–20.5 oz (544–580 g). They have binocular vision (with large eyes), large prominent ears, a large cecum, and large digital pads on their hands and feet for clinging. This species has a pelage color that is medium to light gray on the dorsal side and white to very pale gray on the ventral side. The tail is very light brown in color.

DISTRIBUTION
Extreme southern Madagascar; primarily in the Didiereaceae forest (spiny desert) and gallery forest.

HABITAT
They live in the vegetation next to rivers, all within the regions of the spiny desert and gallery forest. The population density is 200–810 animals per 0.4 sq mi (1.0 sq km). Home ranges are small but appear to coincide with well-defined, stable territories of the females. The home range of the female averages about 0.44 acres (0.18 hectares), but can range from 0.37–0.79 (0.15–0.32 hectares). Male home ranges average 0.74 acres (0.30 hectares), but can range from 0.49–1.14 acres (0.20–0.46 hectares). The home range of a large male may overlap the ranges of up to five females, but a small male's home range may only overlap the ranges of 1–2 females. Adult females who share ranges and males within the ranges of other females will sometimes forage together during the night. Such mates will often groom each other as a social activity, which is preceded by nose touching and followed by a period of rest; mothers and their offspring perform the activity most often.

BEHAVIOR
They are an arboreal and nocturnal species; and basically solitary, but some contact may be present among related females. They sleep in nests within tropical vines, on branches, and sometimes in hollow trees. Often in the afternoons, they will poke their heads out of their hole or nest while they doze off and on during the rest of the day. Territorial defense against members of the same sex is very aggressive, and often occupies a large part of the nighttime activities. They often spend many hours observing their home range (and neighbors) from a high branch in order to protect their home range from invaders. Defense tactics include visual displays, vocalizations, chases, and on occasion severe fights.

Vocalizations can include a range of weak squeals to powerful, high-pitched sounds (the male can sometimes sound like a crow); with purposes including communication and territorial protection. The "loud" calls are used more often as male territorial calls, to demarcate a male's territory and to advise other males that an area is taken. The sounds start out as a series of harsh "hein" calls, and then followed by high-pitched "hee" type calls. Both calls can be also sounded separately. Mothers often use the "contact" call in order to keep in contact with their infants that are set on tree branches as they forage for food. The "contact-rejection" call often occurs when an individual approaches another one. It consists of a series of resonant hissing calls, which is followed by a two-phase vocalization.

White-footed sportive lemurs move through the forest by vertical clinging and leaping. This species is more unique in its locomotion than the other species in that is uses more oblique and vertical supports, and substrates that are 16.4–49.2 ft (5.0–15.0 m) in height.

FEEDING ECOLOGY AND DIET
Primarily it is a folivorous species. Unlike the other species in the family, this species feeds primarily on thick, juicy leaves (mostly from the species *Tamarindus indica* and *Euphorbia tirucalli*) and various vine species. It is also a cecotroph, which means it will often re-ingest part of their fecal material in order to further break down the cellulose in the previously eaten leaves. The diet of the white-footed sportive lemur does not change from the different seasons of its habitat in Madagascar.

REPRODUCTIVE BIOLOGY
The mating season is the period from May to July or August. They are a polygynous species; where the male will visit each female mate during the mating season. A single young is born from mid-September to November or December. Mothers raise offspring usually in a hollow tree. The gestation period has been reported from 120–150 days. The weight of the newborn is about 1.8 oz (50 g). Mothers often will leave babies

clinging to branches while they forage. Weaning occurs at about four months, but youngsters may continue to rely on their mothers for more than the first year of its life. Sexual maturity is reached at around 1.5 years. Captive animals have reached 12 years of age.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN. Also listed on CITES Appendix I and as endangered by the U.S. ESA. Total populations are estimated to number more than 100,000, and the species is threatened with destruction of its habitat.

SIGNIFICANCE TO HUMANS
Hunted for food. ◆

Weasel sportive lemur
Lepilemur mustelinus

SUBFAMILY
Lepilemurinae

TAXONOMY
Lepilemur mustelinus I. Geoffroy, 1851, north of Tamataire, Madagascar.

OTHER COMMON NAMES
French: Grand lépilémur; Spanish: Lémur juguetón comadreja.

PHYSICAL CHARACTERISTICS
Body and head length of 11.0–13.8 in (28.0–35.0 cm); tail length of 9.8–11.8 in (25.0–30.0 cm) and weight of 20.6–22.9 oz (583–650 g). It has binocular vision, a large cecum, and large digital pads on hands and feet that are used for clinging. The species has a pelage color that is brown dorsally and gray-brown ventrally, with a gray coloring on their heads.

DISTRIBUTION
Northern part of eastern forests of Madagascar, with a southern limit from the right bank of the Lokoho river to the coast.

HABITAT
Forests.

BEHAVIOR
Weasel sportive lemurs are arboreal and nocturnal, and basically solitary animals. They live in hollow trees during drier seasons (usually 19.7–39.4 ft [6–12 m] above the ground), and in nests made of leaves within tropical vines during wetter seasons. When first emerging from their nests at dusk they make very noisy, high-pitched sounds. They move through the forest by vertical clinging and leaping. The social system is based upon mothers and young. Males live solitary lives, but have home ranges that overlap one or more females. All animals fiercely protect their territories, with males sometimes using violence as a means to defend their territories. Communication comes with various sounds. One such sound is a “loud” call that is emitted by adult males in order to demarcate its territorial claims and to tell other males that it already occupies a certain area.

FEEDING ECOLOGY AND DIET
They are a folivorous species (eating mostly leaves), but will also eat small amount of fruits and flowers to supplement the diet. They are also cecotroph, re-digesting their feces in order to help break down the cellulose in previously eaten leaves.

REPRODUCTIVE BIOLOGY
The species is polygynous, where a male will visit several females during the mating season. The gestation period is 130–150 days. Females will give birth to one young. Females will leave their young on branches while they forage for food.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN. Also listed on CITES Appendix I and as endangered by the U.S. ESA. Total populations are estimated to number 10,000–100,000, and the species is threatened with destruction of its habitat.

SIGNIFICANCE TO HUMANS
Hunted for food. ◆

Small-toothed sportive lemur
Lepilemur microdon

SUBFAMILY
Lepilemurinae

TAXONOMY
Lepilemur microdon Forbes, 1894, east of Betsileo, Madagascar.

OTHER COMMON NAMES
Spanish: Lémur juguetón de dientes Pequeños.

PHYSICAL CHARACTERISTICS
Small-toothed sportive lemurs have a head and body length of about 10.2 in (26.0 cm), with a tail length of about 10.6 in (27.0 cm) and weight of about 2.2 lb (1.0 kg). They possess binocular vision, a large cecum, and large digital pads on their hands and feet for clinging. The species is mostly red-brown in color with a dark mid-dorsal line and is yellowish-buff colored laterally and ventrally.

DISTRIBUTION
South and central areas of the Eastern rainforests of Madagascar.

HABITAT
Lives in rainy forests not far from the coast. The population density is 13–100 animals per 0.4 sq mi (1.0 sq km).

BEHAVIOR
Small-toothed sportive lemurs are arboreal and nocturnal. They move through the forest by vertical clinging and leaping. Their social system is based on mothers and their offspring, while males live solitary lives. Male home ranges overlap one or more female home ranges. All members of the species are highly territorial, with males often violently defending their territories. Communication comes with various sounds. One such sound is a “loud” call, similar to the sound of a crow, that is emitted by adult males in order to demarcate its territorial claims and to tell other males that it already occupies a certain area.

FEEDING ECOLOGY AND DIET
They are folivorous (leaf eating), but also will eat small amounts of fruits and flowers to supplement their diet. They are also cecotrophic, re-digesting their feces in order to break down cellulose in already eaten leaves.

REPRODUCTIVE BIOLOGY
The species has a polygynous mating system, where the male visits several females during the mating season. Females give birth to one young. Females leave their infants on branches while they forage for food.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN. Also listed on CITES Appendix I and as endangered by the U.S. ESA. Total populations are estimated to number 10,000–100,000, and the species is threatened with destruction of its habitat.

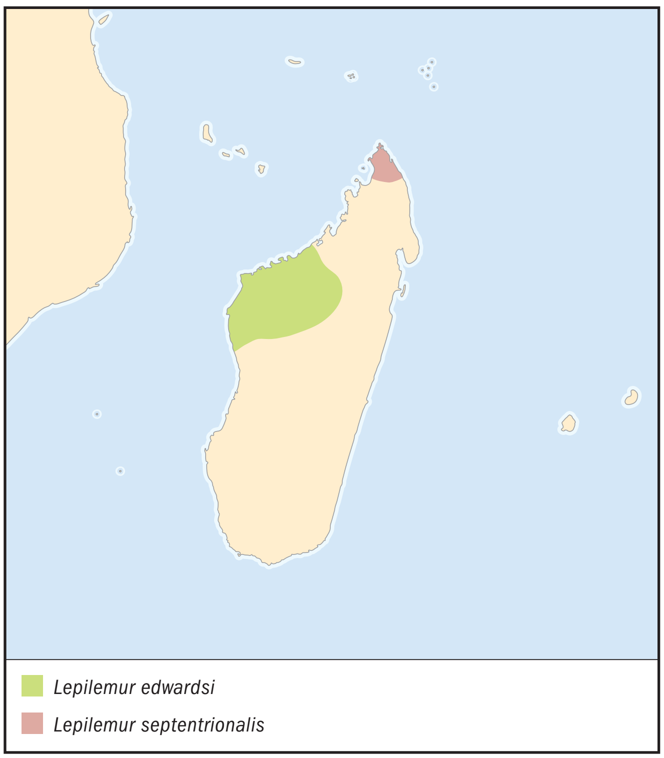
SIGNIFICANCE TO HUMANS
Hunted for food. ◆

Northern sportive lemur
Lepilemur septentrionalis

SUBFAMILY
Lepilemurinae

TAXONOMY
Lepilemur septentrionalis Rumpler and Albignac, 1975, Sahafary Forest, Madagascar.

OTHER COMMON NAMES
Spanish: Lémur juguetón norteño.



PHYSICAL CHARACTERISTICS
Northern sportive lemurs possess binocular vision, a large cecum, and have large digital pads on their hands and feet for clinging. The upper parts of this species are gray, being darkest on the crown and paler in gray color on the rump and the hind limbs. From the crown down the back there is a darker gray median stripe. The under parts are gray in coloration.

DISTRIBUTION
Extreme northern tip of Madagascar from the left bank of the Loky river to the coast.

HABITAT
They live in dry, deciduous forest habitats. The population density is 60–564 animals per 0.4 sq mi (1.0 sq km).

BEHAVIOR
Northern sportive lemurs are arboreal and nocturnal. During the day they sleep in tree holes or bundles of dense foliage and vines. Their social system is based on mothers and their offspring, while males live solitary lives. Male home ranges overlap one or more female home ranges. All members of the species are highly territorial, with males often violently defending their territories. Communication comes with various sounds. One such sound is a "loud" call, similar to the sound made by a crow, which is emitted by adult males in order to demarcate its territorial claims and to tell other males that it already occupies a certain area. Another sound is a "contact-rejection" call that is used when an individual approaches another one. This call consists of a series of resonant hissing calls that is followed by a two-phase vocalization.

FEEDING ECOLOGY AND DIET
They are folivorous (eating mostly leaves), but also will eat small amounts of fruits and flowers to supplement their diet. They are also cecotrophic, re-digesting their feces in order to break down cellulose in already eaten leaves

REPRODUCTIVE BIOLOGY
The Northern sportive lemur has a polygynous mating system, where the male visits several females during the mating season. Females give birth to one young during the year. Females leave their infants on branches while they forage for food.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN. Also listed on CITES Appendix I and as endangered by the U.S. ESA. Total populations are estimated to number 10,000–100,000, and the species is threatened with destruction of its habitat.

SIGNIFICANCE TO HUMANS
Hunted for food. ◆

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William Arthur Atkins

▲

Aye-ayes

(Daubentoniidae)

Class Mammalia

Order Primates

Family Daubentoniidae

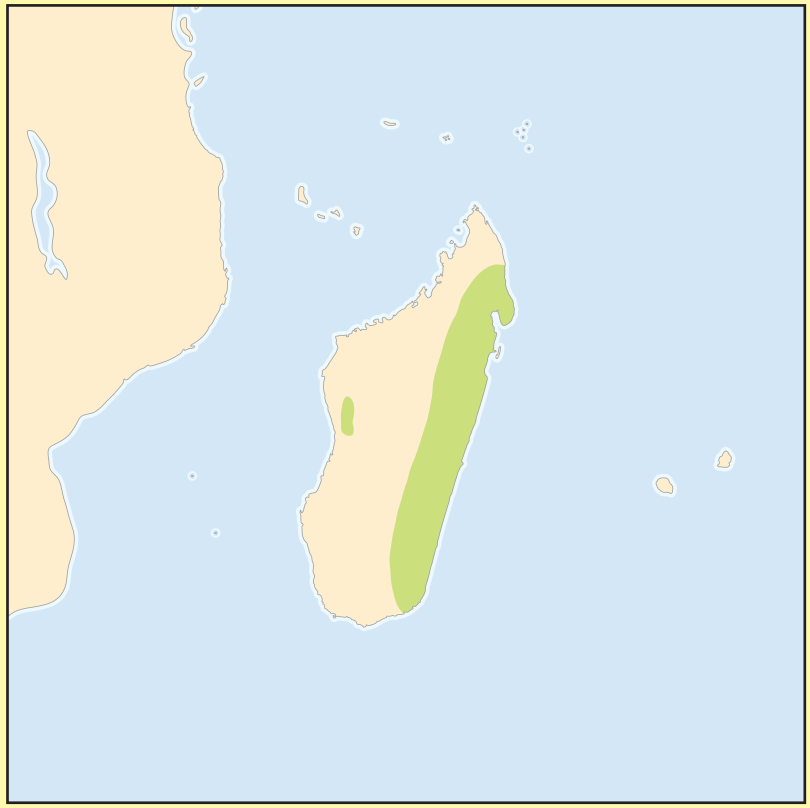
Thumbnail description
Medium-sized nocturnal and arboreal primates

Size
6 lb (2.7 kg); body and tail length average 16 in (40 cm) and 22 in (55 cm), respectively; body size of the extinct aye-aye is estimated at three times that of *D. madagascariensis*

Number of genera, species
1 genera; 1 extant species; 1 extinct species

Habitat
Rainforest, dry deciduous forest, and some cultivated areas

Conservation status
Endangered



Distribution
Madagascar

Evolution and systematics

The aye-aye (*Daubentonia madagascariensis*) is the only primate with a monotypic family, genus, and species. Because of their highly specialized characteristics, aye-ayes were initially difficult to classify and were lumped with several diverse groups until being firmly identified as prosimian in the mid-1800s. Recent genetic research shows that the aye-aye is not more closely related to one lemur family than another.

The taxonomy for this species is *Daubentonia madagascariensis*, (Gmelin, 1788), northwestern Madagascar.

Physical characteristics

Aye-ayes are the largest nocturnal primate. Their pelage consisted of two layers: the short, soft underlayer is light in color and thick on the back; the outer guard hairs are coarse, dark brown to black at the roots, and gray-white at the tips similar to a didelphid North American possum (*Didelphis virginiana*). Some aye-aye guard hairs have measured 7 in (18 cm). Fur above the eyes and on the throat is often light yellow or beige. Eyes are amber and are not frontally oriented. The body mass of males and females is not significantly different, with an average of 6 lb (2.7 kg). Body length averages at 16 in (40 cm), tail length at 22 in (55 cm). The tail is very bushy, more like a fox, than a primate. The ears are bare, flexible, and very large: 4 in (10 cm) length by 2.8 in (7 cm) width, probably the largest for the body size of any primate. The evergrowing incisors have enamel on the buccal side only, with a long dental gap before the molars, like a rodent, not a primate. The molars are flat and wear down quickly. Legs and arms are about the same length and aye-ayes walk on all fours. The third and fourth fingers of aye-ayes are elongated and the last knuckle on the middle digit has a ball and socket joint, allowing rotation. The female mammary glands are located iguanally, between her legs, not under her arms as seen in other primates. Aye-ayes have a nictitating membrane, a character shared with reptiles and birds but few other mammals. The male aye-aye has a penis bone that is 1.2 in (3 cm). Aye-ayes have the largest brain to body weight ratio of any prosimian. The isolated incisors and the arrangement of hand bones for percussive foraging suggest the robust extinct aye-aye (*D. robusta*) had a similar locomotion and lifestyle to the living smaller species.

The aye-aye (*Daubentonia madagascariensis*) has an extraordinarily long third digit. (Photo by © Gallo Images/Corbis. Reproduced by permission.)

An aye-aye (*Daubentonia madagascariensis*) eats the contents of an egg. (Photo by Animals Animals ©D. Haring, OSF. Reproduced by permission.)

Distribution

On Madagascar in forested regions from north (Marojejy National Park, Sambava) to south (Andohahela National Park, Tolagnaro, and throughout the humid rain forest in the east from the coast (Mananara Nord National Park, Manombo Reserve) to the mountains (Andrigitra National Park, Ranomafana National Park). In the west aye-ayes have been sighted in isolated localities, namely Tsiombikibo Forest, Tsingy of Bemaraha National Park and Kirindy Forest. The extinct species was found only in the southwest and south central region of Madagascar.

Habitat

The smaller living species is found in Madagascar in low and mid-altitude rainforest, dry deciduous forests, and some cultivated areas, particularly coconut and lychee plantations. The extinct aye-aye foraged in gallery and deciduous dry forests in the southwest and south-central region of Madagascar.

Behavior

Aye-ayes forage primarily alone. However, when a female is in estrus, she is followed by up to six males. Foraging associations are occasionally observed in the wild between two adult males, adult and young males, and adult males and females. Male home ranges (300–530 acres; 120–215 ha) overlap greatly with one another, while female home ranges (77–100 acres; 31–41 ha) do not overlap with other female

An aye-aye (*Daubentonia madagascariensis*) eats sugar cane. (Photo by Connie Bransilver/Photo Researchers, Inc. Reproduced by permission.)

A juvenile aye-aye (*Daubentonia madagascariensis*). (Photo by Will McIntyre/Photo Researchers, Inc. Reproduced by permission.)

ranges. The average nightly path length of radio-collared females is 4,270 ft (1,300 m) with a maximum of 6,000 ft (1,830 m). The average nightly path length of males is 7,380 ft (2,250 m) with a maximum of 14,400 ft (4,390 m). These are the longest path lengths recorded for any nocturnal primate, and is especially remarkable considering the steep and wet terrain. Locomotion is by four-legged walking, climbing, and jumping; aye-ayes spend 25% of time walking on the ground. The mean height during travel is 23 ft (7 m) and the mean height during feeding is 43 ft (13 m). Aye-ayes are one of the top three terrestrial lemurs (ring-tailed lemurs, greater bamboo lemurs, and aye-ayes all spend a quarter to a third of their time on the ground). Aye-ayes sleep solitarily during the day in round nests about 72 ft (22 m) high in large trees with many vines; the round nests have one entrance and are constructed of branches with many fresh leaves. None of these nests is occupied by more than one individual on the same day, although nests may be serially occupied by other individuals. For example, one male serially shared nests with four other study animals, both males and females. Aye-ayes give up to 15 different vocalizations, including a contact "eep" call, an aggressive "aack" spacing call to other aye-ayes, "plea" calls given by females in estrus, a "fishing reel" call given when animals are feeding, a "sneeze alarm" call, a "hai-hai" alarm call (a pulsed snit cry when individuals are fighting over food), and a begging "bird call" given by young aye-ayes wanting to feed with older animals. Females scentmark frequently using both urine and anogenital rubbing for 10 days before and the three days of estrus.

Feeding ecology and diet

Aye-ayes use their specialized anterior teeth and middle finger to harvest three main food sources—insect larvae from dead trees, inside nutmeat of seeds from the giant *Canarium* tree (Burseraceae family) and cankerous fungus growing on *Intsia* (Fabaceae family) trees. The fourth component of the diet is nectar from Traveller's palm (*Ravenala madagascariensis*) flowers. Ants were occasionally eaten. Using their evergrowing incisors to open the hard exterior of the seed, aye-ayes then scrape the interior out of the *Canarium* or coconut with their middle finger. *Canarium* seeds are 60% fat. Using the large ears to listen to dead wood, the aye-aye tap

Aye-aye (*Daubentonia madagascariensis*). (Illustration by Brian Cressman)

The aye-aye (*Daubentonia madagascariensis*) has the ability to hear grubs and insects burrowing within the bark of a tree. (Photo by Harald Schütz. Reproduced by permission.)

to determine the location of the larvae, then gnaw open the beetle canals, emerge and rotate their long, thin, mobile fingertip to snag the beetle inside the log and pull it out. The insect larva were from cerambicid, scarab, and other beetle larvae that consume dead wood. These large larvae could weigh 0.2 oz (5 g) and are high in protein (44–70%) and fat (33–44%).

Reproductive biology

Aye-ayes are a polygynous group that sleep and forage solitarily, and in contrast to all other lemurs, mating can occur in different months of the year (October, February, December, May). Ten days prior to full estrus, as determined by genital swelling, females increase scent-marking frequency and often visit nests occupied by males, a behavior not seen outside the mating season. During the three days of estrus, females call repeatedly, starting well before dusk. Up to six males surround the calling female, with the males engaging in agonistic chases and biting. Eventually one male will copulate with the female, maintaining hold of the female for about an hour. The pair are suspended by their back feet from a branch during the long copulation. After copulating, females travel quickly 1,640–1,970 ft (500–600 m) and call again. Females mate with more than one male on the first day. The gestation is 4–5 months. The infant remains in a nest with the mother for the first weeks, and lactation continues for two years. Age at first birth is 36–48 months, with an interbirth interval of 24–36 months. Only one offspring is born at one time.

Conservation status

Endangered. Hunting and loss of habitat due to logging and crop cultivation are main concerns.

Significance to humans

Because of their odd appearance, aye-ayes fall victim to superstitious fear in the north of Madagascar and are often killed on sight—one belief is that upon seeing an aye-aye, a member of the observer's family will die unless the animal is killed. Subfossil incisor teeth of *D. robusta* had symmetrical holes, perhaps for hanging as necklaces or amulets. Aye-ayes carry no economic importance except as crop raiders in coconut plantations.

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Organizations

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▲

Tarsiers

(Tarsiidae)

Class Mammalia

Order Primates

Family Tarsiidae

Thumbnail description
Very small nocturnal primates with huge eyes, extremely long hind limbs, and a long and thin more or less sparsely haired tail; all species are brownish or grayish ochre in color

Size
11–16.4 in (28–42 cm); 3.1–5.1 oz (90–145 g)

Number of genera, species
1 genus; 6 or more species

Habitat
Secondary and primary rainforest, scrub, agroforestry plantations, grass, mangroves

Conservation status
Lower Risk/Near Threatened: 1 species; Lower Risk/Conservation Dependent: 1 species; Data Deficient: 4 species

Distribution
Parts of the Southeast Asian archipelagos including Sumatra, Borneo, Sulawesi, and some of the Philippine Islands

Evolution and systematics

Although bearing many derived modern features, the extant tarsiers are the most ancestral haplorhine (tarsiers, monkeys, apes, and humans) living primates. The undisputed oldest fossil representative of tarsiers, *Xanthorhysis tabrumi*, is not less than 50 million years old, and was unearthed by Beard and colleagues in Eocene sediments in China. Once, the tarsiiform primates were widely distributed, fossil remains being found, for example, in Egypt, Germany, France, Thailand, and North America (Wyoming, New Mexico). The extinct tarsiiform family of Omomyidae shares quite a number of traits with the extant *Tarsius*, such as the olfactory bulb lying above the interorbital septum. But at present, the mosaic of shared and less similar characters does not allow a definitive decision about the probable direct ancestors of the present day tarsiers.

Like all other haplorhine primates, the tarsiers are very probably derived from diurnal ancestors, as they have lost the tapetum lucidum in their eyes, a reflecting layer that maximizes light-gathering capacity. By contrast, this reflecting tapetum is characteristic of all nocturnal strepsirhine (prosimian) primates. Sharing a central fovea in the retina of their eyes, a fused frontal bone, and a posteriorly closed orbit with anthropoid primates, as well as many other features, the tarsiers are recognized, today, as a sister group of the anthropoid primates. Their closest living relatives are South American platyrrhine monkeys. This is also supported by recent findings in molecular genetics.

Therefore, anthropoid primates and tarsiers, together, have to be united in the suborder Haplorhini. As Groves found in 1998, the term prosimian is no longer appropriate in a formal taxonomic sense, but belongs in the realm of folk taxonomy. To include tarsiers within the prosimians, i.e. together with the lemurs, galagos, etc., however, is somewhat misleading, as it groups these higher, haplorhine primates falsely with the less closely related Strepsirhini.

At present, the single extant family, Tarsiidae, includes only one genus, *Tarsius*, although the validity of a second genus *Rabienus* was seriously discussed by Groves in 1998. Until 1984 only three tarsier species were recognized, but currently six

A spectral tarsier (*Tarsius spectrum*) in Sulawesi, Indonesia. (Photo by Anup Shah/Naturepl.com. Reproduced by permission.)

The Philippine tarsier (*Tarsius syrichta*) has a head and body only about 6 in (15.2 cm) long. (Photo by Ron Austing/Photo Researchers, Inc. Reproduced by permission.)

A western tarsier (*Tarsius bancanus*) can turn its head almost 360°. (Photo by Frans Lanting/Minden Pictures. Reproduced by permission.)

species are recognized. Two or three more species may be added within the coming years.

Physical characteristics

Tarsiers are very small nocturnal and crepuscular primates. They possess a short-snouted, round head, ranging between 1.4 and 1.7 in (3.5–4.4 cm) in length, and middle-sized to very large, skinny, mobile ears. Their eyes are huge, with one eye weighing nearly as much as the whole brain. The eyes do not fit into the cranial orbit, but protrude from their sockets like an egg in an egg cup. The owl-like appearance of tarsiers is a consequence of many common features in the biology of both these nocturnal predators. More than 30 such convergences of tarsiers with owls have been described, such as the same pelage color in both sexes, similarities in the anatomy of the eyes, the semicircular canals in the inner ear, and the sensory biology for prey location. The dental formula for tarsiers is (I2/2 C1/1 P3/3 M3/3) $\times$ 2 = 36.

The fur of all species shows the colors of dead leaves, i.e., the tarsiers are sand-colored to ochre or grayish buff, with a considerable variation towards reddish or brownish. The Philippine species (*Tarsius syrichta*) tends to be lighter than the western tarsier (*T. bancanus*) and the Sulawesi species (*T. spectrum*). The fur is velvet-like but sometimes somewhat curly. A curly pelage seems to be more frequent in tarsiers from higher altitudes. All sparsely haired or naked parts of

The Philippine tarsier (*Tarsius syrichta*) emits a high pitched squeak when threatened. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

the skin are pigmented ranging from a more sandy color, e.g. in the Philippine species, to a rich dark brown, e.g., in Dian's tarsier (*T. dianae*). Orange skin color at the testicles or dark brown patches in the ears, however, are caused by secretions from skin glands.

The slender body, reaching up to about 4 in (10 cm) in length, often appears round in the clinging or sitting animals. The hands are equipped with long or even extraordinarily long, very prehensile fingers for clinging and climbing, but especially for catching prey. Their tips have round discs of finger pads for an enhanced grip when clinging to vertical stems. The thumb is opposable to the palm and the fifth digit through movements in its basal joint. As an extreme adaptation to leaping between vertical supports, the hind limbs are longer in relation to body size than in any other mammal, reaching 2.3 times the length of the precaudal spine. As a portion of the hind extremity, the foot is proportionately longer than the thigh and the lower leg, which is mainly due to the strongly elongated calcaneal and navicular bones. There is a strong, opposable great toe. Except for toilet claws on the second and third toes, all toes and fingers have nails.

The tail of all species is long and rodlike. Except for the pygmy tarsier (*T. pumilus*), where it is certainly shorter, the tail measures between 7.8 and 9.8 in (20–25 cm), which is about 2.5 times the trunk length. In the Sulawesi tarsiers, the tail retains scaly skin structures, a most ancestral and, therefore, most spectacular feature, which is not found in any other primate. The tails of all species appear to be naked, at least partially. This is most obvious in the Philippine tarsier, which possesses only a thin, roughly 2.4 in (6 cm) long, sparsely haired tuft, the length of the single hair being only about 0.1 in (3 mm) long. In the western tarsier, the tuft hair is about 0.3 in (7 mm) long, whereas in the Sulawesi species the single hairs may measure 0.2–0.5 in (5–12 mm). Although far from being bushy, more than half of the distal part of the tail of the Sulawesi tarsiers is hairy.

There is a sensitive skin area on the ventral side of the tail of all tarsier species. Being endowed with papillary skin ridges, this is friction skin that is used as a support area. Tarsiers spare much of their energy budget by sitting on their tails when resting on a vertical support, much like woodpeckers do.

Distribution

Tarsiers are found from southeastern Sumatra in the west to the Philippine island of Mindanao in the east, and from the Philippine island of Samar in the north to the Indonesian island of Selayar in the south. Thus their range extends from 102°E to 127°E and from 13°N to 7°S—about 1,700 mi (2,750 km) longitudinal range and about 1,300 mi (2,100 km) latitudinal range.

Habitat

All tarsiers are predominantly arboreal and are considerably adapted to more or less vertical supports.

Western tarsiers strongly prefer vertical supports of 0.4–1.6 in (1–4 cm) in diameter. Leaping between vertical tree trunks, they use only a very thin layer of the space of their habitat, foraging more than 80% of the time below 3 ft (1 m) above the ground. Soil contacts make up roughly 5% of all leaps, but they consume only about 1% of the time budget. Sleeping sites of the western tarsier (for single individuals) are often found between 6.6 and 16.4 ft (2–5 m) above the ground.

A spectral tarsier (*Tarsius spectrum*) family in the rainforest of Sulawesi, Indonesia. (Photo by Michael Fogden. Bruce Coleman, Inc. Reproduced by permission.)

The western tarsier (*Tarsius bancanus*) uses its extremly large eyes to help it see during the night. (Photo by Art Wolfe/Photo Researchers, Inc. Reproduced by permission.)

Spectral tarsiers (*T. spectrum*) sleep in small groups, often in hollow trees or densely growing vines, mostly between 3 ft (1 m) and roughly 60 ft (20 m) above the ground.

Also, some tarsiers may venture into other neighboring habitats like mangrove areas, grassland, or diverse forms of plantations, provided that both suitable supports for clinging and leaping are present and prey animals are found in sufficient numbers. Habitat choice above the ground between vertical supports must be a very efficient mechanism for predator avoidance, as tarsiers produce very few offspring.

Behavior

Although they are social primates, as demonstrated, for example, by their territorial scent marking behavior, tarsiers are not or not very gregarious during their activity phase. Scent marking behavior includes the deposition of urine and secretions from skin glands within their lips, on their chest, and in their anogenital region. Group or duetting vocalizations near or at the sleeping site, known from all Sulawesi forms, may be an expression of pair or group coherence. The Philippine and the western tarsiers are not silent, but territorial group vocalizations or duetting have never been reported.

Tarsiers are nocturnal animals, but at least some of the species also show high crepuscular activity. Vocalizations near sleeping sites in the Sulawesi species and subspecies may mark the temporal transition from non-gregarious nocturnalism and diurnal gregarious primates in each of the species concerned.

Tarsiers are vertical clingers and leapers. They are world champions in backward leaping, catapulting themselves backward from a vertical support, turning around in mid-leap, and landing forward on the next tree sapling. With one leap they may cover the distance of 45 times their body length.

Feeding ecology and diet

All tarsiers eat animal food exclusively; no field or captive studies have documented any plant food in their diet. Tarsiers locate their prey by sound or by sight, their closest com-

A western tarsier (*Tarsius bancanus*) eats a cicada. (Photo by Frans Lanting/Minden Pictures. Reproduced by permission.)

petitors being insectivorous bats and small owls. They catch and relish all sorts of arthropods. Birds up to their own body weight have been observed to be caught in mid-flight and killed on the ground, their head, brain, and beak being completely eaten. Lizards and even poisonous snakes can be killed and eaten. Their unselective menu may be a kind of life insurance, as they may, in times of seasonal scarcity, just switch to a different kind of prey.

Tarsiers prefer to eat during vertical clinging. Although this behavior seems to be the best predator prevention, when the animal is distracted and chewing noisily, the sympatric slow loris may catch a tarsier. Also, a constricting snake was observed killing a tarsier, in spite of being heavily mobbed by other tarsiers.

Thus far, only the western tarsier has been studied for parasites. Without exception, all individuals investigated were infested by endoparasites. According to a yet unpublished feces analysis, the same seems to be true also for spectral tarsiers.

Reproductive biology

Tarsiers give birth to a single offspring and never have twins. This is due to the fact that at birth an infant tarsier weighs almost one-quarter of its mother's weight, an accomplishment that is unique among the primates and probably among mammals as well. About 100 years ago Hubrecht investigated some 600 pregnant uteri, finding only one pair of twins at a very early stage (one of which could have easily been resorped at a later stage). Tarsiers have an ovarian cycle of about 28 days. Through 2003, seasonal births had been observed in three tarsier species.

Although there are indications of pair bonding (e.g., snuggling behavior at a shared common sleeping site), the greater home rages of males and the presence of sexual dimorphism (though weaker than in many other primates) indicate a certain degree of polygamy in the tarsiers' reproductive system.

Conservation status

Although tarsiers do not appear to be rare in many areas, they are very sensitive to changes in their environment. For example, Merker found the population density of Dian's tarsier to be 268 individuals per 0.04 mi^2 (1 km^2) in undisturbed primary forest, 130–190 in slightly or medium disturbed areas, and 45 in plantations outside natural forest. Neri-Arboleda found 16 males and 41 females of the Philippine tarsier per 0.04 mi^2 (1 km^2), mainly in early mid-succession forest. All authors agree that rapid habitat destruction is the major threat to the tarsiers. The spectral tarsier is listed by the IUCN as

A Philippine tarsier (*Tarsius syrichta*) clings to a tree trunk. (Photo by Bernard Walton/Naturepl.com. Reproduced by permission.)

Lower Risk/Near Threatened; Dian's tarsier as Lower Risk/Conservation Dependent; and the Philippine, pygmy, western, and Sangihe tarsiers are listed as Data Deficient.

Significance to humans

Tarsiers are too small to be hunted. With only one young per year they do not have the potential to be pests. Since they eat many harmful insects including grasshoppers, moths, and caterpillars, they may play an unquantified role as pest control agents in agroforestry. However, tarsiers are at risk, if insecticides are applied by humans. With their huge eyes tarsiers appear in very different kinds of art, from an edging of the famous "Vienna School" to the cover of a science fiction novel. Also, the famous extraterrestrial movie creature *E.T.* undoubtedly shows the features of a tarsier.

1. Philippine tarsier (*Tarsius syrichta*); 2. Dian's tarsier (*Tarsius dianae*); 3. Western tarsier (*Tarsius bancanus*); 4. Spectral tarsier (*Tarsius spectrum*). (Illustration by Barbara Duperron)

Species accounts

Philippine tarsier
Tarsius syrichta

TAXONOMY
Tarsius syrichta Linnaeus, 1758, southern Philippine Islands.

OTHER COMMON NAMES
French: Tarsier des Philippines; German: Philippinenkobold-maki.

PHYSICAL CHARACTERISTICS
11.5–15.9 in (29.–40.2 cm); 3.9–5 oz (110–142 g); light buff or sand-colored, more gray than the other species; tail tuft very sparse and short.

DISTRIBUTION
Southeastern Philippine islands of Samar, Marippi, Biliran, Leyte, Dinagat, Siargao, Bohol, and Mindanao.

HABITAT
Secondary lowland rainforest in early mid-succession, rarely shrubs or bamboo, not in grassland or plantations.

BEHAVIOR
Family groups with one male and one or two females with their offspring. The home ranges of males and their (first) female overlap to about 40%. Males and females sleep separately. Nocturnal and crepuscular; generally silent, but make contact calls.

FEEDING ECOLOGY AND DIET
Hunting for small invertebrates and vertebrates, mostly 3–6 ft (1–2 m) above the ground, leaping to about 85% between vertical stems.

REPRODUCTIVE BIOLOGY
Likely polygamous. One offspring is born, in most cases by the end of the rainy season between April and July. Gestation lasts approximately six months.

CONSERVATION STATUS
Data Deficient.

SIGNIFICANCE TO HUMANS
None known. ◆

Western tarsier
Tarsius bancanus

TAXONOMY
Tarsius bancanus Horsfield, 1821, eastern Sumatra, Borneo, and adjacent island.

OTHER COMMON NAMES
English: Horsfield's tarsier; French: Tarsier occidental; German: Sundakoboldmaki.

PHYSICAL CHARACTERISTICS
12.6–14.6 in (32–37 cm); 3.8–4.8 oz (107–135 g); buff, sometimes sand-colored; tail tuft short, but well developed. Biggest eyes in relation to head size in any mammal.

DISTRIBUTION
Southeastern Sumatra and Borneo, and the islands of Bangka, Belitung, Karimata, and Serasan.

HABITAT
Secondary and primary rainforest, shrubs, plantations.

BEHAVIOR
Scent marking is very traditional, indicating very stable home ranges. Males and females sleep separately. Rather silent, nocturnal and crepuscular.

FEEDING ECOLOGY AND DIET
Western tarsiers eat anything that moves and does not defend itself too effectively, from ants and beetles to bats and birds, even animals up to the tarsier's own body weight. On one occasion, a western tarsier was observed catching and eating a poisonous snake.

REPRODUCTIVE BIOLOGY
Different field studies suggest pair bonds or polygynous social organization. Births occur throughout the year, with a conspicuous increase in frequency by the end of the rainy season between February and June. The giant baby, weighing about one quarter of its mother's weight, is able to climb on the first day of its life. Some skeletally adult males have small testes, suggesting the existence of a social category of reproductively inactive "spare males."

CONSERVATION STATUS
Data Deficient.

SIGNIFICANCE TO HUMANS
This tarsier was considered an omen animal by the formerly head-hunting Iban people in Sarawak, Borneo. Since their extremely flexible cervical spine allows head rotations of at least 360°, their head was considered to be loose. If a head hunter encountered a tarsier, he was obliged to turn around immediately, because otherwise, the spell of the spirits might hit him and his community. ◆

Spectral tarsier
Tarsius spectrum

TAXONOMY
Tarsius spectrum Pallas, 1778, northern Sulawesi.

OTHER COMMON NAMES
English: Eastern tarsier, Sulawesi tarsier; French: Tarsier spectral, tarsier des Célèbes; German: Minahassakoboldmaki.

PHYSICAL CHARACTERISTICS
About 13.8 in (35 cm); 3.3–5.1 oz (94–154 g); buff, but generally darker and more gray than the western tarsier; tail tuft bushy and long, tail scaly; big skinny ears.

DISTRIBUTION
At least on Minahassa Peninsula of northern Sulawesi.

HABITAT
Spectral tarsiers inhabit secondary and primary forest, large grasslands, and, less often, plantations. They sleep, however, in hollow trees, crowns of coconut palms, or in thick vines.

BEHAVIOR
Not very gregarious. On the average, one intergroup encounter and 1–4 intragroup encounters per night. Group members were found to forage mostly between 66 ft (20 m) and 180 ft (55 m) apart from each other, depending from prey availability. During intragroup encounters, allogrooming or copulations may occur. Sleeping group associations consist mostly of an adult pair with or without offspring. Gursky found that 12% of the sleeping groups had a second adult female. Snuggling occurs more often at the sleep tree, while scent marking or play can be observed at the sleeping site or elsewhere at similar frequencies. Female home ranges are about 5.7 acres (2.3 ha), those of males 7.7 acres (3.1 ha). During the day spectral tarsiers may sleep for about nine hours and use slightly more than two additional hours of the day for social interactions. Duet songs usually last longer than 2 minutes and consist of repeated short phrases, the average duration of which is 11 sec. Average single calls last 190 msec in females and 140 msec in males.

FEEDING ECOLOGY AND DIET
About 60% of the predominantly insect prey is caught on leaves or branches, about 5% on the ground, and the remaining third is caught in the air. Moths and butterflies, including many caterpillars, form the greatest percentage of the insect prey (32%) followed by orthopterans (grasshoppers, cockroaches, etc., 24%), ants (13%), and beetles (11%). These averages vary between the dry and wet seasons.

REPRODUCTIVE BIOLOGY
Polygamous. There is one birth per year; the gestation period is around 190 days. The main birth season is April and May at the end of the monsoon rainy period. The young are weaned after 2.5 months. The adult male of the group and subadult females care for the young more than the subadult males.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Dian's tarsier
Tarsius dianae

TAXONOMY
Tarsius dianae Niemitz Nietsch, Warter and Rumpler, 1991.

OTHER COMMON NAMES
French: Tarsier de Dian; German: Dianakoboldmaki.

PHYSICAL CHARACTERISTICS
13–13.8 in (33–34.9 cm); 3.4–3.9 oz (95–110g); fur somewhat curly, buff-tinged gray, bright hairs on upper lip; tail tuft long and bushy; finger and toe nails dark brown and keeled.

DISTRIBUTION
Central montane areas of Sulawesi.

HABITAT
Seems to be most abundant in primary rainforest, about 270 individuals per 0.04 mi^2 (1 km^2). In secondary forest density was about 190 individuals per 0.04 mi^2 (1 km^2). Compared with primary forest, only half the density was found in agroforestry patches. In areas with stronger disturbance, density was still lower.

BEHAVIOR
Like the spectral tarsier, Dian's tarsier spends about 50% of its time below 5 ft (1.5 m) above the ground. But in contrast, Dian's tarsier spends about 23% of its time above 10 ft (3.1 m). Also, this species uses horizontal supports more than the spectral tarsier and the western tarsier. An average duet song lasts about 45 sec and is not divided into phrases. Average singe calls last about 80 msec in both sexes.

FEEDING ECOLOGY AND DIET
Moths, crickets, and lizards have been observed to be eaten.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Lower Risk/Conservation Dependent.

SIGNIFICANCE TO HUMANS
None known. ◆

Sangihe tarsier
Tarsius sangirensis

TAXONOMY
Tarsius sangirensis Meyer, 1897.

OTHER COMMON NAMES
French: Tarsier de Sangihe; German: Sangihekoboldmaki.

PHYSICAL CHARACTERISTICS
Less woolly than the neighboring spectral tarsier with a poorly marked postauricular spot (this spot is conspicuous and almost white in the spectral tarsier); large, broad skull with long tooth rows and short lateral incisors and canines.

DISTRIBUTION
Islands of Sangihe and Siau (between Sulawesi and Mindanao).

HABITAT
Nothing is known.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Data Deficient.

SIGNIFICANCE TO HUMANS
None known. ◆

Pygmy tarsier
Tarsius pumilus

TAXONOMY
Tarsius pumilus Miller and Hollister, 1921, central Sulawesi. Treated as a spectral tarsier subspecies for many decades, it regained species level by Niemitz in 1985, which was confirmed later by several authors.

OTHER COMMON NAMES
English: Lesser spectral tarsier, mountain tarsier; French: Tarsier naïn; German: Zwergkoboldmaki; Spanish: Tarsero piemeno.

PHYSICAL CHARACTERISTICS
Head and body length, 3.8–4.1 in (9.5–10.5 cm); Fur color similar to spectral tarsier, but more curly. Considerably smaller than any other tarsier species.

DISTRIBUTION
Central Sulawesi montane regions (e.g., about 2,625 ft [800 m] above sea level).

HABITAT
Montane foggy rainforests.

BEHAVIOR
Nocturnal and crepuscular. Duetting vocalizations, long high-pitched whistling notes by the female, and a series of calls by the males (about 3 calls/sec).

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Data Deficient.

SIGNIFICANCE TO HUMANS
None known. ◆

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Carsten Niemitz, PhD

New World monkeys I: Squirrel monkeys and capuchins

(Cebidae)

Class Mammalia
Order Primates
Family Cebidae
Subfamily Cebinae

Thumbnail description
Squirrel monkeys have slender bodies while capuchins are more robust and have prehensile tails; both genera have rounded heads with flat faces and short muzzles; some capuchins have tufts of fur on their heads; all are arboreal and move quadrupedally

Size
Squirrel monkey body weight, 1.2–2.75 lb (0.55–1.25 kg); Capuchin body weight, 2.4–7.3 lb (1.1–3.3 kg)

Number of genera, species
2 genera; 12 species

Habitat
Forest-living, occurring in a range of forest types from dry forest to dense evergreen tropical rainforest

Conservation status
Critically Endangered: 1 species, 2 subspecies; Endangered: 2 subspecies; Vulnerable: 1 species

Distribution
Both genera are widely distributed over parts of Central and South America, with some species being isolated in very small populations in certain countries

Evolution and systematics

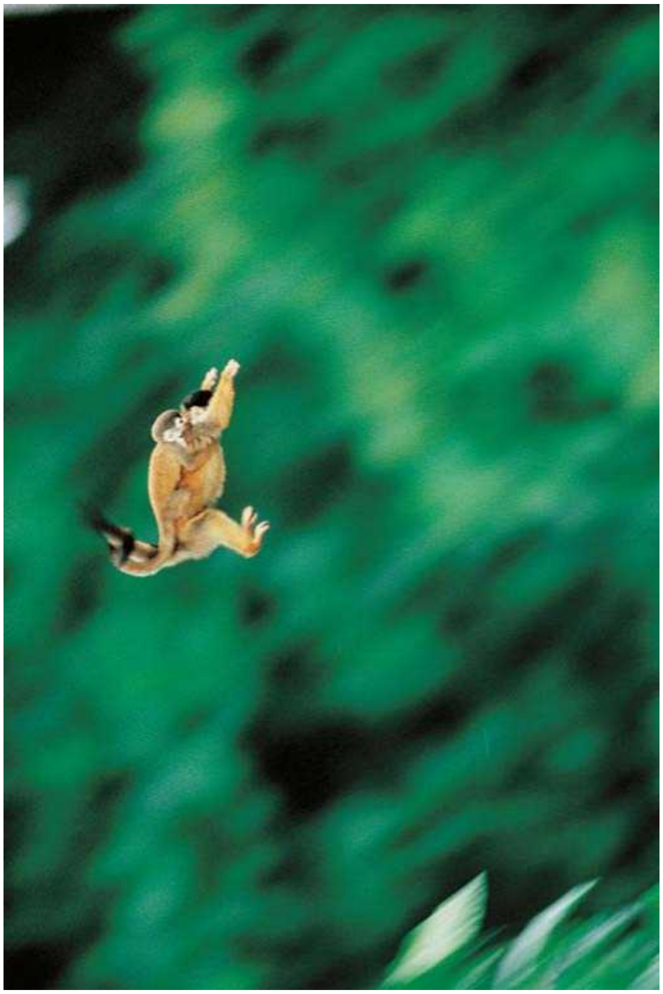
Monkeys in the New World are classified into the infraorder Platyrrhini, which are distinguished from the Old World monkeys by nostrils that are widely separated and open to the side. Within this infraorder are three families, one of which is the Cebidae. Dentition is 36 teeth with a dental formula of (I2/2 C1/1 P3/3 M3/3) $\times$ 2 = 36. Within the Cebidae are five subfamilies including the Cebinae. The Cebinae includes the squirrel monkeys (genus *Saimiri*) and the capuchins (genus *Cebus*).

Initially all squirrel monkeys were grouped in one species, *Saimiri sciureus* (Linnaeus, 1758). Hershkovitz (1984) then split the genus *Saimiri* into four distinct species: *Saimiri boliviensis* (with two subspecies), *Saimiri oerstedii* (with two subspecies), *Saimiri sciureus* (with four subspecies), and *Saimiri ustus*. In 1985 a fifth species (*Saimiri vanzolinii* Ayers, 1985) was delineated in a small pocket of forest in northwestern Brazil based on chromosomal differentiation. This taxonomy is now generally accepted and validated based on chromosomal evidence.

Capuchin systematics is more cloudy and disputed, as it has been from early times. This is due to a high degree of individual variation, changes in coloration associated with age, sexual differentiation, and occasional hybridization. The current taxonomy follows the divisions established by Hershkovitz (1955) of one "tufted" species: *Cebus apella* (10 subspecies); and three "untufted" species: *Cebus albifrons* (11 subspecies), *Cebus capucinus* (4 subspecies), and *Cebus olivaceus* (5 subspecies). A fifth species (*Cebus xanthosternos* Weid-Neuwied, 1826) was formally recognized (formerly a subspecies of *Cebus apella*) in 1997. A controversial recent revision by Groves (2001) has clouded the systematics by further elevating former subspecies of *Cebus apella* to two additional species: *Cebus libidinosus* (4 subspecies) and *Cebus nigritus* (3 subspecies).

Physical characteristics

All Cebinae are characterized by round heads with large forward facing eyes and relatively rounded muzzles that do



A red-backed squirrel monkey (*Saimiri oerstedii*), leaping with young from a branch 80 ft (24.4 m) above the ground in coastal rainforest south of Golfo Dulce, Costa Rica. (Photo by Gregory G. Dimijian/Photo Researchers, Inc. Reproduced by permission.)

not protrude much from the face. The bodies of the squirrel monkeys are small and rather slender, with adult males being larger than adult females, especially prior to and during the breeding season. Squirrel monkey bodies are covered with dense short fur. Color varies from gray to black on the crown of the head, the muzzle is black, the back is yellow to golden to reddish, the shoulders are gray to olive, the undersides are white to yellow, and the forearms, hands, and feet are yellow to golden. The tail is fully furred, nonprehensile, and typically longer than the body length. Head and body length is 10.8–14.6 in (27.5–37 cm); tail length is 14.2–17.8 in (36–45.2 cm). Body mass is 1.2–2.75 lb (0.55–1.25 kg).

Scientists have grouped the squirrel monkeys into two groups based on the shape of the white arch of supraorbital fur above their eyes: Gothic (pointed) and Roman (rounded). *Saimiri boliviensis* and *Saimiri vanzolinii* have Roman arches, while *Saimiri oerstedii*, *Saimiri sciureus*, and *Saimiri ustus* have Gothic arches.

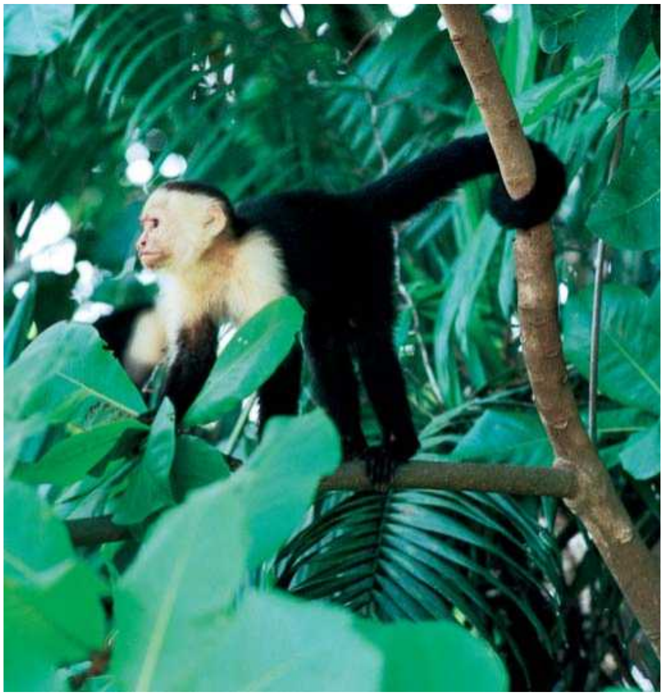
Capuchins have robust, medium-size bodies. Adult males are slightly larger than adult females, and head shape and body proportions differentiate the sexes. Capuchin bodies are fully furred, with short fur around their faces, and short to longer dense fur on the rest of their bodies. Fur coloration varies from black to brown to buff, with patches of white on chests and shoulders. Undersides are generally lighter from yellow to brown, and the crown of the head is usually darker, with some species having delineated black caps. Capuchins all have opposable thumbs and opposable big toes. Tails are fully furred and prehensile. Head and body length is 12.6–22 in (32–56 cm); tail length is 15–22 in (38–56 cm). Body mass is 2.4–7.3 lb (1.1–3.3 kg).

Capuchins have been grouped according to the presence (*Cebus apella* and *Cebus xanthosternos*) or absence of tufts (*Cebus albifrons*, *Cebus capucinus*, and *Cebus olivaceus*) on their heads.

Distribution

Squirrel monkeys are found throughout the Amazon basin from central Colombia to Bolivia and northeastern Brazil (including Ecuador, French Guiana, Guyana, Peru, Suriname,

The common squirrel monkey (*Saimiri sciureus*) is able to balance on its hind legs while picking leaves to eat. (Photo by Norman O. Tomalin. Bruce Coleman, Inc. Reproduced by permission.)



A white-throated capuchin (*Cebus capucinus*) in the rainforest of Costa Rica. (Photo by Animals Animals ©Mickey Gibson. Reproduced by permission.)

and Venezuela). The *Saimiri oerstedii* species range in Costa Rica and Panama.

Capuchins are found in Central and South America from Belize, throughout the Amazon basin and Brazilian coastal forests and south to Argentina. Countries include Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Guyana, Honduras, Nicaragua, Panama, Paraguay, Peru, Suriname, Trinidad and Tobago, and Venezuela.

Habitat

Squirrel monkeys have a wide distribution in primary and secondary forest types from gallery to low canopy hillside and riverine forests, palm forests, high and lowland rainforest, swamp, mangrove, and marsh forests. Squirrel monkey habitat ranges in altitude from sea level to 6,500 ft (2,000 m).

Capuchins inhabit virtually every type of forest in the Neotropics including dry forests, deciduous forests, and rainforests. Capuchin habitat ranges from sea level to 8,500 ft (2,700 m) in altitude in the Colombian Andes.

Behavior

Both genera of the subfamily Cebinae are diurnal and arboreal in habit. In the wild, squirrel monkeys are found in multimale-multifemale groups of 10–55 animals, with some groups as large as 300 individuals observed. Larger groups tend to break into smaller groups for foraging during the day, aggregating together at night. Sex ratio is close to 1:1, with some species having fewer adult males than adult females. Society generally revolves around the adult females, as studies show that all age/sex classes including adult males are most attracted to the adult females. Females are responsible for determining spatial relations between adult animals through affiliative and agonistic interactions. In *Saimiri boliviensis* and to some extent in *Saimiri oerstedii*, males are peripheral to the group in the nonbreeding season and are actively chased away when they approach non-estrus adult females. Adult females of these species are dominant to adult males except during the breeding season. Adult males are more integrated into the groups in *Saimiri sciureus*, and all adult males are dominant to all females. Juvenile and adult animals will huddle together during times of rest, with adult animals huddling almost exclusively in same-sex groupings. The huddling behavior is distinct, with animals in lateral contact and each animal's head tucked against its chest and its tail curled over its head and body.

Capuchins live in multimale-multifemale groups of 8–30 animals, with some larger groups of up to 50 animals noted for *Cebus oliveceus*. Sex ratio is 1:1 in some species, with other species having more females than males. Troops generally have one male who is dominant to all other individuals, and who aggressively defends the group against other groups. Males typically emigrate from their natal groups at between 2 and 4 years of age. *Cebus capucinus* groups have been reported to have frequent turnover of adult male group membership. Some species are reported to have males that are occasionally solitary or nomadic. All capuchin species are territorial. Capuchin individuals are active throughout most of the day traveling and foraging within their range.

A weeper capuchin (*Cebus olivaceus*) sits at the end of a log. (Photo by Animals Animals ©J. & J. Sohns. Reproduced by permission.)

A white-throated capuchin (*Cebus capucinus*) sleeping in Costa Rica. (Photo by J-C Carton. Bruce Coleman, Inc. Reproduced by permission.)

Communication is both vocal and visual. Both genera are vulnerable to predation and give alarm calls in response to large carnivorous mammals, boas, and birds of prey. It has been reported that *Cebus apella* males have an alarm call directed towards harpy eagles. This call is a distinctive barking that varies in frequency and loudness to indicate to other group members the relative proximity of the eagle. Squirrel monkeys are known to emit more than 24 different vocalizations including predator alarm calls and distancing calls that allow individuals to locate each other when out of sight while foraging. Unique visual signals include the so-called "genital displays" of the squirrel monkey. One leg is extended outward, presenting a view of the genitals to another animal. Both male and female individuals use this signal as a greeting when one animal flashes another its genitals from a distance (open genital display). The genital display is also used to establish and exert dominance when a dominant animal approaches another at very close proximity and exposes its genitals to the other while averting its gaze (closed genital display). The submissive animal will huddle quietly facing the display. Erections and occasionally the squirting of urine often accompany closed genital displays by males.

Both squirrel monkeys and capuchins practice urine washing of the fur with their hands; this may help an animal scent mark its surroundings and other olfactory communication. Capuchins are known to throw things towards potential predators in their aggressive displays. Boinski reports *Cebus capucinus* in Costa Rica throwing branches, fruit, and other objects at coatimundis, tayras, opossums, and humans. She describes one incident in which a capuchin threw a squirrel monkey at her when it had depleted its supply of readily detachable branches.

Capuchins are also noted for their manual dexterity and ability to manipulate objects. They have comparatively large and developed brains for their body size. Their high level of intelligence has made them one of the primates of choice for animal behavior and cognitive research. Young capuchins in captivity are easily trained, leading to their popularity in the pet market. Older animals become problematic as pets once reaching sexual maturity, and male capuchin pets are sometimes castrated or have their teeth pulled to try and control their aggressive tendencies. This trainability of young capuchins in the past led to their being used as organ grinder monkeys in many parts of the world. Now some capuchin females are being trained as helper animals for paraplegics and other wheelchair-bound humans. With a capuchin's ability to move in three-dimensional space and retrieve items desired by their human hosts, they have proven themselves much more helpful than canine companions. In captivity they are avid tool users, and in the wild have been observed using rocks to open oysters and one was seen using a branch as a club to kill a snake that had been caught under a fallen branch. In captivity they have been observed to use their prehensile tails to manipulate and play with objects.

Social and self-grooming is a common behavior in capuchin monkeys and social grooming helps to reinforce the group dynamics. Dominant animals are groomed more than less dominant animals. Squirrel monkeys have rarely been observed to engage in social grooming, with the exception of some mothers grooming their infants. They do engage in high frequencies of self-grooming using both fingers and toes to groom their fur. Capuchins also engage in self-anointing behavior, often rubbing fragrant items on their chests and other body parts. This behavior is also seen in captivity, with onions being of particular interest.

Feeding ecology and diet

Both genera are omnivorous. Squirrel monkeys are primarily frugivorous and insectivorous. They require a high level of protein in their diets, most of which is acquired by the consumption of animal prey. Diet includes fruits, nuts, flowers, buds, seeds, leaves, gum, insects, spiders, crabs, and some smaller vertebrates including frogs and bats. Capuchins are primarily frugivorous, but also include animal prey in their diet. This animal prey includes insects and smaller vertebrates (bird eggs, small birds, nestling squirrels, and lizards). *Cebus capucinus* have been observed eating oysters and using rocks to crack open the shells. Capuchins also beat fruit or nuts against hard surfaces to tenderize them or crack them open to get the seeds inside. Squirrel monkeys and capuchins overlap in much of their range and tolerate each other, even sharing food sources, eating side by side in the same fruiting trees. The squirrel monkeys are able to exploit more of the resources since their smaller size and lighter weight allows them to forage on smaller branches and to reach the tips of larger branches. Squirrel monkeys in Panama have been reported to spend 95% of the day traveling or foraging during the dry season. When fruit is not plentiful in the dry season, capuchins substitute pith and seeds for fruit and increase their daily ranging to try and locate the few fruiting trees available. When one troop member discovers a fruiting tree, it vocalizes to alert the rest of the troop to its location. Dominant *Cebus* *apella* males control access to preferred food items during times of scarcity, restricting other animals' access until they have eaten their fill.

Reproductive biology

Both genera have a polygamous mating system with promiscuous mating. Single births are the rule for both genera. Squirrel monkeys have a yearly reproductive cycle with a 2–3 month breeding season and a corresponding 2–3 month birthing season. The birth season (approximately 5.5–6 months after the breeding season) is correlated with the wet season and food abundance in their specific range. Unique among primates is an annual change in the males' physiology that occurs just prior to the breeding season. Adult males increase in body weight 10–30% (primarily in the upper body), and the testes double or triple in size, accompanied by the onset of spermatogenesis. These males are referred to as "fatted males." During the breeding season females have an estrus cycle of 12–14 days. The gestation period varies from 155–180 days. Females generally reach sexual maturity at three years with males not reaching full sexual maturity (evidenced by attaining the fatted stage) until 5–6 years. The ratio of infant size to mother size is the largest for any mammal, approaching 1:6. Infant birth weight is 3.2–3.9 oz (90–110 g).

Some species of capuchins are reported to be seasonal breeders, while others breed year round with a peak of births in a certain season. For many capuchin species paternity is often unknown as females have been seen to mate with more than one male. Estrus females follow and solicit mating from males, and males rarely fight over access to females. Female *Cebus apella* tend to groom and breed only with the dominant male, which is thought to create a bond so that he will protect the infants that he has sired. Females reach sexual maturity at 4–5 years; males do not reach full maturity until 8–10 years of age. Female estrus cycles are 18 days for *Cebus apella*, and the gestation period for *Cebus* varies from 149 to 168 days. Infants at birth are about 8.5% of the mother's weight, about 8 oz (220 g).

Both infant squirrel monkeys and capuchins are dependent on their mothers for parental care. An infant squirrel monkey clings to its mother's back from day one. It rides in the middle of her back with its head turned to one side, clutching her fur tightly with hands and feet and wrapping its tail tightly around her body. When nursing, the infant crawls forward and positions its head under her arm, rooting around under her armpit until it finds the nipple. Infants ride this way for several months. At 3–4 weeks other animals attempt to carry the infant and the mother may allow older females without young to carry the infant, but the mother always maintains visual contact. Juvenile females are occasionally allowed to carry infants, but the mother always remains nearby, ready to retrieve the infant at the first sound of trouble. It is thought that this is the way in which young females learn mothering skills. Infants begin to be weaned at five months and are independent from the mother by 11–12 months, just prior to their mother giving birth during the next birthing season. The youngster still maintains a close relationship with its mother and often travels nearby her and the new infant. Capuchin infants initially

A common squirrel monkey (*Saimiri sciureus*) eating flower petals. (Photo by Norman O. Tomalin. Bruce Coleman, Inc. Reproduced by permission.)

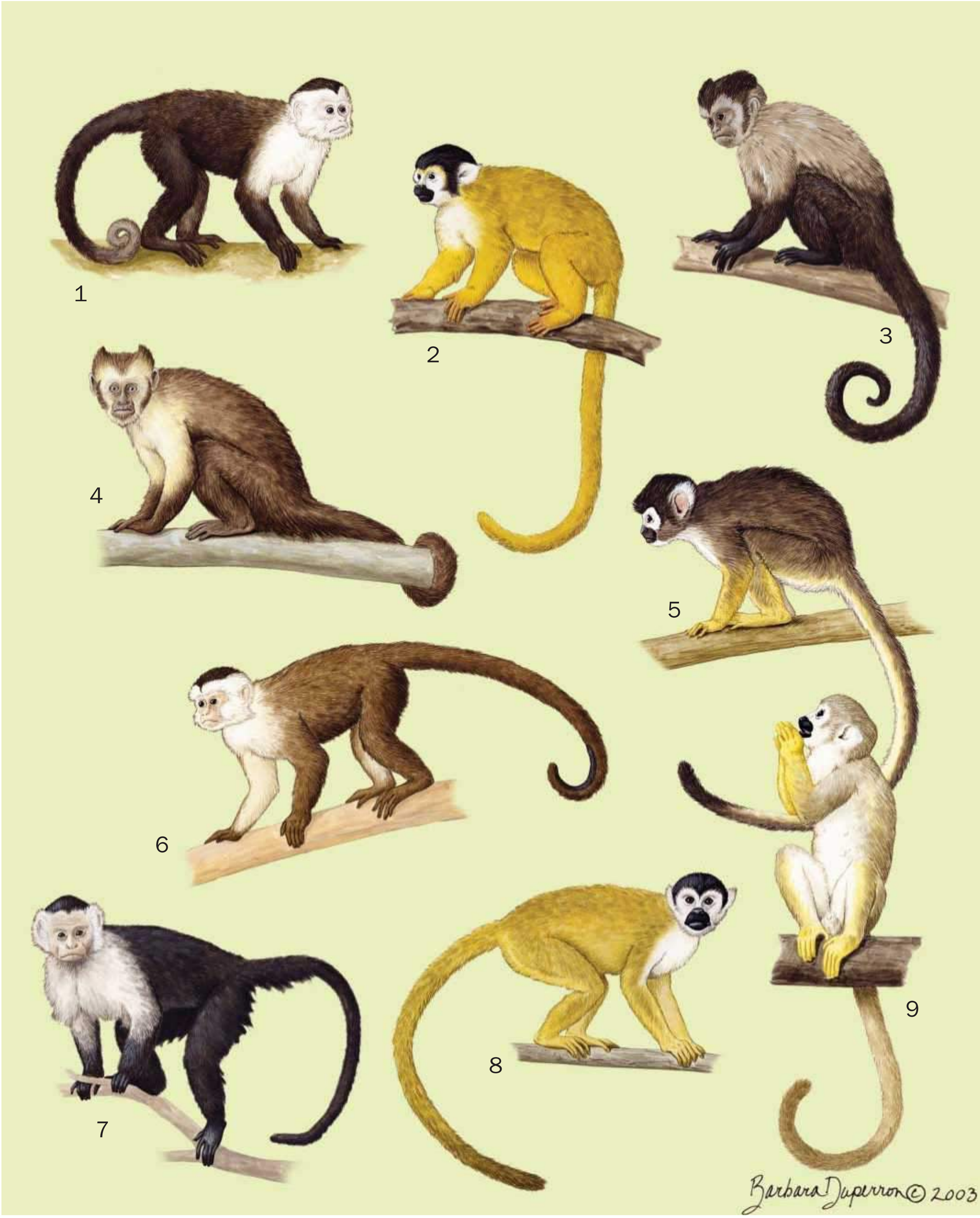
cling to the mother's underside or across her shoulders, and at about six weeks align their bodies along the mother's back. As infants and juveniles, both genera return to the mother for protection and security when stressed. At 2–3 months they begin to explore their environment and develop social relationships with other group members and begin to play with similar aged infants. Social play helps animals learn the subtleties of proper social behavior and the control of aggressive responses. It also helps to develop sexual behavior and to integrate the young into the group.

Conservation status

Both genera are widespread in parts of their range and extremely restricted in other areas. All are at least listed in Appendix 2 of CITES. The IUCN lists one subspecies of *Saimiri oerstedii* (*S. o. oerstedii*) as Endangered and the other (*S. o. citrinellus*) as Critically Endangered due to a severely fragmented population, low population numbers, and continued habitat loss and degradation. The IUCN lists *Saimiri vanzolinii* as Vulnerable due to a limited range, fragmented populations, low population numbers, and continued habitat loss and degradation. During the 1960s and 1970s over 25,000 squirrel monkeys per year were exported from Peru alone for the research and pet markets. Annual export quotas limit the number of squirrel monkeys to a sustainable harvest, although the quality of monitoring has come under question. The IUCN lists one subspecies of *Cebus apella* (*C. a. robustus*) as Endangered due to continued habitat loss and degradation. *Cebus xanthosternos* is listed as Critically Endangered by IUCN since only one small population is known, and this population suffers from continued habitat loss and degradation as well as hunting for food. International captive breeding programs are underway for both of these Endangered *Cebus* populations. Annual export quotas for *Cebus apella* from Guyana are imposed by CITES.

Significance to humans

Both genera are used as a model for human research in many forms: biomedical, pharmacological, physiological, behavioral/social, etc. Members of both genera are commonly found as pets and zoo animals throughout the world. Capuchins and squirrel monkeys are hunted for food (bushmeat) in major portions of their range. In the United States captive breeding programs have been established to help supply the scientific, biomedical, and zoological communities. Squirrel monkeys were used in the space program prior to the use of human astronauts.



1. White-fronted capuchin (*Cebus albifrons*); 2. Bolivian squirrel monkey (*Saimiri boliviensis*); 3. Black-capped capuchin (*Cebus apella*); 4. Yellow-breasted capuchin (*Cebus xanthosternos*); 5. Blackish squirrel monkey (*Saimiri vanzolinii*); 6. Weeper capuchin (*Cebus olivaceus*); 7. White-throated capuchin (*Cebus capucinus*); 8. Red-backed squirrel monkey (*Saimiri oerstedii*); 9. Common squirrel monkey (*Saimiri sciureus*). (Illustration by Barbara Duperron)

Species accounts

Bolivian squirrel monkey

Saimiri boliviensis

SUBFAMILY
Cebinae

TAXONOMY
Saimiri boliviensis (I. Geoffroy and Blainville, 1834), Guarayos Mission, Rio San Miguel, Santa Cruz, Bolivia. Four subspecies. Elevated from subspecies of *Saimiri sciureus* in 1984.

OTHER COMMON NAMES
English: Black-headed squirrel monkey.

PHYSICAL CHARACTERISTICS
Fur is sexually dichromatic—males gray and females black. Yellow at base of crown, on forearms, hands, and feet. Roman (rounded) arch over eyes. Head and body length is 12.2 in (31 cm). Tail length is 14.2 in (36 cm). Weight is 24.7–38.4 oz (700–1,088 g).

DISTRIBUTION
Brazil, Bolivia, Colombia, Peru, and Venezuela.

HABITAT
Primary and secondary tropical rainforest.

BEHAVIOR
Diurnal and arboreal. Multimale-multifemale groups of 20–50 animals. During breeding season males form hierarchy, and are dominant over females. For the rest of the year males are peripheral and subordinate to the females. Both males and females use genital display towards conspecifics. Female social aggression is common.

FEEDING ECOLOGY AND DIET
Predominately eat fruits, seeds, and animal prey including frogs, snails, insects, and spiders. Fruit is eaten earlier in the day, with animal protein eaten later.

REPRODUCTIVE BIOLOGY
Promiscuous mating. Males become "fatted" with upper body weight gain, an increase in testes size, and active spermatogenesis just prior to the breeding season. Males compete with each other for dominance during the breeding season. Breeding season is followed six months later by a birth season (coinciding with the wet season) when food is most abundant. Females reach sexual maturity at 36 months and gestation is 155–170 days. Births are single.

CONSERVATION STATUS
Widespread and uncommon to locally common. Main pressures on populations include habitat degradation, deforestation, hunting for food, and collection for laboratories. Listed in Appendix 2 of CITES.

SIGNIFICANCE TO HUMANS
Hunted for food in those areas of range where larger mammals have been depleted. Collected for pet, zoo, and research market. ◆

Saimiri oerstedii

Saimiri boliviensis

Red-backed squirrel monkey

Saimiri oerstedii

SUBFAMILY
Cebinae

TAXONOMY
Saimiri oerstedii (Reinhardt, 1872), David, Chiriquí, Panama. Two subspecies. Elevated from subspecies of *Saimiri sciureus* in 1984.

OTHER COMMON NAMES
English: Panamanian squirrel monkey; French: Saïmiri à dos roux, Singe-écureuil à dos rouge; Spanish: Barizo dorsirrojo, mono tití.

PHYSICAL CHARACTERISTICS
Black crown; rust-orange back, hands, and feet; olive-gray hips, shoulders, and tail base. Tail tip is black. Gothic (pointed) arch over eyes. Head and body length is 10.6 in (27 cm). Tail length is 14.3 in (36 cm). Weight is 21.2–33.5 oz (600–950 g).

DISTRIBUTION
Costa Rica and Panama.

HABITAT
Subtropical and tropical lowland rainforest.

BEHAVIOR
Diurnal and arboreal. Multimale-multifemale groups of 20–55 animals. Males integrated into group structure year-round, yet

are peripheral in behavior during the non-breeding season. Males are vigilant and aggressive to outside threats and other groups. Males remain in natal group, females emigrate. Mothers groom infants, unseen in other squirrel monkey species.

FEEDING ECOLOGY AND DIET
Predominately eat fruits, seeds, leaves, and insects.

REPRODUCTIVE BIOLOGY
Promiscuous mating. Males become "fatted" with upper body weight gain, an increase in testes size, and active spermatogenesis just prior to the breeding season. Breeding season in January and February, birth season in July. Births are single.

CONSERVATION STATUS
Scattered small populations throughout range. Main pressures on populations include habitat loss, degradation, and deforestation. Listed as Endangered by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Common squirrel monkey
Saimiri sciureus

SUBFAMILY
Cebinae

TAXONOMY
Saimiri sciureus (Linnaeus, 1758), Cayenne, French Guyana. Taxonomy is disputed, has four subspecies.

OTHER COMMON NAMES
French: Saimiri écureuil; German: Totenkopfaffchen; Spanish: Mono ardilla.

PHYSICAL CHARACTERISTICS
Fur is gray to black crown; olive-gray back; light yellow underside; yellow-orange forearms, hands, and feet; white ears and around eyes. Head and body length is 10.8–14.6 in (27.5–37 cm). Tail length is 15–17.8 in (26.5–45 cm). Weight is 19.5–44.1 oz (559–1,250 g).

DISTRIBUTION
Brazil, Colombia, French Guiana, Guyana, Suriname, and Venezuela.

HABITAT
Primary and secondary rainforest, riverine forest, and mangrove swamps from sea level to 6,600 ft (2,000 m).

BEHAVIOR
Diurnal and arboreal. Multimale-multifemale groups of 20–300 animals. Strict male dominance hierarchy with males dominant over females and integrated within the group year-round. Male emigration upon sexual maturity.

FEEDING ECOLOGY AND DIET
Squirrel monkeys have a high need for protein. Predominately eat fruit and animal prey including frogs, snails, crabs, insects, spiders, and occasionally bats.

REPRODUCTIVE BIOLOGY
Promiscuous mating often with multiple mountings. Males become "fatted", with upper body weight gain, an increase in testes size, and active spermatogenesis just prior to the breeding season. This is followed six months later by a birth season (coinciding with the wet season) when food is most abundant. Females reach sexual maturity at 30–36 months and gestation is 168–180 days. Births are single.

CONSERVATION STATUS
Widespread and uncommon to locally common. Main pressures on populations include habitat degradation, deforestation, hunting for food, and collection for laboratories. Listed in Appendix 2 of CITES.

SIGNIFICANCE TO HUMANS
Collected for the pet and research markets. Annual export quotas from Guyana to U. S. laboratories. Hunted for food in some areas of its range. ◆

Blackish squirrel monkey
Saimiri vanzolinii

SUBFAMILY
Cebinae

TAXONOMY
Saimiri vanzolinii Ayers, 1985, left bank of Lago Mamirauá, mouth of Rio Japura, Amazonas, Brazil.

OTHER COMMON NAMES
English: Black squirrel monkey.

PHYSICAL CHARACTERISTICS
Fur is gray or black back with a black stripe; gray shoulders; yellow hands and forearms; Roman (rounded) arch over eyes. Head

and body length is 10.8–12.6 in (27.5–32 cm). Tail length is 16.3–17.5 in (41.5–44.5 cm). Weight is 22.9–33.5 oz (650–950 g).

DISTRIBUTION
A small tract of 367 sq mi (950 sq km) in northeastern Brazil.

HABITAT
Swamp and white-water flooded tropical moist forest.

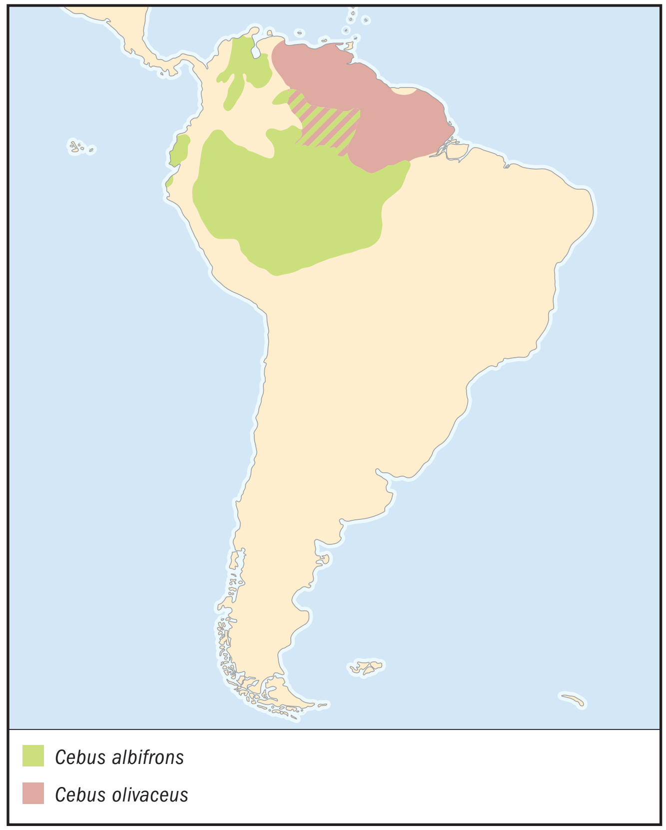
BEHAVIOR
Diurnal and arboreal. Multimale-multifemale groups of up to 50 animals.

FEEDING ECOLOGY AND DIET
Predominately eat fruit and animal prey including insects and spiders.

REPRODUCTIVE BIOLOGY
Promiscuous mating. Males become "fatted" with upper body weight gain, an increase in testes size, and active spermatogenesis just prior to the breeding season. Breeding season is followed six months later by a birth season (coinciding with the wet season) when food is most abundant. Births are single.

CONSERVATION STATUS
Smallest distribution of any squirrel monkey. Main pressures on populations include habitat degradation and deforestation. Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆



White-fronted capuchin
Cebus albifrons

SUBFAMILY
Cebinae

TAXONOMY
Cebus albifrons (Humboldt, 1812), Orinoco River, Venezuela. Eleven subspecies.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Fur color varies from light to dark brown with a dark wedge-shaped cap and white-yellow underside. Head and body length is 14.1–18.1 in (35.8–46 cm). Tail length is 15.8–18.7 in (40.1–47.5 cm). Weight is 3.1–7.2 lb (1.4–3.3 kg).

DISTRIBUTION
Bolivia, Brazil, Colombia, Ecuador, Guyana, Peru, Trinidad and Tobago, and Venezuela.

HABITAT
Primary deciduous, gallery, mangrove, and flooded forest up to 6,500 ft (2,000 m).

BEHAVIOR
Diurnal and arboreal. Multimale-multifemale groups of 10–30 individuals with more adult females than males. Group is led by one dominant male, and all animals are in a dominance hierarchy. Males emigrate from natal group.

FEEDING ECOLOGY AND DIET
Predominantly eat fruit and animal prey. Diet includes fruit, seeds, nectar, pith, insects, and small vertebrates.

REPRODUCTIVE BIOLOGY
Polygamous, both sexes mate promiscuously. Females reach sexual maturity at 3.5–4 years. Gestation is 5.5 months. Births are single. Birth peak February–July.

CONSERVATION STATUS
Widespread and uncommon to locally common. Main pressures on populations include habitat degradation, deforestation, and hunting for food. Listed in Appendix 2 of CITES.

SIGNIFICANCE TO HUMANS
Hunted for food (bushmeat) and kept as pets in Brazil. Considered crop pests in parts of their range and killed. ◆

Black-capped capuchin
Cebus apella

SUBFAMILY
Cebinae

TAXONOMY
Cebus apella (Linnaeus, 1758), French Guiana. Ten subspecies.

OTHER COMMON NAMES
English: Brown or tufted capuchin; French: Sapajou apelle; Spanish: Capuchino de copete.

PHYSICAL CHARACTERISTICS
Fur is dark to light brown on body with underside and shoulders sometimes lighter; hands and feet always black. Adults

have two tufts of erect fur on crown of head. Head and body length is 13.8–19.2 in (35–48.8 cm). Tail length is 14.8–19.2 in (37.5–49 cm). Weight is 3–10.6 lb (1.4–4.8 kg).

DISTRIBUTION
Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, and Venezuela.

HABITAT
Primary and secondary rainforest to semi-deciduous and montane forest up to 8,800 ft (2,700 m).

BEHAVIOR
Diurnal and arboreal. Multimale-multifemale groups of 8–16 individuals with sex ratio of 1:1. One male is dominant to all group members. Dominant males fight when two groups meet at food trees. Males emigrate from natal group.

FEEDING ECOLOGY AND DIET
Predominantly eat fruit, seeds, nectar pith, and animal prey including insects, frogs, reptiles, birds, bats, and other small mammals.

REPRODUCTIVE BIOLOGY
Polygamous, both sexes mate promiscuously, although dominant male guards estrus females during part of their cycle. Females reach sexual maturity at 4–5 years. Gestation is 149–158 days. Estrus cycle is 18 days. Birth season is October–January. Births are single.

CONSERVATION STATUS
Widespread and uncommon to locally common. Main pressures on populations include habitat degradation, deforestation, and hunting for food. Listed in Appendix 2 of CITES. One subspecies, *Cebus apella robustus*, is listed as Endangered by IUCN.

SIGNIFICANCE TO HUMANS
Hunted for food and as crop pests, collected and exported for pet and scientific research markets. ◆

White-throated capuchin
Cebus capucinus

SUBFAMILY
Cebinae

TAXONOMY
Cebus capucinus (Linnaeus, 1758), northern Colombia. Four subspecies.

OTHER COMMON NAMES
English: White-shouldered capuchin; French: Sajou à gorge blanche; Spanish: Mono capuchino.

PHYSICAL CHARACTERISTICS
Fur: white to yellowish throat, head, and shoulders; black back, tail, arms, and legs. Head and body length is 13.2–17.8 in (33.5–45.3 cm). Tail length is 13.8–21.7 in (35–55 cm). Weight is 5.9–8.6 lb (2.7–3.9 kg).

DISTRIBUTION
Colombia, Costa Rica, Honduras, Nicaragua, and Panama.

HABITAT
Primary and secondary evergreen forest, rainforest, mangroves, and deciduous dry forest from sea level to 6,900 ft (2,100 m).

BEHAVIOR
Diurnal and arboreal. Multimale-multifemale groups of 10–20 individuals with more adult females than males. Males defend the groups' territory. Communicate vocally when out of sight while foraging. Threat displays towards humans and other animals. Males emigrate from natal group.

FEEDING ECOLOGY AND DIET
Fruits, leaves, berries, nuts, seeds, shoots, buds, flowers, and animal prey including insects, spiders, crabs, and small vertebrates (birds, baby squirrels, lizards). Males will forage on forest floor.

REPRODUCTIVE BIOLOGY
Polygamous, both sexes mate promiscuously. Females reach sexual maturity at 3–4 years, although females have been documented to give birth as young as 28 months. Gestation is 157–167 days. Birth season is December–April. Births are single.

CONSERVATION STATUS
Widespread and uncommon to locally common. Main pressures on populations include habitat degradation, deforestation, and hunting for food. Listed in Appendix 2 of CITES.

SIGNIFICANCE TO HUMANS
Hunted for food and as crop pests in parts of their range. Collected for zoo and pet trade in past. ◆

Weeper capuchin
Cebus olivaceus

SUBFAMILY
Cebinae

TAXONOMY
Cebus olivaceus Schomburgk, 1848, southern base of Mt. Roraima, 3,050 ft (930 m), Bolivar, Venezuela. Five subspecies.

OTHER COMMON NAMES
English: Wedge-capped capuchin.

PHYSICAL CHARACTERISTICS
Fur is tawny brown on body, with lighter shoulders and upper arms; brownish yellow head with black wedge on cap. Head and body length is 14.7–18.1 in (37.4–46 cm). Tail length is 15.7–21.8 in (40–55.4 cm). Weight is 5.3–6.6 lb (2.4–3 kg).

DISTRIBUTION
Brazil, French Guiana, Guyana, Suriname, and Venezuela.

HABITAT
Evergreen rainforest, lowland forest, cloud forest, dry forest, and submontane forest up to 6,500 ft (2,000 m).

BEHAVIOR
Diurnal and arboreal. Multimale-multifemale groups of 8–50. One male is dominant to all group members and is the breeding male. Dominant display by branch shaking, jumping up and down and bouncing. Males emigrate from natal group as young as two years of age.

FEEDING ECOLOGY AND DIET
Fruits, seeds, and animal prey including snails and social insects. Feed on the ground and in the canopy.

REPRODUCTIVE BIOLOGY
Polygamous, but only one breeding male at any time. Females reach sexual maturity at 5–6 years. Gestation is 5–6 months. Birth season is May–August. Births are single.

CONSERZVATION STATUS
Widespread and uncommon to locally common. Main pressures on populations include habitat degradation, deforestation, hunting for food, and collection for research. Listed in Appendix 2 of CITES.

SIGNIFICANCE TO HUMANS
Hunted for meat in parts of their range. Some exported annually from Guyana for research market. ◆

Yellow-breasted capuchin
Cebus xanthosternos

SUBFAMILY
Cebinae

TAXONOMY
Cebus xanthosternos Wied-Neuwied, 1826. Monotypic; elevated from subspecies of *Cebus apella* in 1997.

OTHER COMMON NAMES
English: Yellow-bellied capuchin.

PHYSICAL CHARACTERISTICS
Fur is dark to light brown on body with underside and shoulders yellowish gold. Adults have two tufts of erect fur on crown of head. Head and body length is 13.8–19.2 in (35–48.8 cm). Tail length is 14.8–19.2 in (37.5–49 cm). Weight is 3–10.6 lb (1.4–4.8 kg).

DISTRIBUTION
Atlantic forest of Southern Bahia, Brazil.

HABITAT
Coastal forest.

BEHAVIOR
Not known in the wild, but assumed to be similar to *Cebus apella*.

FEEDING ECOLOGY AND DIET
Not known in the wild, but assumed to be similar to *Cebus apella*.

REPRODUCTIVE BIOLOGY
Not known in the wild, but assumed to be similar to *Cebus apella*.

CONSERVATION STATUS
Listed as Critically Endangered by the IUCN. Main pressures on populations include habitat loss and degradation, hunting for food, and collection for pet and scientific research markets in the past.

SIGNIFICANCE TO HUMANS
Hunted to near extinction. An international captive breeding program has been in place since 1992. ◆

Resources

Books

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Rosenblum, Leonard A., and Robert W. Cooper, eds. *The Squirrel Monkey.* New York: Academic Press, 1968.

Rowe, Noel. *The Pictorial Guide to Living Primates.* East Hampton, NY: Pogonias Press, 1996.

Smuts, Barbara B., et al. *Primate Societies.* Chicago: The University of Chicago Press, 1986.

Wolfheim, Jaclyn H. *Primates of the World: Distribution, Abundance, and Conservation.* Seattle: University of Washington Press, 1983.

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Jack, K., and L. Fedigan. "Life History of Male White-faced Capuchins (*Cebus capucinus*), Santa Rosa National Park, Costa Rica." *American Journal of Primatology* 54, Supplement 1 (2001): 50.

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Other

Vermeer, Jan. *The Nutrition of Squirrel Monkeys* (Saimiri): *Report of an EEP-Survey*. Romagne: La Vallee des Singes, 2000.

Kenneth C. Gold, PhD

New World monkeys II: Marmosets, tamarins, and Goeldi's monkeys

(Callitrichidae)

Class Mammalia

Order Primates

Family Callitrichidae

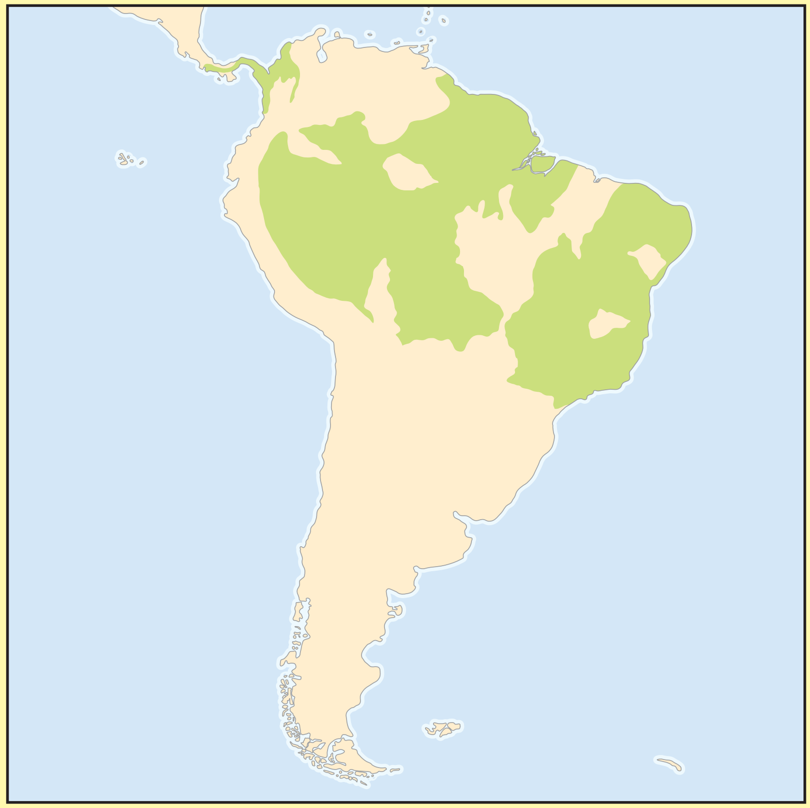
Thumbnail description
Small-sized monkeys with claws on all digits except large toe; long non-prehensile tails; several species with elongated hairs on crown, ears, or face

Size
Head and body length: 5.5–11.4 in (14–29 cm), tail length: 7.9–15.8 in (20–40 cm); weight: 3.9–21.9 oz (110–620 g)

Number of genera, species
6 genera; 41 species

Habitat
Tropical and subtropical forests

Conservation status
Critically Endangered: 3 species; Endangered: 5 species; Vulnerable: 6 species; Data Deficient: 2 species



Distribution
South and Central America

Evolution and systematics

The family includes six extant genera: tamarins (*Saguinus*, 15 species), lion tamarins (*Leontopithecus*, 4 species), Goeldi's monkey (*Callimico*, 1 species), eastern Brazilian marmosets (*Callithrix*, 6 species), Amazonian marmosets (*Mico*, 14 species), and pygmy marmosets (*Cebuella*, 1 species). Their closest allies among the primates are the capuchins and squirrel monkeys, family Cebidae. The monotypic Goeldi's monkey (*Callimico goeldii*) has often been classified as a member of its own family Callimiconidae, but genetic studies demonstrate its position within the Callitrichidae as a sister-group to the clade formed by the three marmoset genera. In 2000, the Amazonian marmosets were reconsidered and placed in their own genus, *Mico*. This classification was based on the recognition that the pygmy marmoset is more closely related to Amazonian marmosets than to eastern Brazilian marmosets. The relative position of tamarins and lion tamarins within the Callitrichidae is still debated, with either of these genera being considered as basal within the family by different authorities.

The evolutionary history of the Callitrichidae is poorly documented. *Lagonimico*, from the middle Miocene (about 13.5 million years ago) of Colombia, is perhaps the earliest known fossil pertaining to the callitrichids.

Physical characteristics

The extant members of the family Callitrichidae are among the smallest primates and represent the smallest true monkeys (simian primates). Adult body mass ranges between 3.9–21.9 oz (110–620 g), head and body length between 5.5–11.4 in (14–29 cm), and tail length between 7.9–15.8 in (20–40 cm). The non-prehensile tail is always longer than the head and body combined. The head is relatively rounded and the snout only slightly pronounced. Except for lion tamarins and Goeldi's monkeys, females are usually larger than males (in contrast to the general trend in primates where males are larger than females), although to a varying degree. The coloration of the dense, silky fur varies considerably between species. Some, like the golden lion tamarins (*Leontopithecus*

Common marmosets (*Callithrix jacchus*) are found in the coastal forests of northeastern Brazil. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

rosalia), are very conspicuously colored, others, like Graell's black-mantled tamarins (*Saguinus graellsi*), are rather dull, and still others show contrasting coloration in different regions of the body. The fur may form a kind of a mantle on the shoulders or a mane in some species. Several marmosets possess ear tufts, while in a few tamarins either the beard or the hair on the crown is quite elongated. Males and females are colored alike. Claw-like nails grow on all fingers and toes except the big toe that has a flat nail. Histological studies revealed that these claws are laterally compressed nails, different from the true claws of other mammals. The thumb cannot be opposed to the other fingers, but the big toe is opposable, as in all other primates. The arms are shorter then the legs, but relative length varies between species, depending on the principal mode of locomotion. The third molar is lacking both in the upper and lower jaw; hence the number of teeth is 32. Goeldi's monkey represents the only exception: it possesses small, third molars, and thus 36 teeth. In tamarins, lion tamarins, and Goeldi's monkey the lower canines are higher then the lower incisors (long-tusked callitrichids), while in eastern Brazilian marmosets and pygmy marmosets they attain the same height (short-tusked callitrichids); Amazonian marmosets are intermediate in this character.

Distribution

The Callitrichidae have a wide distribution over tropical and subtropical South and Central America, from the Panamanian isthmus in the north to southeastern Brazil and northern Paraguay in the south. Tamarins occur in western and central Amazonia west of the Rio Madeira (although one subspecies of saddle-back tamarins, *Saguinus fuscicollis*, has extended its range into a small area east of the Rio Madeira), in the Guyanas and adjacent northern Brazil, and in northwestern Colombia, Panama and southeastern Costa Rica. Lion tamarins have the most restricted distribution of all genera of the family and are endemic to southeastern Brazil. Goeldi's monkey is found in western Amazonia, south of the Rio Japurá, but its exact distribution, particularly the eastern limits, is still poorly known; within the distributional range, its occurrence seems to be very patchy. Pygmy marmosets also occur in western Amazonia, south of the rivers Caquetá and Solimões and west of the Rio Madeira. Amazonian marmosets range in eastern and southern Amazonia, between the Rio Madeira in the west and the rivers Xingu and Tocantins in the east. Eastern Brazilian marmosets are distributed along the Brazilian Atlantic coast and adjacent inland areas.

Habitat

Callitrichids are mainly animals of tropical rainforests; they do, however, occupy a wide range of different habitats. Tamarins and the Amazonian marmosets are typically found in high-ground primary rainforest interspersed with patches of secondary vegetation, caused by natural disturbances (tree falls). Secondary forests provide a different spectrum of fruit and may also bear a higher abundance of insects, making them highly attractive for prey foraging. Some species may also persist in secondary forests with little or no remaining primary vegetation, and close to human settlements. Pygmy marmosets are preferably found in seasonally inundated and riverine forests. Goeldi's monkey mainly ranges in forest with dense undergrowth, such as those found in bamboo forests. Such habitat may occur in widely spaced patches, which is probably one of the reasons why groups and populations of this species may be separated from each other. Tamarins of northwestern Colombia and Central America are also found in relatively dry and semi-deciduous forests. Lion tamarins occur in coastal rainforests and in the often drier inland extensions of the Atlantic forests of eastern Brazil. Eastern Brazilian marmosets live in Atlantic coastal forests, gallery forests, and in forest patches within open habitats like the Cerrado and Caatinga (Brazil) and Chaco (Paraguay and Bolivia).

Behavior

All marmosets and tamarins live in groups. Group sizes range between 3–15 individuals, but most species are typically found in groups of 4–9. Groups of two animals usually represent migrating individuals without a home range or incipient groups. On average, group size is smaller in tamarins and lion tamarins compared to Amazonian and eastern Brazilian marmosets. Large groups of 20 or more individuals reported in the literature most likely represent the temporal association of two or more neighboring groups.

Based on captive findings where keeping an adult pair together with their non-breeding offspring was the most stable situation, marmosets and tamarins have traditionally been classified as living in family groups. However, callitrichid social organization is much more complex in the wild. In the best-studied species—that of the saddleback tamarin—social organization varies within populations, with groups being composed of one adult female plus two or more adult males, one adult female plus one adult male, one adult male plus two or more adult females, and two or more adults of both sexes plus immature individuals. During its existence, a single group may pass through these different forms of organization. Other species for which long-term data are available—like the common marmoset (*Callithrix jacchus*) and the moustached tamarin (*Saguinus mystax*)—have also been reported to be highly flexible in their social organization.

All tamarins and marmosets are diurnal and usually leave their sleeping sites at sunrise. The length of their daily activity period is, however, variable between species. Moustached tamarins and saddleback tamarins are active for ten hours and retire on average two hours before sunset, while pygmy marmosets (*Cebuella pygmaea*) and common marmosets are active for 11–12 hours, almost until dusk. Many species sleep in dense tangles of vines and epiphytes, but the base of palm fronds or the forking of trunks and large branches are also used. Saddleback tamarins and lion tamarins make intensive use of tree hollows, while moustached tamarins have never been observed in this kind of shelter.

Home-range size is highly variable both within and between species. The smallest home ranges are found in pygmy marmosets, which occupy areas of 0.25–1.24 acres (0.1–0.5 hectares). They are centered upon one or a few major sources of plant exudates; once these sources have been exhausted, pygmy marmoset groups shift to another area. In marmosets of the genera *Callithrix* and *Mico*, home-range size is related to the relative importance of exudates in their diet: highly exudativorous species usually occupy much smaller ranges (1.2–16.1 acres [0.5–6.5 hectares] in common marmosets, 3.2–11.1 acres [1.3–4.5 hectares] in black tufted-ear marmosets, *Callithrix penicillata*) compared to the less exudativorous species (27–40 acres [11–16 hectares] in buffy tufted-ear marmosets, *Callithrix aurita*, and about 69 acres [28 hectares] in the Aripuanã marmoset, *Mico intermedius*). In tamarins, home-range size varies between 20 acres [8 hectares] and almost 495 acres [200 hectares], but reasons underlying this variation are less well known; it is likely to be related to the productivity of the habitat. The largest home ranges for any callitrichid have been reported for golden-rumped lion tamarins (*Leontopithecus chrysopygus*) who may range over 682 acres [276 hectares].

The overlap between home ranges of neighbors also varies between species and populations. Home ranges of pygmy marmosets and Goeldi's monkey do not overlap and may not even be contagious, while in golden lion tamarins overlaps of up to 60% have been observed. Neighboring groups meet and interact in these overlap areas regularly, normally during the first hours of the day. Interactions may be aggressive, including chasing and fighting, but may also include friendly interactions like grooming and playing; in common marmosets, saddleback tamarins, and mustached tamarins, individuals from neighboring groups have been observed to be involved in sexual interactions. While the function of these between-group encounters is often seen as resource defense, it also provides the opportunity for immature individuals and non-breeding adults to familiarize with potential mates from neighboring groups. Additionally, during between-group encounters animals may migrate from one group to another without an intervening solitary phase.

Within-group social behavior is characterized by much affiliation. Social grooming is the most frequent interaction and

The emperor tamarin (*Saguinus imperator*) may be threatened due to destruction of its environment. (Photo by J-C Carton. Bruce Coleman, Inc. Reproduced by permission.)

is usually performed during prolonged resting periods. It is usually the adult and subadult group members who are involved in grooming, and the breeding female of a group can be the primary focus of the grooming activity. One individual laying down in front of another one and presenting the body in a posture not taken during solitary resting often initiates a grooming session. Apart from grooming, animals also huddle together for extended periods. While adults and subadults are grooming, youngsters are involved in social play, which involves chasing each other to-and-fro, grabbling, wrestling, and smooth, inhibited biting. Aggressive behavior between group members is generally rare and limited to threats and displacements. It may occur in small food resources that cannot accommodate several individuals; severe aggression with fighting is extremely rare in the wild.

Callitrichids are highly vocal animals. In the wild, marmosets and tamarins can best be detected by listening to their calls. All species possess a long call, a vocalization of high intensity that is audible to the human ear over a distance of at least 500–650 ft (150–200 m). Long calls are composed of two

A male tassel-eared marmoset (*Callithrix humeralifera*) peers out among the trees of the Brazilian Amazon. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

or more (up to about 30) notes, and are different between species, populations, and individuals; within an individual, the structure of long calls may also vary according to social context. Long calls function in intragroup cohesion and in the regulation of space between neighboring groups; in tamarin mixed-species troops they also function in the establishment of association. Long calls are most often heard in the early morning and usually precede and accompany encounters between neighboring groups.

Apart from long calls, all marmosets and tamarins possess a diversity of other calls. Specific alarm calls are emitted upon seeing a raptorial bird. Other group members (and even members of other species) "understand" these calls and may react in the appropriate way without seeing the raptor itself. Infant and juvenile tamarins utter squawks when soliciting and stealing food from another group member. Harsh and atonal calls are given during aggressive interactions. Many vocalizations are related to the cohesion of the group and coordination of activity. Pygmy marmosets vary the structure of their trills in relation to the distance to the nearest group member. In golden lion tamarins, different calls provide information about the sender's current location, activity, and intention.

Playback experiments with naturally recorded and with synthesized vocalizations revealed that pygmy marmosets show categorical perception, and that they respond to individual and contextual differences. Learning seems to be involved in the development of the vocal repertoire in marmosets and tamarins, since infants "babble" intensively and use vocalizations out of their proper context.

In contrast to most other simian primates, olfactory communication, that is communication by means of scent signals, plays an important role in the social life of marmosets and tamarins. Most callitrichids are equipped with scent glands in areas on and around the genitals (anogenital or circumgenital glands), on the lower abdomen above the genitals (suprapubic glands), and on the midline of the chest (sternal gland). The secretions of these glands consist of highly complex mixtures of fatty acids and their esters, proteins, and other organic compounds. Alone or mixed with urine, these secretions contain information about species and subspecies, sex, reproductive state, and individual identity of the sender. Scent gland secretions are applied to the environment through ritualized rubbing movements. Depending on the type of gland employed, this behavior is called anogenital, suprapubic, or sternal scent marking. The frequency with which the different types of scent marking behavior are employed varies between species. In most species, anogenital marking is the dominant mode, but in the Aripuanã marmoset suprapubic marking prevails, and black-mantled tamarins, *Saguinus nigricollis*, most often use sternal marking.

Usually, scent gland secretions are applied to branches, trunks, and lianas, but some species also mark members of their group. In saddleback tamarins this behavior culminates in scent-marking "parties" where most or all group members mark each other and objects of the environment for 2–3 minutes. The sympatric moustached tamarin lacks this kind of performance. Reasons for such interspecific variation are suggested to rest in subtle differences in the social structure and mating strategies.

In tamarins, adult females scent mark significantly more than adult males, while in lion tamarins and marmosets, rates of scent marking are usually balanced between sexes or may be male-biased as in golden-headed lion tamarins, *Leontopithecus chrysomelas*. In common marmosets, Aripuanã marmosets, saddle-back tamarins, and moustached tamarins scent marking is performed throughout the home range, and the spatial distribution of scent marks usually follows the patterns of home-range use. While this does not completely exclude a territorial function of scent marking, it is more consistent with a function in intragroup communication. In common marmosets scent marking by subordinate females may serve in the attraction of potential mates from neighboring groups.

In a few tamarin species urine washing has been observed, a behavior known from several other New World primates, particularly from squirrel monkeys (*Saimiri*). The behavior is, however, very rare and its function not known. Another behavior pattern related to olfactory communication is the

A lion tamarin (*Leontopithecus rosalia rosalia*) vocalizing. (Photo by Animals Animals ©John Chellman. Reproduced by permission.)

anointing of the tail with scent-gland secretions and urine, as observed in Goeldi's monkey.

Marmosets and tamarins also employ visual signals in social communication. When they are aroused, the hair on the head, ears, shoulders, or the whole body is raised. This is particularly notable in species that possess hairy ornaments like the long crown hair of cotton-top tamarins (*Saguinus oedipus*) and the ear tufts of several marmoset species. Facial expressions like frowning, open mouth threats, and head shaking, are used in agonistic interactions. When threatening another individual—whether in their own group or in another group—several marmoset species turn around, lift their tail, and display their genitals. Lion tamarins and marmosets walk with an arched back and raised hair during agonistic interactions and in situations of social tension.

Due to their small body size, callitrichids are susceptible to a wider array of predators than larger primates. Successful and unsuccessful attacks by raptorial birds—Guianan crested eagles (*Morphnus guianensis*), ornate hawk eagles (*Spizaetus ornatus*), bicolored hawks (*Accipiter bicolor*)—and snakes—anacondas (*Eunectes murinus*), rainbow boas (*Boa constrictor*), jararacas (*Bothrops jararaca*)—have been witnessed. Tayras (*Eira barbara*) have been seen carrying dead tamarins in their mouths and hairs of tamarins were found in feces of ocelots (*Felis pardalis*). Callitrichids respond to predators by alarm calling, escaping, and hiding. If a raptor attacks while animals are exposed in an open tree crown and no escape to dense vegetation is possible, they may let themselves drop as a last resort. Once a predator has been detected and can no longer hunt by surprise, marmosets and tamarins may approach and intensively mob the predator with specific vocalizations. Saddleback tamarins have been observed striking at a resting snake, and moustached tamarins were observed attacking a rainbow boa in order to rescue a group member.

As a counterstrategy against being surprised by a predator, marmosets and tamarins are constantly vigilant. They frequently interrupt their ongoing activity to scan the surroundings. Adult male marmosets and tamarins perform such vigilance more often than other group members.

In areas south of the Amazon, saddle-back tamarins form mixed-species troops (interspecific associations) with sympatric congeners, either moustached tamarins, red-bellied tamarins (*Saguinus labiatus*), or emperor tamarins (*Saguinus imperator*). In these troops, one group of saddlebacks and one group of the other tamarin species spend much of their active time together and jointly exploit plant resources, and their home ranges overlap almost completely. The species separate for the night, and contact is often re-established the next morning by means of long calls. Although species participating in mixed-species troops use all layers of the forest from the ground to the emergent trees, the smaller saddle-back tamarins range on average at lower heights than the associated larger species. Species forming mixed-species troops also differ in their strategies of foraging for prey. In northern Bolivia, Goeldi's monkeys regularly participate as the third party in associations of saddleback tamarins and red-bellied tamarins. Members of the different species in a mixed-species troop rarely interact directly with each other. If such interactions occur, they are usually agonistic and involve displacements or mild aggression by a member of the larger species

A juvenile white-lipped tamarin (*Saguinus leucopus*) rests on a tree branch. (Photo by Roy P. Fontaine/Photo Researchers, Inc. Reproduced by permission.)

A pygmy marmoset (*Cebuella pygmaea*) eats fruit in the Upper Amazon Basin. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

towards a member of the smaller species. Agonistic interactions mainly occur in food resources of limited size. There are also friendly interactions between members of the associated species, and particularly juveniles and subadults have been observed playing intensively.

Major benefits of mixed-species troops are seen in increased safety from predators and increased foraging efficiency. By associating with another species, group size is increased without compromising the social organization and mating patterns. Increased group size may reduce the risk for each individual of being the target of an attacking predator. Studies on associations of moustached and saddleback tamarins on the Urucu River in Brazilian Amazonia have revealed that the two species may also benefit from a "division of labor" with regard to their vigilance: moustached tamarins, which use higher strata of the forest, are more likely to detect aerial threats, while saddleback tamarins use lower strata of the forest and are more likely to detect threats coming from below. Saddleback tamarin may also derive a benefit from the association by capturing prey that has been flushed by and escaped from mustached tamarins.

Like most New World monkeys and unlike Old World monkeys and apes, all callitrichid males and one-third of the females are dichromats, that is, they can only distinguish two colors, while two-thirds of the females are trichromats, that is, they possess normal color vision. While the gene for the short wavelength is located on chromosome 7, the genes coding for the middle and long wavelength are located on chromosome X. Having only one chromosome X, males possess only two different color vision genes. Whether females are dichromat or a trichromat depends on whether they are homozygotous or heterozygotous at the respective gene locus on the chromosome X. The reasons for the maintenance of this polymorphic color vision system are unknown. It has been suggested that trichromats are better at detecting ripe fruits, while dichromats may have an advantage in detecting camouflaged prey and predators.

Feeding ecology and diet

All callitrichids include fruit, gums and other plant exudates, and insects in their diet. Most species also feed on nectar, other arthropods (e.g., butterflies and spiders), and small vertebrates (e.g., frogs, lizards, bird eggs, and nestlings). Leaves and buds are very rarely consumed. The relative proportion of different dietary components varies considerably between species. Eastern Brazilian marmosets and pygmy marmosets rely heavily on plant exudates that they procure by gouging through the bark of trees and lianas, a behavior facilitated by their short-tusked condition. Amazonian marmosets are also able to gouge, but depend on plant exudates much less than the other marmosets. Given their long-tusked condition, tamarins and lion tamarins cannot gouge and rely on exudate flow stimulated by damage of the bark through

A golden lion tamarin (*Leontopithecus rosalia*) rests in a tree. (Photo by Wolfgang Bayer. Bruce Coleman, Inc. Reproduced by permission.)

such things as windbreak and wood-boring insects. In contrast to marmosets, their diet is dominated by a high diversity of fruits; saddleback tamarins and moustached tamarins may include up to about 150 different fruit species in their diet. The spectrum of fruits ranges from soft, tiny berries of less than 0.2 in (0.5 cm) in diameter to large, leathery legume pods of more than 12 in (30 cm) in length. Tamarins swallow the seeds of many of the plant species whose fruits they consume and void them with their feces after the adhering pulp has been fully or partially digested. These seeds remain viable after gut passage; tamarins thus contribute to seed dispersal and to the natural regeneration of the forest. Many of the swallowed seeds are large (diameter up to 0.4 in [1 cm], length 0.6–0.8 in [1.5–2 cm]) in relation to tamarin body size, and it has been suggested that this habit possesses a curative function (displacement of gastro-intestinal parasites and stimulation of gut motility).

During seasonal shortages in fruit availability, nectar or gum may become the principal dietary alternative for frugivorous species. Goeldi's monkeys exploit fungi as an alternative diet during periods of reduced fruit availability. In contrast, fungi are an important dietary component throughout the year for buffy tufted-ear marmosets. In saddleback tamarins and emperor tamarins nectar may account for 50–75% of all plant food consumed during periods of fruit scarcity.

Strategies for the search and capture of insects and other prey vary between species. Lion tamarins and saddleback tamarins are mainly manipulative foragers. They probe with their hands (which are particularly elongated in lion tamarins) into tree holes and crevices, break up dead bark, turn around leaf litter, and dip into bromeliads to obtain hidden prey. Most other tamarins and the marmosets are "surface gleaners" that obtain camouflaged prey from the surface of leafs and branches; they stealthily approach this prey and then rapidly snatch or grab. For many callitrichids, foraging for prey is the most time-consuming activity, accounting for up to about 45% of the waking hours, and katydids are the top prey for most species. When capturing a katydid, the first bite is directed towards the head; thus they avoid being bitten by the often formidable mandibles.

Differences in prey foraging strategies are an important factor for the sympatric co-existence of different tamarin species and for the formation of mixed-species troops. By searching for and capturing prey at different strata of the forest and with different techniques, saddleback tamarins and moustached tamarins overlap much less in the spectrum of their principal prey items (katydids) in comparison to the plant component of their diet; saddleback tamarins also capture more lizards and other small reptiles, while mustached tamarins feed more often on frogs.

Several marmoset species and saddleback tamarins also forage over swarms of army ants and capture insects and other arthropods that try to escape from the ants.

Reproductive biology

As with social organization, the mating system of callitrichids is quite variable, both within and between species.

Goeldi's monkey (*Callimico goeldii*) has claws instead of nails. (Photo by Norman Owen Tomalin. Bruce Coleman, Inc. Reproduced by permission.)

In all marmosets and tamarins (once again with the exception of Goeldi's monkey) each group includes only a single breeding (dominant) female, which may mate with a single male (monogamy), or with two or more males (polyandry). While monogamy is found in all callitrichids, polyandry has been observed in saddleback and moustached tamarins, golden lion tamarins, Aripuanã marmosets, and pygmy marmosets. Breeding by multiple females is the norm in Goeldi's monkey, but also occurs in different tamarin species, in golden lion tamarins, and in common marmosets. In golden lion tamarins, secondary breeding females are usually the daughters of the primary breeding female, but their rearing success is much lower. In common marmosets, dominant females have even been observed committing infanticide; that is, actively killing the infants of other breeding females in their group. This behavior has been related to the competition for resources, particularly helpers for infant care.

In captivity, the limitation of breeding to a single female in each group is based on the lack in subordinate females of fertile ovarian cycles in marmosets and tamarins, and the

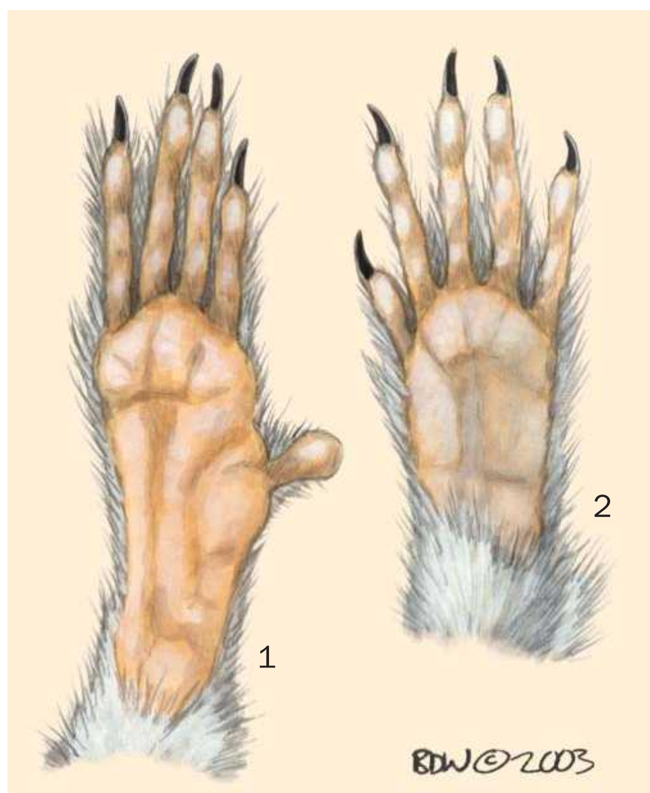
A cotton-top tamarin (*Saguinus oedipus oedipus*) in northwest Colombia. (Photo by Gail M. Shumway. Bruce Coleman, Inc. Reproduced by permission.)

dominant female's interference with matings between subordinate females and males in golden lion tamarins. It has been suggested that olfactory cues (pheromones) released by breeding females through scent marking "suppress" ovarian cycling in subordinate females. However, the presence of ovarian cycles in subordinate females and of multiple breeding females in groups suggest that the mechanism is much more complex and that subordinate females play an active role in determining whether or not they will breed.

Callitrichid mating behavior is rather inconspicuous. In many species, for example, in moustached tamarins and in pygmy marmosets, copulations are not preceded by any soliciting behavior, while in common marmosets tongue flicking may initiate copulations. There is no external sign of estrus, although some swelling of the vulva during the supposed receptive phase has been observed in wild mustached tamarins. During the receptive period of the female estrus cycle, males are often more closely associated with females than during other times. During this period, males also perform more genital controls by sniffing and licking the genitals and the urine of females. In captivity, pygmy marmoset and cotton-top tamarin males are able to detect the receptive period through olfactory signals, and it is likely that the same is true for other species and in the wild. Golden lion tamarin males increase their body mass in the month before the highest probability that females come into estrus, and mustached tamarin males have larger testes during the months when most conceptions occur.

In captivity, all callitrichids may give birth twice per year. However, in the wild this has been observed regularly only in marmosets and in pygmy marmosets. In most tamarins and in golden lion tamarins normally only one birth per year occurs. In these species, births peak during 2–3 months, mainly in the early and middle wet season. Through this timing of births, the energetically costly lactation and carrying of infants and the critical process of weaning take place during periods of high fruit availability. In golden lion tamarins, a female may give birth a second time only if the first birth took place early in the birth season.

The duration of pregnancy varies between 129 days in golden lion tamarins and 183 days in cotton-top tamarins, but for most marmosets and tamarins it is around 145–150 days. All callitrichids except for Goeldi's monkey give birth to dizygotic twins. Births take place during the night. At birth, the combined body mass of twins accounts for up to 20% of maternal body mass, which is among the highest proportion in mammals and the highest in primates except for tarsiers. The infants are carried on the back, and most or all adult and subadult group members may participate in infant carrying. In



Marmosets and tamarins have claws on all digits on the hand (2) and foot (1), except the large toe. (Illustration by Bruce Worden)

Scent-marking in callitrichids: 1. Sternal marking (Goeldi's monkey); 2. Anogenital marking with simultaneous sniffing of marking site (moustached tamarin); 3. Suprapubic marking (Geoffrey's tamarin). (Illustration by Jarrod Erdody)

tamarins, it is the adult males who carry the infants most of the time, often from the day of birth on, while in lion tamarins and common marmosets infant carrying is more evenly shared between mothers and fathers or other adult males. In Goeldi's monkey, infants are first carried by group members other than the mother only from about the second week of life on.

Carrying the heavy offspring is a strong, energetic burden. Studies of captive cotton-top tamarins have shown that carrying males may lose up to 10% of body mass in the weeks after the birth of infants, even though they do not have to travel and search for food. It is thus evident that in the wild, where tamarins may have to travel 0.6–1.2 mi (1–2 km) per day to find sufficient food, infant carrying represents a considerable cost to the caregivers. In pygmy marmosets, infants may be "parked" at protected places after the second week of life, and may spend most of their waking hours on their own. This behavior is unique among simian primates (while many lemurs, lorises, and tarsiers park their infants routinely), and only feasible because the activities of pygmy marmosets are usually focused around a single major food resource.

Infant callitrichids make the first short excursions from the back of a carrier and take the first solid food during the third or fourth week of life, but continue to suckle milk from the mother until the end of the third month. Locomotor independence is also attained by the end of the third month, although even at a later age infants may be picked up and carried by an adult group member in threatening situations or when the group has to travel very fast.

An adult silvery marmoset (*Callithrix argentata*) carries its young. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

Apart from carrying, the cooperative rearing system of callitrichids includes the transfer of food from adults and subadults to infants. Infants approaching another group member and emitting a squawk, and then taking the food item, can initiate this transfer. In a number of species (e.g., golden lion tamarins and in buffy-headed marmosets, *Callithrix flaviceps*), animals in possession of a food item may also initiate the transfer; that is, a specific chattering vocalization is emitted in order to attract the infant. Items transferred include animal prey or opened fruits that are otherwise difficult for infants to process. The frequency of food transfer and the willingness of the food possessor to concede decrease with increasing age of the offspring and cease after the first year of life. Sexual maturity is attained between 12–24 months of age; marmosets (except pygmy marmosets) and Goeldi's monkey are matured at an earlier age than tamarins and lion tamarins.

Conservation status

The family includes very common and widely distributed species that are not threatened, but also a number of Critically Endangered, Endangered, and Vulnerable species with very restricted and shrinking distributional ranges. With perhaps fewer than 350 individuals remaining, the black-faced lion tamarin (*Leontopithecus caissara*) is among the 25 most endangered primate species. The principal reason for declining populations is the ongoing destruction of suitable habitats. In the past, several species (e.g., cotton-top tamarins) have also suffered from heavy trapping of wild animals for exportation to the Northern Hemisphere, both as laboratory animals and as pets. While large-scale trade-trapping has been banned, illegal activities continue. For Critically Endangered species like the lion tamarins, even the removal of a few individuals from the already reduced wild populations represents a substantial loss.

Ironically, threats to marmosets and tamarins also emerge from closely related species. The common marmoset expands its range due to introduction by humans, and displaces or interbreeds with resident species. The Critically Endangered pied tamarin (*Saguinus bicolor*), which lives in a limited area close to the Amazonian city of Manaus, suffers from range expansion by the Midas tamarin (*Saguinus midas*).

Significance to humans

Common marmosets are one of the most widely used primate species in biomedical research, and cotton-top tamarins are an important primate model for the study of colitis and colon cancer. Other callitrichids like moustached tamarins and red-bellied tamarins are also used in different areas of biomedical research. Today, most marmosets and tamarins in biomedical research are captive bred. In their habitat countries, marmosets and tamarins are appreciated as pet monkeys. In the 1960s and 1970s, several species (e.g., golden lion tamarins and cotton-top tamarins) were heavily trapped and exported to the Northern Hemisphere. Due to their small body size, marmosets and tamarins are rarely hunted for food, quite in contrast to larger primate species.

Recent research has pointed to the possibility that common marmosets may represent a reservoir for rabies in Brazil.

1. Aripuanã marmoset (*Mico intermedius*); 2. Buffy-headed marmoset (*Callithrix flaviceps*); 3. Saddleback tamarin (*Saguinus fuscicollis*); 4. Pygmy marmoset (*Cebuella pygmaea*); 5. Common marmoset (*Callithrix jacchus*). (Illustration by Joseph E. Trumpey)

1. Goeldi's monkey (*Callimico goeldii*); 2. Golden lion tamarin (*Leontopithecus rosalia*); 3. Cotton-top tamarin (*Saguinus oedipus*); 4. Golden-headed lion tamarin (*Leontopithecus chrysomelas*). (Illustration by Joseph E. Trumpey)

Species accounts

Cotton-top tamarin
Saguinus oedipus

TAXONOMY
Simia oedipus Linnaeus, 1758, Colombia.

OTHER COMMON NAMES
French: Pinché; German: Lisztaffe; Spanish: Tití blanco.

PHYSICAL CHARACTERISTICS
Weight: 12.4–15.9 oz (350–450 g); head and body length: 7.9–11 in (20–28 cm); tail length: 12.2–16.1 in (31–41 cm); conspicuous long white hair on the crown.

DISTRIBUTION
Northwestern Colombia, between Rio Magdalena and Rio Atrato.

HABITAT
Tropical rainforest, seasonally dry tropical forest.

BEHAVIOR
Cotton-top tamarins usually live in groups of 3–10 individuals, including 1–2 adults of each sex and immature offspring of different ages. Both sexes may disperse and join neighboring groups. Home-range areas are 19–25 acres (7.8–10 ha), and daily path length is 0.9–1.1 mi (1.5–1.7 km). The diverse and complex vocal repertoire includes long calls of much lower frequency (1–1.5 kilohertz) than those of tamarin species distributed in Amazonia. Scent-marking involves the anogenital and suprapubic glands, sternal marking is extremely rare. The conspicuous crown hair is raised when animals are agitated.

FEEDING ECOLOGY AND DIET
Cotton-top tamarins are primarily frugivorous and insectivorous, but complement their diet with exudates, nectars, and small vertebrates. They use all strata of the forest during feeding and foraging, and may also come down to the ground to feed on fallen fruits.

REPRODUCTIVE BIOLOGY
Breeding is usually restricted to a single female per group, but groups with two pregnant females have been observed. Whether females mate with more than one adult male is not known. Estrus cycle duration is 23–25 days, and gestation length is 180–185 days (longer than other tamarin species). Usually one birth per year takes place between March and June, if pregnancies fail or if infants die, females may conceive a second time and give birth later in the year. Infants are mainly carried by adult males.

CONSERVATION STATUS
Cotton-top tamarins are Critically Endangered due to ongoing habitat destruction and trapping.

SIGNIFICANCE TO HUMANS
Used in biomedical research and popular as pets. ◆

Saddleback tamarin
Saguinus fuscicollis

TAXONOMY
Midas fuscicollis Spix, 1823, Brazil. Twelve subspecies (some or most of which may represent their own species).

OTHER COMMON NAMES
French: Tamarin à dos brun; German: Braunrückentamarin; Spanish: Bebeleche (Colombia), chichico (Ecuador), pichico (Peru).

PHYSICAL CHARACTERISTICS
Weight: 10.2–14.8 oz (290–420 g); head and body length: 7.9–10.6 in (20–27 cm); tail length: 11.4–15 in (29–38 cm). It is the smallest member of the genus. Fur occurs on the dorsal side of the head and body tripartite, with an agouti-colored saddle in the middle.

DISTRIBUTION
Central and western Amazonia.

HABITAT
Tropical rainforest.

BEHAVIOR
Saddle-back tamarin groups comprise 3–10 individuals, with 1–2 adults of each sex, and immature individuals of different ages. Home-range size varies between 25–495 acres (10–200 ha), according to population. Most or all group members at the same place perform scent marking throughout the home range, often simultaneously. In areas of sympatry, saddle-back tamarins form mixed-species troops with mustached tamarins, red-bellied tamarins, and emperor tamarins. East of the Rio Madeira, saddleback tamarins have also been observed in association with a marmoset species.

FEEDING ECOLOGY AND DIET
Saddle-back tamarins are primarily frugivorous and insectivorous, but supplement their diet with exudates, nectar, small vertebrates, and soil from arboreal termite mounds. Depending on availability, nectar or exudates may become the dietary staples when fruits are scarce. They search for prey in the leaf litter, and dip into tree holes, crevices, and bromeliads.

REPRODUCTIVE BIOLOGY
Flexible mating system includes polyandry, monogamy, and polygyny. Reproduction is moderately seasonal, usually one birth per year. Estrus cycle duration averages about 25.7 days, and gestation length is 148–152 days. Adult males are the principal carriers of infants.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
They are kept as pets in habitat countries and used as models in biomedical research. ◆

Golden lion tamarin
Leontopithecus rosalia

TAXONOMY
Simia rosalia Linnaeus, 1766, Rio de Janeiro, Brazil.

OTHER COMMON NAMES
French: Singe lion; German: Goldener Löwenaffe; Portuguese: Mico-leão-dourado.

PHYSICAL CHARACTERISTICS
Male weight: 21.9 oz (620 g), female weight: 21.1 oz (598 g); head and body length: 8.9–11 in (22.5–28 cm); tail length: 10.4–15.8 in (26.5–40 cm). Entirely covered with golden fur, except for a naked face.

DISTRIBUTION
Remnants of Atlantic coast forest in the state of Rio de Janeiro, Brazil.

HABITAT
Mature lowland forest, secondary forest.

BEHAVIOR
Group size ranges between 2–11 individuals, most often including more than one adult of each sex. Both sexes may migrate, but may also inherit the breeding status in the natal group. Home range comprise 52–180 acres (21–73 ha), overlap with neighboring home ranges is around 60%. Groups travel between 0.8–1 mi (1.3–1.6 km) per day. Males and females scent mark with equal rates. Tree holes are preferred for sleeping.

FEEDING ECOLOGY AND DIET
Golden lion tamarins are primarily frugivorous and insectivorous, but supplement their diet with nectar, exudates, and small vertebrates; nectar may become the principal food source when fruits are scarce. Forage for prey mainly in epiphytic bromeliads, but also in dead leaves, epiphytes, tree bark, etc., using their long fingers to probe for embedded prey.

REPRODUCTIVE BIOLOGY
Flexible mating system (monogamy, polyandry, polygyny). In groups with more than one adult male, mate guarding occurs during the receptive phase of the breeding female. Gestation length is 125–130 days and twins are the rule. Females give birth usually once per year, and breeding and births are seasonal. Adult males participate in infant carrying.

CONSERVATION STATUS
Critically Endangered due to habitat destruction and fragmentation. Golden lion tamarins are the focus of strong conservation efforts, where protection of natural habitat, captive breeding, and reintroduction of captive-bred animals into the wild are combined.

SIGNIFICANCE TO HUMANS
Golden lion tamarins are kept as pets; one was the famous pet of Madame de Pompadour. They are featured on the back of the Brazilian 20 Reais cash note, and is the flagship species for conservation efforts in the Brazilian Atlantic region. ◆

Golden-headed lion tamarin
Leontopithecus chrysomelas

TAXONOMY
Midas chrysomelas Kuhl, 1820, Bahia, Brazil.

OTHER COMMON NAMES
French: Singe lion à tête d'or; German: Goldkopf-Löwenaffe; Portuguese: Mico-leão-de-cara-dourada.

PHYSICAL CHARACTERISTICS
Male weight: 21.9 oz (620 g), female weight: 18.9 oz (535 g); head and body length: 8.7–10.2 in (22–26 cm); tail length: 13.0–15.4 in (33–39 cm). Rump with black fur; arms, part of tail, and fringe around face is golden in color.

DISTRIBUTION
Forest remnants in the southern part of the state of Bahia, Brazil.

HABITAT
Tropical rainforest in coastal region, semi-deciduous forest further inland.

BEHAVIOR
Groups of 3–9 individuals, with usually two adult males and one adult female, plus immature individuals. Home-range size is 163–213 acres (66–86 ha), and groups travel 0.9–1.4 mi (1.4–2.2 km) per day. Where living in the same forest with Wied's black-tufted-ear marmoset (*Callithrix kuhli*), short term associations are formed.

FEEDING ECOLOGY AND DIET
Golden-headed lion tamarins are mainly frugivorous and insectivorous; the diet is supplemented with flowers, exudates from the pods of a legume, and nectar. Prey is mainly searched in epiphytic bromeliads and includes cryptic or concealed insects, but also small vertebrates and snails.

REPRODUCTIVE BIOLOGY
Little known, probably a flexible mating system (monogamy, polyandry).

CONSERVATION STATUS
Critically Endangered due to ongoing habitat destruction.

SIGNIFICANCE TO HUMANS
Kept as pets. ◆

Goeldi's monkey
Callimico goeldii

TAXONOMY
Hapale goeldii Thomas, 1904, Acre, Brazil.

OTHER COMMON NAMES
French: Tamarin de Goeldi; German: Springtamarin; Portuguese: Mico-de-Goeldi; Spanish: Chichico diablo (Colombia), supay pichico (Peru).

PHYSICAL CHARACTERISTICS
Average male weight: 12.9 oz (366 g), female weight: 12.5 oz (355 g) (both in the wild); male weight: 19.5 oz (554 g), female weight 18.6 oz (526 g) (both in captivity); head and body length: 8.4–9.2 in (21.3–23.4 cm); tail length: 10.6–12.8 in (27–32.4 cm). Fur is entirely black; the only callitrichid with 36 teeth.

DISTRIBUTION
Patchily distributed in western Amazonia, south of the Rio Japurá.

HABITAT
Tropical rainforest with dense undergrowth, bamboo forest.

BEHAVIOR
Groups include 2–9 individuals; 1–3 adult males and females per group. Home-range size is 198–370 acres (80–150 ha); home ranges of different groups are not contagious. They are frequently found in mixed-species troops with saddle-back tamarins and red-bellied tamarins, often occupying the lowest levels of the forest when in association.

FEEDING ECOLOGY AND DIET
Goeldi's monkeys are basically frugivorous and insectivorous, but fungus may become the dominant dietary item during several months of fruit scarcity. Prey foraging in the understory on thin branches, but also in the leaf litter; orthopterans are the principal prey item.

REPRODUCTIVE BIOLOGY
Flexible mating system (monogamy, polyandry). Groups include 1–2 breeding females, each of which gives birth to a single infant. Estrus cycle duration is 23–24 days, gestation length is 147–157 days. Breeding is perhaps seasonal, with possibly two births per year. Mothers are the principal carriers of infants.

CONSERVATION STATUS
Vulnerable. Threatened by habitat destruction, at least in the southern part of its geographic range.

SIGNIFICANCE TO HUMANS
Little is known even by local people; they are occasionally kept as pets. ◆

Common marmoset
Callithrix jacchus

TAXONOMY
Simia jacchus Linnaeus, 1758, Pernambuco, Brazil.

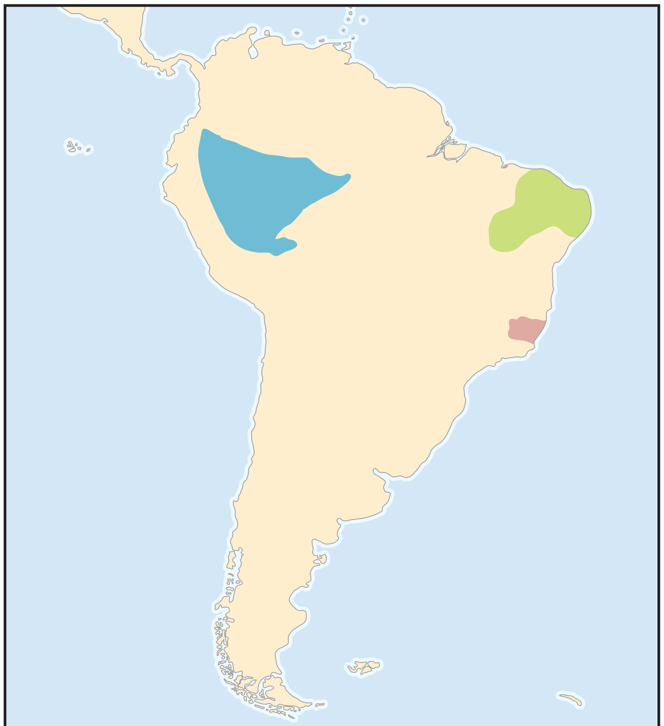
OTHER COMMON NAMES
French: Ouistiti à toupet blanc; German: Weisspinselaffe; Portuguese: Sagüi-do-nordeste.

PHYSICAL CHARACTERISTICS
Average weight: 11.3 oz (320 g); head and body length: 7.3–9.8 in (18.5–25 cm); tail length: 11.6–13.8 in (29.5–35 cm). They display prominent white ear tufts.

DISTRIBUTION
Northeastern Brazil; introduced in eastern and southeastern Brazil.

HABITAT
Coastal forest, gallery forest, forest patches in open Caatinga and Cerrado bush land.

BEHAVIOR
Group size ranges between 3–15, with usually several adults of both sexes plus immature individuals. Home-range size is 1.2–16.1 acres (0.5–6.5 ha), daily path length is 0.3–0.6 mi (0.5–1 km). Home range overlap with neighboring groups is variable. Encounters between neighboring groups are frequent, usually initiated by long calling. Most interactions between members from different groups are hostile, involving chasing and genital displays, but copulations between members from different groups have also been observed during these encounters. Within-group social relations are highly affiliative. Grooming is the major social activity, and breeding adults are most frequently involved in grooming interactions. Aggression



between group members is rare in the wild and usually occurs only during feeding in exudates trees. In the dominance hierarchy, the breeding adults are at the top, and the non-breeding group members are arranged according to age with older individuals ranking higher than younger ones.

FEEDING ECOLOGY AND DIET
Common marmosets feed primarily on exudates and insects; eating only a little fruit and occasionally small vertebrates. Exudate flow is stimulated through gouging into the tree bark.

REPRODUCTIVE BIOLOGY
They usually breed in monogamous pairs, but breeding by two females in the same group is quite common in the wild. Genetic data suggest that only one male breeds in a group. Despite observation of copulations between males and females from different groups, no infants seem to be fathered by extra-group males. Estrus cycle duration is 28–29 days, and gestation length is 141–146 days. In captivity, subordinate females do not show an estrus cycle. Two births per year are common both in captivity and in the wild. When two females are breeding simultaneously in the group, rearing success is lower in the subordinate female; even killing of subordinate female infants by the dominant female has been observed in a wild population. Adult males and other group members participate in infant carrying.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
One of the most widely used laboratory primates; also kept as pets. They have been introduced to areas outside their natural range. ◆

Buffy-headed marmoset
Callithrix flaviceps

TAXONOMY
Hapale flaviceps Thomas, 1903, Espírito Santo, Brazil.

OTHER COMMON NAMES
French: Ouistiti à tête jaune; German: Gelbkopfbüschelaffe; Portuguese: Sagüi-da-serra.

PHYSICAL CHARACTERISTICS
Average weight: 14.3 oz (406 g); head and body length: 8.7–9.8 in (22.2–24.8 cm); tail length: 11.7–13.8 in (29.8–35 cm); Fur appears on the head and ear tufts are buffy-yellowish in color.

DISTRIBUTION
Forest remnants in the states of Espírito Santo and Minas Gerais.

HABITAT
Seasonal, altitudinal Atlantic coastal forest.

BEHAVIOR
Group size varies between 5–15; a single group that was monitored over six years living together included 11–15 individuals; 3–6 adult males, and 1–6 adult females. Home-range size is around 88 acres (35.5 ha), and daily path length is about 0.75 mi (1.2 km).

FEEDING ECOLOGY AND DIET
Buffy-headed marmosets feed primarily on exudates and insects; exudates are procured through gouging on tree bark. However, they often eat more fruit when it becomes more abundant in their highly seasonal habitat.

REPRODUCTIVE BIOLOGY
Despite the large number of adult females that may live in a group, only one of them breeds. A daughter may inherit the position of the breeding female, while the mother still remains in the group and contributes to infant care, along with other adult and subadult group members. Mating is monogamous, but mating with more than one male (polyandry) is suspected. Two births per year is normal, and probably seasonal.

CONSERVATION STATUS
Endangered. Habitat fragmentation and loss are the major threat.

SIGNIFICANCE TO HUMANS
Often captured for the pet trade; this species is also a draw for ecotourists. ◆

Aripuanã marmoset
Mico intermedius

TAXONOMY
Callithrix humeralifer intermedius Hershkovitz, 1977, Rio Aripuanã, Brazil.

OTHER COMMON NAMES
French: Ouistiti à camail; German: Weissschulterseidenaffe; Portuguese: Sagüi-de-Aripuanã.

PHYSICAL CHARACTERISTICS
Average head and body length: 9.4 in (24 cm); tail length: 12.6

in (32 cm). The head and upper half of the body is creamy white, while the lower half is brown.

DISTRIBUTION
Brazilian Amazonia, between Rio Aripuanã and Rio Roosevelt.

HABITAT
Tropical rainforest, both in mature and secondary vegetation.

BEHAVIOR
Groups are normally between 4–13 individuals, usually including more than one adult of each sex. Home-range size is around 69 acres (28 ha), overlap with neighboring groups is around 22%. Daily path length is 0.5–1.3 mi (0.8–2.1 km). Scent marking performed most frequently with suprapubic gland, but sternal marking is also quite common, and by both sexes with similar rates. Scent marks are distributed throughout home range, but more in peripheral areas, and also more often during encounters with neighboring groups.

FEEDING ECOLOGY AND DIET
They primarily feed on fruits and arthropods; exudates are much less important than in eastern Brazilian marmosets, and tree gouging rarely employed. Occasionally small vertebrates are taken. They have been observed to forage over swarms of army ants (*Eciton burchelli*).

REPRODUCTIVE BIOLOGY
Mating is not confined to a single pair, but several adult males and females have been seen copulating. However, only a single female gives birth. Births occur seasonally, with two peaks at the end of the dry season and the second half of the wet season. Adult males and other group members participate in infant carrying.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Pygmy marmoset
Cebuella pygmaea

TAXONOMY
Jacchus pygmaeus Spix, 1823, Tabatinga, Brazil. Two subspecies.

OTHER COMMON NAMES
French: Ouistiti mignon; German; Zwergseidenaffe; Spanish: Leoncito (Peru, Ecuador), mono de bolsillo (Colombia).

PHYSICAL CHARACTERISTICS
Average male weight: 3.9 oz (110 g), female weight: 4.3 oz (122 g); head and body length: 5.4–6 in (13.6–15.2 cm); tail length: 6.8–9 in (17.2–22.9 cm). Coat is yellow-brown; tail has faint rings. It is the smallest New World monkey.

DISTRIBUTION
Western Amazonia, south of the rivers Caquetá and Solimões and west of the Rio Madeira.

HABITAT
Tropical rainforest, prefers seasonally inundated and riverine forest.

BEHAVIOR
Groups include 2–9 individuals, with usually a single adult pair and their offspring. Both sexes disperse from their natal group. They occupy very small home ranges (0.25–1.25 acres; 0.1–0.5 ha), which are shifted once the exudate yield of the principal feeding tree has dropped below a critical level. Neighboring home ranges are usually not contagious. Genital display is used as an aggressive signal towards other individuals (both within and between groups) and human observers.

FEEDING ECOLOGY AND DIET
They feed mostly on exudates of over 60 plant species and on arthropods; fruits are of little importance. They gouge 0.4–0.8 in (10–20 mm) wide and 0.2–0.7 in (4–18 mm) deep holes into the bark with specialized dentition to stimulate exudate flow. Foraging for prey in the crowns of small- to medium-sized trees often occurs, but occasionally they also forage on the forest floor.

REPRODUCTIVE BIOLOGY
Usually monogamous. Estrus cycle duration is 27–28 days, gestation length is 135–146 days. Births occur throughout the year, but peak around May-June and October-January. Infants are carried by mothers and other group members, but also parked at safe sites.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Sometimes kept as pets. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Emperor tamarin *Saguinus imperator*	Hairy face, long white moustache extends to shoulders. Head and body length 6.9–12.2 in (17.5–31 cm), tail length 9.8–17.3 in (25–44 cm).	Can be found in tropical forests, open woodlands, and secondary growth. Groups of 1 to 3 individuals.	Western Brazil and eastern Peru.	Consists of fruit, tender vegetation, insects, spiders, small vertebrates, and bird eggs.	Not threatened
Midas tamarin *Saguinus midas*	Lacks white area around mouth, blackish face, orange or yellowish hands and feet. Head and body length 6.9–12.2 in (17.5–31 cm), tail length 9.8–17.3 in (25–44 cm).	Can be found in tropical forests, open woodlands, and secondary growth. Extremely agile. Groups of 1 to 20 individuals.	Northern Brazil, Guyana, French Guiana, and Suriname.	Consists of fruit, tender vegetation, insects, spiders, small vertebrates, and bird eggs.	Not threatened
Mottle-faced tamarin *Saguinus inustus*	Mottle-faced, dense crown of hair except for sides of face, unpigmented face, melanistic pelage. Head and body length 6.9–12.2 in (17.5–31 cm), tail length 9.8–17.3 in (25–44 cm).	Can be found in tropical forests, open woodlands, and secondary growth. Extremely agile. Small groups of individuals associate together.	Northwestern Brazil and southwestern Colombia.	Consists of fruit, tender vegetation, insects, spiders, small vertebrates, and bird eggs.	Not threatened
Geoffroy's tamarin *Saguinus geoffroyi*	Forehead, crown, cheeks, and temples covered with long hairs. Head and body length 6.9–12.2 in (17.5–31 cm), tail length 9.8–17.3 in (25– cm).	Can be found in tropical forests, open woodlands, and secondary growth. Small number of individuals associate in groups.	Canal Zone of Panama.	Consists of fruit, tender vegetation, insects, spiders, small vertebrates, and bird eggs.	Not threatened
Pied tamarin *Saguinus bicolor*	Yellowish or white forequarters, grayish brown hindquarters. Bare, black face. Head and body length 6.9–12.2 in (17.5–31 cm), tail length 9.8–17.3 in (25–44 cm).	Can be found in tropical forests, open woodlands, and secondary growth. Three to 12 individuals in a group, tendency toward seasonal reproduction.	Northern Brazil; perhaps northeastern Peru.	Consists of fruit, tender vegetation, insects, spiders, small vertebrates, and bird eggs.	Endangered
Golden-rumped lion tamarin *Leontopithecus chrysopygus*	Mostly black, with gold rump and thighs. Head and body length 7.9–13.2 in (20–33.6 cm), tail length 12.4–15.7 in (31.5–40 cm).	Can be found primarily in tropical forests, less commonly found in secondary forest and areas under partial cultivation. Seasonal breeder.	São Paulo region of Brazil.	Mainly insects and fruit but also eats spiders, snails, small lizards, birds' eggs, and small birds.	Critically Endangered
Black-faced lion tamarin *Leontopithecus caissara*	Black face, long silky pelage. Head and body length 7.9–13.2 in (20–33.6 cm), tail length 12.4–15.7 in (31.5–40 cm).	Can be found primarily in tropical forests, less commonly found in secondary forest and areas under partial cultivation. Seasonal breeder.	Superagui Island, Brazil.	Mainly insects and fruit, but also eats spiders, snails, small lizards, birds' eggs, and small birds	Critically Endangered
Silvery marmoset *Callithrix argentata*	Black-tailed or silvery marmoset, fine, silver pelage. Head and body length 7.1–11.8 in (18–30 cm), tail length 6.8–15.9 in (17.2–40.5 cm).	Can be found in tropical or subtropical forests. Diurnal, quick and jerky movements.	Northern and central Brazil, and eastern Bolivia.	Consists of insects, spiders, small vertebrates, birds' eggs, fruit, and tree exudates.	Not threatened
Tassel-eared marmoset *Callithrix humeralifera*	Pelage is whitish, back is black and flecked with white. Tail is black, underparts orange. Head and body length 7.1–11.8 in (18–30 cm), tail length 6.8–15.9 in (17.2–40.5 cm).	Can be found in tropical or subtropical forests. Diurnal, quick and jerky movements.	Brazil, between Madeira and Tapajós Rivers, south of the Amazon.	Consists of insects, spiders, small vertebrates, birds' eggs, fruit, and tree exudates.	Not threatened

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Organizations

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Eckhard W. Heymann, PhD

▲

Night monkeys
(Aotidae)

Class Mammalia
Order Primates
Family Aotidae

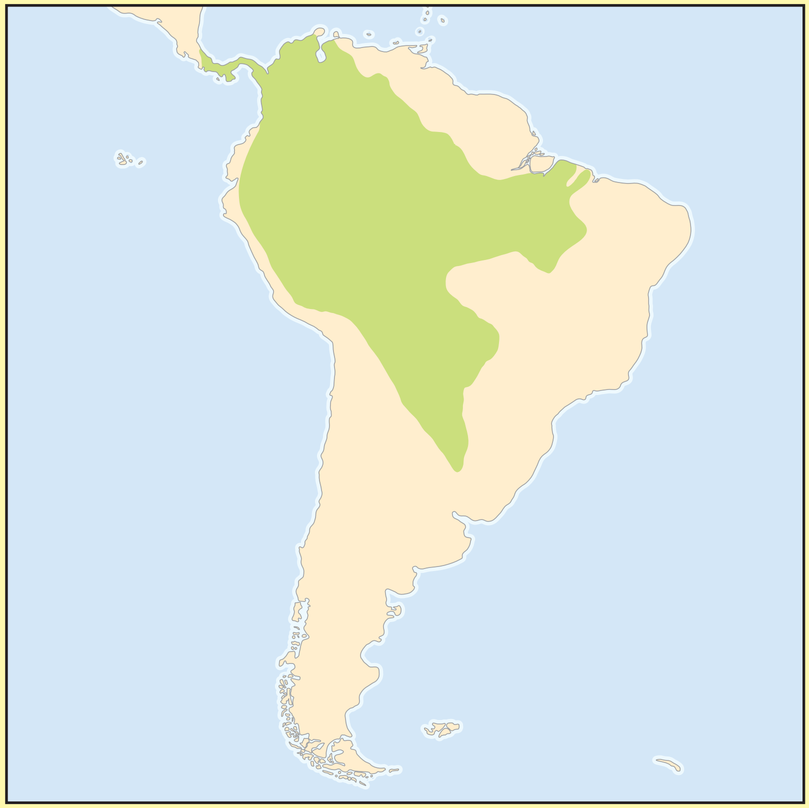
Thumbnail description
Gracile monkeys with a slender body and a rounded head; face flat with short muzzle; nocturnal habits reflected by remarkably large eyes, resulting in the alternate name "owl monkeys," and inconspicuous pelage coloration

Size
Medium-sized monkeys weighing approximately 2 lb (910 g)

Number of genera, species
1 genus; 8 species

Habitat
Evergreen tropical rainforest, gallery forest, and mixed deciduous forest

Conservation status
Vulnerable: 2 species; Data Deficient 1 species



Distribution
After howler monkeys (genus *Alouatta*), this is the second most widely distributed genus among the New World monkeys, occurring over a vast range including Panama and a large part of South America

Evolution and systematics

Traditionally, only a single night monkey species (*Aotus trivirgatus*) was recognized, but chromosomal evidence revealed considerable diversity. This is hardly surprising, given the extensive geographical range covered by *Aotus*. It is now widely accepted that there are between five and nine night monkey species, and eight species can be recognized as a basic minimum. Night monkeys provide a graphic example of a persistent failure to recognize cryptic species among nocturnal primates, because they differ relatively little in visually obvious characters. Molecular evidence indicates that some individual night monkey species diverged at a very early stage and also suggests that there is no close relationship between the night monkey lineage and any other group of New World monkeys. It is hence appropriate to recognize a separate family Aotidae for the night monkeys, rather than just a subfamily (Aotinae). It has been customary to include the titi monkeys (genus *Callicebus*) with the night monkeys in the subfamily Aotinae, but molecular evidence does not indicate any phylogenetic association between *Aotus* and *Callicebus*, so there is no justification for classifying these two genera together.

The night monkeys can be divided into a gray-neck group of four species occurring essentially north of the River Amazon (*Aotus hershkovitzi*, *Aotus lemurinus*, *Aotus trivirgatus* and *Aotus vociferans*) and a red-necked group of four species occurring almost exclusively south of the Amazon (*Aotus azarai*, *Aotus miconax*, *Aotus nancymaae* and *Aotus nigriceps*).

As is the case for New World monkeys, generally, there is very little fossil evidence to document the evolution of night monkeys. However, some fragmentary remains from the early Miocene of the La Venta site in Colombia have been allocated to a species in the modern genus *Aotus* (*Aotus dindinensis*). The lower jaw and teeth closely resemble those of the modern night monkey and a fragment of the skull indicates that large eyes were present, suggesting that nocturnal habits were already present as in living species.

Physical characteristics

The body is slender and covered with dense fine hair, varying in color from gray to brown dorsally and from yellow to

A pair of three-striped night monkeys (*Aotus trivirgatus*). (Photo by © Michael J. Doolittle/The Image Works. Reproduced by permission.)

The three-striped night monkey (*Aotus trivirgatus*) has large eyes to collect a lot of light. A reflective coating behind their eyes reflects the light back out. Their color cones can "read" light both coming in, and after reflection. (Photo by © Michael J. Doolittle/The Image Works. Reproduced by permission.)

The Azari's night monkey (*Aotus azarai*) does not have a prehensile tail. (Photo by Aníbal Parera. Reproduced by permission.)

Azari's night monkey (*Aotus azarai*). (Photo by Peter Oxford/Naturepl.com. Reproduced by permission.)

The three-striped night monkey (*Aotus trivirgatus*) is monogamous. (Photo by © Kevin Schafer/Corbis. Reproduced by permission.)

orange ventrally. Conspicuous white or pale gray patches surround the eyes and the mouth, and the white areas above the eyes are emphasized to varying extents by three spurs of dark fur in the midline and on either side of the crown. The head is rounded and the muzzle does not protrude. The tail, which is not prehensile, is typically longer than the body and densely furred. Average head and body length is 13.5 in (34 cm); average tail length is 15 in (37 cm). There is no sexual dimorphism in size and the average body mass for both sexes is approximately 2 lb (910 g).

Distribution

Widely distributed in Central and South America, from the foothills of the Andes eastward. Occurs in Panama, Nicaragua, Colombia, Peru, Bolivia, Brazil, Venezuela, and Paraguay.

Habitat

Wide distribution throughout evergreen tropical rainforests and certain dry forest areas, between sea level and 10,700 ft (3,200 m).

Behavior

Uniquely among higher primates, night monkeys are typically nocturnal, although cathemeral activity (mixed day and night activity) has been reported for some populations. Several lines of evidence indicate that they have become secondarily adapted for nocturnal life, following divergence from a diurnal ancestor. During the daytime, they typically sleep in tree hollows. Their basal metabolism is relatively low and this is reflected in quite sluggish movement and limited ranging during the nocturnal phase of activity. Olfactory marking is performed with urine and with marking glands. There is a small marking gland on the chest and a diffuse glandular area on the underside of the tail base. Night monkeys also perform "urine washing," in which the palms of the hands and the soles of the feet are impregnated with urine that is then deposited during locomotion.

Feeding ecology and diet

Primarily consume fruits, with a supplement of arthropods (mainly insects) and perhaps small vertebrates and eggs.

The three-striped night monkey (*Aotus trivirgatus*) has the ability to see in color. (Photo by Erwin & Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

Reproductive biology

Field studies have consistently indicated that night monkeys are monogamous, living in pairs along with any immature offspring. The testes are relatively small and spermatogenesis seems to take place with a remarkably low turnover. For *Aotus lemurinus griseimembra*, the ovarian cycle is 15–16 days long and the gestation period was found to be 133 days from a single timed mating. The latter figure is likely to apply to all night monkeys, as an overall range of gestation periods of 122–141 days has been reported for a captive colony containing *Aotus azarai*, *A. lemurinus*, *A. nancymaae*, and *A. vociferans*. Single births are typical. The infant is carried clinging to an adult's fur, and both parents participate in infant carriage.

Conservation status

Two species are listed as Vulnerable (*Aotus lemurinus*, *A. miconax*); one species is Data Deficient (*A. hershkovitzi*).

Significance to humans

Because of their nocturnal habits, night monkeys are relatively protected from human interference, but they may occasionally be hunted for food. Several night monkey species have been used in medical research, notably because they can be infected with human malaria.

1. Nancy Ma's night monkey (*Aotus nancymaae*); 2. Three-striped night monkey (*Aotus trivirgatus*); 3. Gray-bellied night monkey (*Aotus lemurinus*). (Illustration by Bruce Worden)

Species accounts

Gray-bellied night monkey
Aotus lemurinus

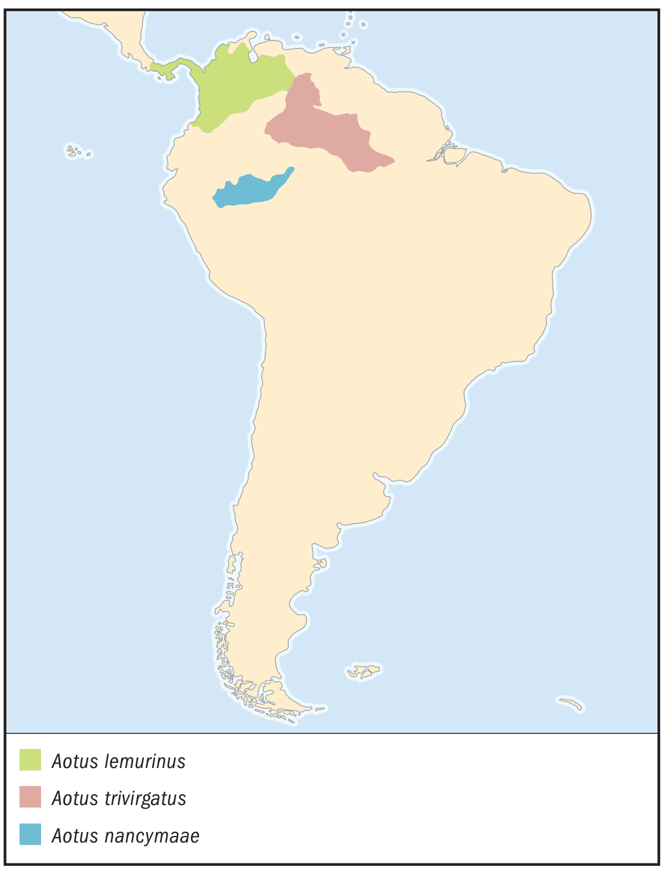
SUBFAMILY
Aotinae

TAXONOMY
Aotus lemurinus (I. Geoffroy, 1843), Quindio, Dept. of Caldas, Colombia. Originally included in the species *Aotus trivirgatus*, the gray-bellied night monkey is now allocated to the separate species *Aotus lemurinus*, containing 4 subspecies (*lemurinus*, *brumbacki*, *griseimembra*, and *zonalis*). It is quite possible that one or more of these subspecies may actually be a full species, and that one may be the same as *A. lemurinus lemurinus*.

OTHER COMMON NAMES
English: Gray-bellied owl monkey, gray-bellied douroucouli; French: Douroucouli à ventre gris; German: Graubauch-nachtaffe.

PHYSICAL CHARACTERISTICS
Fur gray to buff-agouti dorsally and yellow to pale orange ventrally. Because of previous uncertainty over taxonomy, no reliable data on body dimensions are available for this species alone. Body mass: males 2 lb (920 g); females 1 lb 15 oz (875 g).

DISTRIBUTION
Panama, northern Colombia, and northwestern Venezuela.



HABITAT
Predominantly evergreen tropical rainforest, including montane forest.

BEHAVIOR
Nocturnal. Little-studied in the wild.

FEEDING ECOLOGY AND DIET
Feeds primarily on fruits with a supplement of arthropods (mainly insects).

REPRODUCTIVE BIOLOGY
Presumably monogamous. Ovarian cycle 15–16 days long; gestation period approximately 133 days. Single births are typical, but twins often occur.

CONSERVATION STATUS
Listed as Vulnerable.

SIGNIFICANCE TO HUMANS
Occasionally hunted for food. Used quite extensively for medical research. ◆

Nancy Ma's night monkey
Aotus nancymaae

SUBFAMILY
Aotinae

TAXONOMY
Aotus nancymaae Hershkovitz, 1983, Loreto, Peru. Originally included in the species *Aotus trivirgatus* but recognized as a separate species because of chromosomal features.

OTHER COMMON NAMES
English: Nancy Ma's owl monkey, Nancy Ma's douroucouli; French: Douroucouli de Nancy Ma; German: Nancy Ma-Nachtaffe.

PHYSICAL CHARACTERISTICS
Fur gray-agouti dorsally and pale orange ventrally. Facial fur pale gray with three dark brown stripes on the crown. Head and body length: 12.5 in (31 cm); tail length: 15 in (38 cm). Body mass: males 1 lb 12 oz (794 g); females 1 lb 12 oz (780 g).

DISTRIBUTION
Occupies a limited range spanning the border between Peru and Brazil, essentially confined between the Amazon/Marañon in the north and the Juruá in the south.

HABITAT
Evergreen tropical rainforest.

BEHAVIOR
Nocturnal. Little-studied in the wild.

FEEDING ECOLOGY AND DIET
Presumably feeds primarily on fruits with a supplement of arthropods (mainly insects).

REPRODUCTIVE BIOLOGY
Presumably monogamous. Ovarian cycle probably 15–16 days long; gestation period probably approximately 133 days. Single births are typical.

CONSERVATION STATUS
Not regarded as currently threatened.

SIGNIFICANCE TO HUMANS
Occasionally hunted for food. ◆

Three-striped night monkey
Aotus trivirgatus

SUBFAMILY
Aotine

TAXONOMY
Aotus trivirgatus (Humboldt, 1811), Rio Casiquiare, Duida Range, Venezuela.This species once included all night monkeys but it is now restricted to just one of at least 8 species occupying a far smaller geographical range.

OTHER COMMON NAMES
English: Three-striped douroucouli; French: Douroucouli à trois raies; German: Dreistreifennachtaffe.

PHYSICAL CHARACTERISTICS
Fur gray to buff-agouti dorsally and bright orange ventrally. Facial fur pale gray; stripes on crown brown. Conspicuous orange band down the middle of the back. Because of previous uncertainty over taxonomy, no reliable data on body dimensions are available for this species alone. Body mass: males 1 lb 13 oz (810 g); females 1 lb 10 oz (735 g).

DISTRIBUTION
Eastern Colombia, southern Venezuela and part of northern Brazil above the River Amazon.

HABITAT
Predominantly evergreen tropical rainforest.

BEHAVIOR
Nocturnal. Little-studied in the wild.

FEEDING ECOLOGY AND DIET
Presumably feeds primarily on fruits with a supplement of arthropods (mainly insects).

REPRODUCTIVE BIOLOGY
Presumably monogamous. Ovarian cycle probably 15–16 days long; gestation period presumably approximately 133 days. Single births are typical.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Occasionally hunted for food. Used quite frequently for medical research. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Hershkovitz's night monkey *Aotus hershkovitzi*	Pelage is short, dense, semiwoolly, soft. Silver gray to dark gray, underparts brownish. Three dark brown or black lines on face. Small ears, densely furred tail. Head and body length 9.4–14.6 in (24–37 cm), tail length 12.4–15.7 in (31.6–40 cm).	Can be found in forests from sea level to about 6,890 ft (2,100 m). Nocturnal.	Colombia, Dept. of Meta, east side of Cordillera Oriental.	Consists mainly of fruits, nuts, leaves, bark, flowers, gums, insects, and small vertebrates.	Data Deficient
Noisy night monkey *Aotus vociferans*	Pelage is short, dense, semiwoolly, soft. Silver gray to dark gray, underparts brownish. Three dark brown or black lines on face. Small ears, densely furred tail. Head and body length 9.4–14.6 in (24–37 cm), tail length 12.4–15.7 in (31.6–40 cm).	Can be found in forests from sea level to about 6,890 ft (2,100 m). Nocturnal.	Colombia, east of Cordillera Oriental, west of Rio Negro, south to Brazil (north of Amazon-Solimões Rivers).	Consists mainly of fruits, nuts, leaves, bark, flowers, gums, insects, and small vertebrates.	Not threatened
Azari's night monkey *Aotus azarai*	Pelage is short, dense, semiwoolly, soft. Silver gray to dark gray, underparts brownish. Three dark brown or black lines on face. Small ears, densely furred tail. Head and body length 9.4–14.6 in (24–37 cm), tail length 12.4–15.7 in (31.6–40 cm).	Can be found in forests from sea level to about 6,890 ft (2,100 m). Nocturnal.	Bolivia south of Rio Madre de Dios, south to Paraguay and northern Argentina.	Consists mainly of fruits, nuts, leaves, bark, flowers, gums, insects, and small vertebrates.	Not threatened
Andean night monkey *Aotus miconax*	Pelage is short, dense, semiwoolly, soft. Silver gray to dark gray, underparts brownish. Three dark brown or black lines on face. Small ears, densely furred tail. Head and body length 9.4–14.6 in (24–37 cm), tail length 12.4–15.7 in (31.6–40 cm).	Can be found in forests from sea level to about 6,890 ft (2,100 m). Nocturnal.	A small area in Peru between Rio Ucayali and the Andes, south of Rio Marañon.	Consists mainly of fruits, nuts, leaves, bark, flowers, gums, insects, and small vertebrates.	Vulnerable
Black-headed night monkey *Aotus nigriceps*	Pelage is short, dense, semiwoolly, soft. Silver gray to dark gray, underparts brownish. Three dark brown or black lines on face. Small ears, densely furred tail. Head and body length 9.4–4.6 in (24–37 cm), tail length 12.4–15.7 in (31.6–40 cm).	Can be found in forests from sea level to about 6,890 ft (2,100 m). Nocturnal.	Brazil, south of Rio Solimões, west of Rio Tapajós Juruena, west into Peru.	Consists mainly of fruits, nuts, leaves, bark, flowers, gums, insects, and small vertebrates.	Not threatened

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Robert D. Martin, PhD

▲

Sakis, titis, and uakaris

(Pitheciidae)

Class Mammalia
Order Primates
Family Pitheciidae

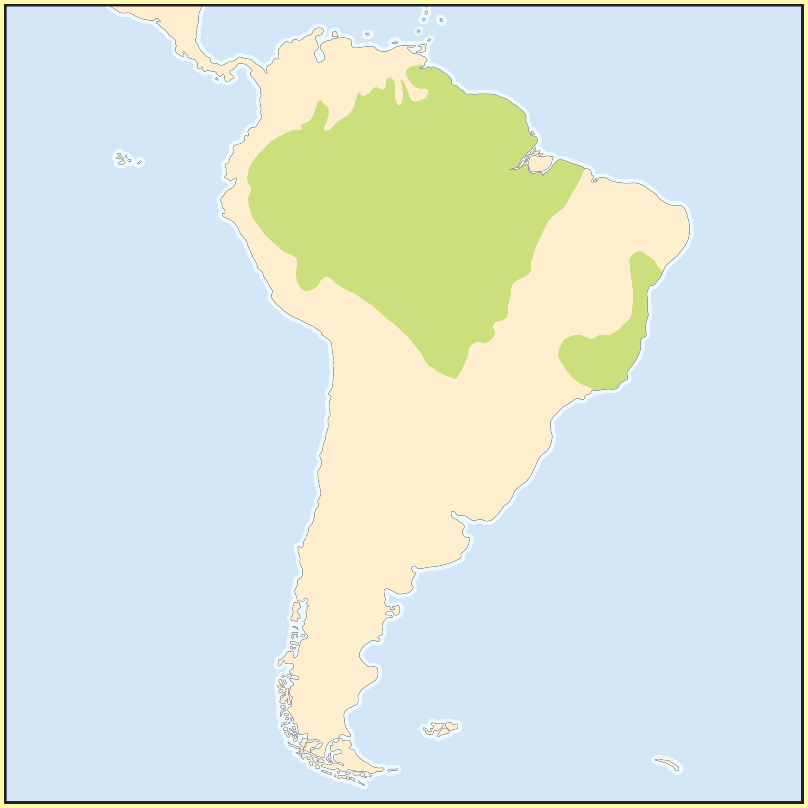
Thumbnail description
Diverse family of small- to medium-sized monkeys with long, thickly haired tails (except *Cacajao*) and long, coarse or dense hair (except *Chiropotes*), which range in color from white, buffy, yellow, and orange to brown, black, gray, and agouti

Size
Length: 9.1–21.7 in (232–550 mm); weight: 1.5–7.6 lb (700–3,450 g)

Number of genera, species
4 genera; 28 species

Habitat
Highland and lowland rainforest, tropical dry forest, liana forest, savanna forest, mountain savanna forest, secondary forest, igapó, várzea, swamp, gallery forest, and disturbed habitat

Conservation status
Critically Endangered: 2 species; Endangered: 1 species; Vulnerable: 9 species; Data Deficient: 2 species



Distribution
Found in South America in the Amazon and Orinoco basins, Atlantic coastal forest of Brazil, parana forests of Bolivia and Paraguay

Evolution and systematics

The platyrrhine family Pitheciidae includes four genera in two subfamilies. The subfamily Pitheciinae includes sakis (*Pithecia*, 5 species, 5 subspecies), bearded sakis (*Chiropotes*, 2 species, 3 subspecies), and uakaris (*Cacajao*, 2 species, 5 subspecies). The subfamily Callicebinae includes only titi monkeys (*Callicebus*, 19 species, 5 subspecies). The genus *Pithecia* is further subdivided into two groups: the *Pithecia pithecia* group containing two subspecies of *Pithecia pithecia*, and the *P. monachus* group (*P. monachus*, 2 subspecies; *P. irrorata*, 2 subspecies; *P. albicans*, and *P. aequatorialis*). *Callicebus* is also further subdivided. Prior to Hershkovitz's revision of the genus in 1990, only three species were recognized. Taxonomies published in 2000 and 2001 modify his revision, listing 19 species in four species groups: the *Callicebus modestus* group (1 species), the *C. donacophilus* group (4 species), the *C. moloch* group (12 species), and the *C. torquatus* group (2 species, 5 subspecies). *Callicebus* taxonomy is in a state of flux.

The saki-uakari group has long been considered a distinctive adaptive radiation and titi monkeys have usually been considered a sister group to it based on both morphological and genetic evidence. Previous classifications have also considered night monkeys (genus *Aotus*) a sister group to the pitheciins, but as of 2001, this genus has been place in its own monogeneric family.

Several fossil primates from early Miocene localities in Argentina (*Soriacebus*, *Proteropithecia*, *Homunculus*, *Carlocebus*), Middle Miocene localities in Colombia (*Cebupithecia*, *Nuciruptor*), and Quarternary localities in the Caribbean (*Xenothrix*, *Antillothrix*, *Paralouatta*) have been aligned with both the Pitheciinae and the Callicebinae. Earlier forms are more primitive and not readily aligned with any extant taxa, but it is possible to identify lineages leading to extant pitheciins in later forms.

Physical characteristics

Pitheciids are small- to medium-sized monkeys. *Callicebus* is the smallest, followed by *Pithecia*, *Chiropotes*, and *Cacajao*. Both *Chiropotes* and *Cacajao* are sexually dimorphic in size, with males 20–23% larger than females. Sexual dichromatism is uncommon, but is found in *Pithecia pithecia* and *P. aequatorialis*.

A black uakari (*Cacajao melanocephalus*) balances on the top of a tree. (Photo by John Giustina. Bruce Coleman, Inc. Reproduced by permission.)

It is most pronounced in *Pithecia pithecia*: males are solid black with a white face and black nose, while females are blackish-agouti with white stripes from under each eye to the corners of the mouth.

Other pitheciids range in color from dark agouti with paler hands and feet and sex-specific patterns of facial hair (*Pithecia* species), black with light to dark brown back and shoulders (*Chiropotes satanas*), silky black with a white nose (*C. albinasus*), reddish orange to orange, or white (*Cacajao calvus*), or black with a reddish brown to orange back, belly, and thighs (*Cacajao melanocephalus*). *Callicebus* is a very diverse genus in terms of coloration. The pelage ranges from black hands (*Callicebus personatus*), or black all over with yellow hands (*Callicebus torquatus*), while other species vary from agouti to roufous to grayish with various facial markings.

The four genera are quite distinct in appearance. *Pithecia* and *Cacajao* have long, coarse, fluffy hair, *Callicebus* has long, dense, fluffy hair, while *Chiropotes* is distinctive in having short body hair. *Pithecia* and *Chiropotes* have long, bushy, nonprehensile tails, *Callicebus* has a long, thickly haired tail, and *Cacajao* is unique in having a short, bushy haired tail that measures only one-third the length of its body. Distinctive beards, bulbous temporal swellings, and distinctive pink scrotums in males and pink vaginal lips in females characterize bearded sakis (*Chiropotes*). The bald uakari (*Cacajao calvus*) is unique in having a bright red, naked face and a bald head

The major defining feature of pitheciids is a shared dental complex. Enormous laterally splayed canines that are functionally separated from the incisors by a diastema are used to open fruits protected by hard, thick husks. The incisors are inclined anteriorly for cropping fruit, and the lower ones are styliform. The molars have low occlusal relief and crenulations. Pitheciids have been characterized as "sclerocarpic foragers" because of their specialization for exploiting heavily protected fruit, such as species of the Brazil nut family (Lecythidaceae).

Distribution

All four pitheciid genera are only found in South America. *Callicebus* has the largest distribution, inhabiting tropical forests in the Amazon and Orinoco basins (*C. moloch* and *C. torquatus* groups), the Atlantic coastal forest in Brazil (*C. personatus*), and the parana forests of Bolivia and Paraguay (*C. donacophilus*). The two *Pithecia* species groups are separated by the Amazon River, with the *Pithecia pithecia* group found in the Guiana Shield north of the Amazon River and east of the Rios Negro and Orinoco, and the *P. monachus* group found

The white-faced saki (*Pithecia pithecia*) does not have a prehensile tail. (Photo by Norman Owen Tomalin. Bruce Coleman, Inc. Reproduced by permission.)

The red bald uakari (*Cacajao calvus rubicundus*) is about the same size as a house cat. (Photo by J. Foott. Bruce Coleman, Inc. Reproduced by permission.)

south of the Amazon and west to the Andean foothills. *Chiropotes* is found north of the Amazon in the Guiana Shield and between Rios Xingu and Garupi south of Amazon (*C. satanas*), while *C. albinasus* is found south of the Amazon in Brazil west of the Rio Xingu. The two species are not sympatric. The genus *Cacajao* is restricted to western Amazon flooded forests, with *Cacajao calvus* inhabiting inundated forests south of the Amazon on whitewater rivers (várzea) in Brazil and Peru, while *C. melanocephalus* is only found in inundated forests on black-water rivers (igapó) north of the Amazon in Brazil and Venezuela.

Habitat

All pitheciid species are predominately or exclusively arboreal, but habitat use by the four genera is variable. Both *Pithecia* and *Callicebus* are found in a wide variety of habitats. *Pithecia* species are found in highland and lowland forests, tropical dry forest, igapó, high várzea, secondary forests, disturbed habitats, liana forest, savanna forest, and mountain savanna forests. *Callicebus* species are found in inundated forests, swamps, and river and lake edges (*C. moloch*), open canopy in mixed, gallery, evergreen, and tall forests near streams (*C. torquatus*), and secondary but not primary forest with low canopy, thickets, and vine tangles in the Atlantic Coastal rainforest (*C. personatus*).

Both *Chiropotes* and *Cacajao* are found in fewer habitat types. *Chiropotes* species are restricted to terra firme, high rainforest, high mountain savanna forest, savanna forest, and high moist forest. They have not been observed in lowland, disturbed, secondary, flooded, or gallery forests. *Cacajao* species are found almost exclusively in igapó and várzea, but have been observed to seasonally migrate to terra firme forest.

Behavior

Pitheciid social organization is quite variable. *Callicebus* is unique among pitheciids in exhibiting a pair-bonded, monogamous social structure, living in groups of 2–6 individuals (adult couple and offspring). *Pithecia* species live in small multimale/multifemale groups. *Chiropotes* lives in

A brown titi (*Callicebus brunneus*) near upper Madre de Dios River in South America. (Photo by © Kevin Schafer/Corbis. Reproduced by permission.)

A southern bearded saki (*Chiropotes satanas satanas*). (Photo by Claus Meyer/Minden Pictures. Reproduced by permission.)

multimale/multifemale groups of 10–30 individuals with a roughly equal sex ratio, while *Cacajao* lives in large multimale/multifemale groups of up to 100 individuals.

Grooming behavior is important in reinforcing social bonds in *Callicebus* and may account for 10% of a day's activity. Group members also twine their tails when sitting together. When aggravated, *Pithecia* exhibits an aggressive display of piloerection, body shaking, an arched posture, and a growling vocalization. *Chiropotes* has a distinctive tail wagging behavior that denotes excitement, and a characteristic high-pitched whistling vocalization. *Cacajao* also exhibits tail wagging and piloerection, and the naked-faced *Cacajao calvus* has the largest repertoire of facial expressions of any platyrrhine.

Callicebus lives in small, well-defined territories that in most species are defended using loud vocalizations (solo male calls and male-female duets). In other species there is overlap of home ranges, and calls are used to define territories without boundary defense. They rarely associate with other primate species, but have been observed occasionally with tamarins (genus *Saguinus*) and marmosets (genus *Callithix*). *Pithecia* generally occupies small home ranges, but some species may have large ones. The home ranges of some species may overlap, while others may have relatively exclusive areas with defined boundaries and little overlap. They have not been observed to form polyspecific associations with other primates. Both *Chiropotes* and *Cacajao* have large home ranges that are not defended. *Chiropotes* has been observed in polyspecific groups with squirrel monkeys (genus *Saimiri*), capuchin monkeys (genus *Cebus*), and *Cacajao*; and *Cacajao* has been observed to associate with squirrel monkeys (genus *Saimiri*), capuchin monkeys (genus *Cebus*), woolly monkeys (genera *Lagothrix*, *Pithecia*, and *Chiropotes*).

Both *Pithecia* and *Chiropotes* have relatively shorter day ranges than do the other two pitheciid species. *Pithecia* has short day ranges, usually less than 0.6 mi (1.0 km). Most *Pithecia* species locomote by vertical clinging and leaping and tend to prefer the lower and middle strata of the forest canopy, although *Pithecia albicans* uses the middle and upper canopy and does little vertical clinging. Some species will forage occasionally on the ground. Day ranges are much longer in *Chiropotes* (0.6–2.8 mi [1.0–4.5 km]), and increase during periods of food scarcity. Groups may fission for feeding. Travel is cohesive but they may also travel in subgroups. *Chiropotes* is an arboreal quadruped that prefers the upper canopy, traveling rapidly between feeding trees and then engaging in intense feeding bouts. *Cacajao* also has very long day ranges (greater than 3 mi [5 km]), and prefers the middle and upper canopy, but will forage on the ground during the dry season due to the paucity of terrestrial mammals in flooded forests. They are arboreal quadrupeds, but employ more leaping and bipedal suspension postures than other pitheciids. All *Callicebus* species are primarily arboreal quadrupeds and rarely forage on the ground. Some species use the lower canopy, some the middle canopy, and some others the upper canopy.

Feeding ecology and diet

The three pitheciin genera, and to a lesser extent *Callicebus*, are specialized seed predators. *Pithecia*, *Chiropotes*, and *Cacajao* all include a large percentage of fruit in their diets, and the majority of these fruit are exploited for the seeds they contain. Most species prefer young seeds from unripe fruit. The

A golden-faced saki (*Pithecia pithecia chrysocephala*). (Photo by Claus Meyer/Minden Pictures. Reproduced by permission.)

A bearded saki (*Chiropotes satanas*) eats a small piece of fruit. (Photo by John Giustina. Bruce Coleman, Inc. Reproduced by permission.)

fruits these primates include in their diets are primarily large, hard, indehiscent fruits with one or a few large seeds, such as the Brazil nut family (Lecythidaceae). *Pithecia* supplements its diet with leaves, flowers, and invertebates, as does *Cacajao*. *Chiropotes* eats fewer leaves, but will eat some invertebrates. Callicebus species eat more fruit pulp and fewer seeds than other pitheciids. Some species supplement their diet with insects while others eat leaves.

Reproductive biology

Saki (*Pithecia*) reproductive biology is variable. All species give birth to single offspring. Some species (*P. pithecia* and *P. monachus*) reproduce seasonally, while others (*P. albicans*) do not. Groups may have a single reproductive female (*P. monachus*) or more than one (*P. pithecia*). Adult coloration may develop in weeks (*P. albicans*), months (*P. pithecia*), or years (*P. monachus*). There is typically no paternal care, although fathers may groom infants. In some species, subadult and adult daughters may help. Offspring are independent at 6–7 months and are weaned at one year of age.

Chiropotes satanas gives birth in the dry season in Suriname and Venezuela. There are occasional copulations year-round with a peak from July to September, and gestation is 4.5–5.5 months. By two months, infants are carried ventrally, but begin a shift to dorsal carrying. Other group members groom infants. At three months, infants are always carried dorsally, and they exhibit some self-locomotion at rest. At six months, infants locomote independently for short distances, but are still carried dorsally for long trips. Infants are fully independent at 10–13 months. *Chiropotes albinasus* does not breed seasonally, but may give birth in February-March or August-September. Adult females exhibit bright red labia during estrus.

In captivity, *Cacajao* mates promiscuously and has seasonal births of single offspring. Females show no external sign of estrus, and gestation length is unknown. Only mothers carry offspring, and infants are carried ventrally for three months, and then are carried dorsally. At 12 months, infants independently locomote but may still sleep with the mother. Suckling and sleeping on proximity to the mother may last two years. The birth season for wild *Cacajao* in Peru is December to March.

Callicebus also breeds seasonally and gives birth to a single offspring. These monkeys are unique among pitheciids in that males provide nearly all of the infant care. Male titis begin carrying infants within 48 hours of birth, and infants return to the mother only to nurse. Infants are carried until 4–6 months of age, and weaning occurs at this time. Offspring reach maturity at 3–4 years, at which time they abruptly leave the natal group. No aggression accompanies the departure.

A bald uakari (*Cacajao calvus*) in the trees of Brazil. (Photo by R. A. Mittermeier. Bruce Coleman, Inc. Reproduced by permission.)

Conservation status

The IUCN lists Miller's monk saki (*Pithecia monachus milleri*) as Vulnerable due to habitat loss, fragmented populations, and declining numbers of adults. The Napo monk saki (*P. monachus napiensis*) is listed as Data Deficient.

The IUCN lists Uta Hick's bearded saki (*Chiropotes satanas utahicki*) as Vulnerable due to habitat loss and the southern bearded saki (*C. satanas satanas*) as Endangered due to habitat loss and the fragmenting and decline of population sizes. The white-nosed bearded saki (*Chiropotes albinasus*) is listed as CITES Appendix I.

Bald uakaris (*Cacajao calvus*) are generally listed as Vulnerable due to severe hunting in many parts of Peru and Brazil. The IUCN also lists the Ucayali bald uakari (*Cacajao calvus ucayalii*) as Vulnerable due to a loss of habitat, and lists three other subspecies, the white bald uakari (*C. calvus calvus*), Novae's bald uakari (*C. calvus novaesi*), and the red bald uakari (*C. calvus rubicundus*) as Endangered due to habitat fragmentation and population decline. All *Cacajao* species are CITES Appendix I.

A number of *Callicebus* species are also listed by the IUCN. Two species, the northern Bahian blond titi (*Callicebus barbarabrownae*) and Coimbra's titi (*C. coimbrai*), are Critically Endangered. Six additional species, Medem's collared titi (*C. medemi*), the southern Bahian masked titi (*C. melanochir*), the black fronted titi (*C. nigrifrons*), the Andean titi (*C. oenathe*), the ornate titi (*C. ornatus*), and the masked titi (*C. personatus*), are considered Vulnerable. One species, the Beni titi (*C. olallae*), is listed as Data Deficient.

Significance to humans

All pitheciid genera are either hunted for food or captured to be sold locally or exported as pets. *Pithecia* and *Chiropotes* are often hunted solely for their long, bushy tails, which are used as dusters.

1. Masked titi (*Callicebus personatus*); 2. Collared titi (*Callicebus torquatus*); 3. White-faced saki (*Pithecia pithecia*); 4. Bearded saki (*Chiropotes satanas*); 5. Dusky titi monkey (*Callicebus moloch*); 6. Bald uakari (*Cacajao calvus*). (Illustration by Marguette Dongvillo)

Species accounts

White-faced saki
Pithecia pithecia

SUBFAMILY
Pitheciinae

TAXONOMY
Pithecia pithecia Linnaeus, 1766, French Guiana.

OTHER COMMON NAMES
English: Flying jack, Guianan saki; Spanish: Parauacu.

PHYSICAL CHARACTERISTICS
Head and body length is 13.2–13.8 in (335–350 mm); tail length is 13.5–17.5 in (342–445 mm); and weight is 27.5–88.2 oz (779–2,500 g). They possess long, coarse, fluffy hair and long, thickly haired, non-prehensile tail. Males are colored black with a white face and black nose. Females possess agouti with white stripes along the sides of the nose.

DISTRIBUTION
Guiana Shield forests north of the Amazon River and east of the Rios Negro and Orinoco.

HABITAT
Primary and secondary forests, tropical dry forests, gallery forests, savanna forests, palm swamps.

BEHAVIOR
Diurnal and predominately arboreal. They live in small multi-male/multi-female groups, and forage in the lower to middle canopy and occasionally on the ground.

FEEDING ECOLOGY AND DIET
Seed predators. Fruit, seeds, flowers, leaves, and invertebrates.

REPRODUCTIVE BIOLOGY
Variable mating system. Females give birth to a single off-spring from December to April. There is no paternal care. Infants are weaned at four months, and are sexually mature at 24–36 months.

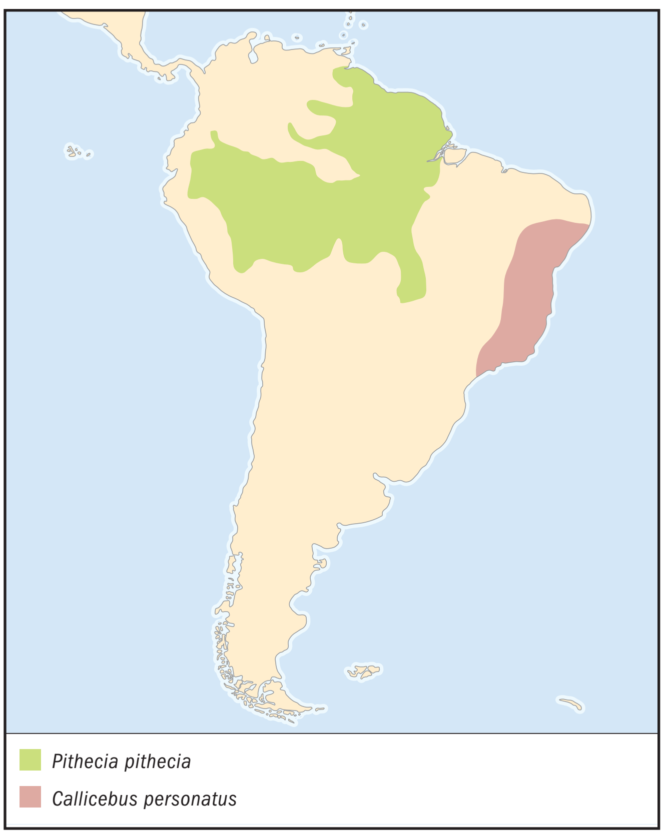
CONSERVATION STATUS
CITES Appendix II. Relatively rare but not threatened.

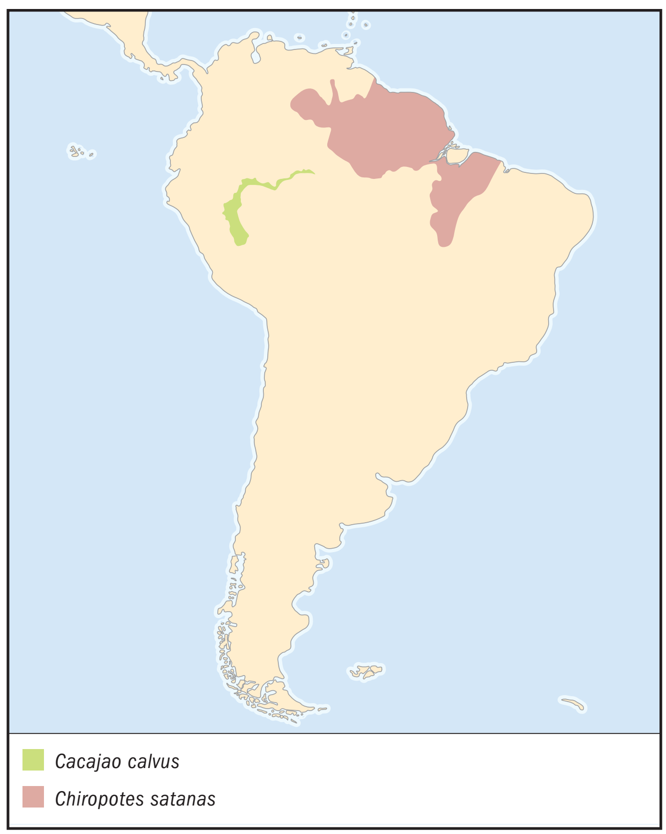
SIGNIFICANCE TO HUMANS
None known. ◆

Bearded saki
Chiropotes satanas

SUBFAMILY
Pitheciinae

TAXONOMY
Chiropotes satanas Hoffmannsegg, 1807, Brazil.





OTHER COMMON NAMES
English: Black bearded saki; French: Saki noire; Spanish: Capuchino del Orinoco, mono capuchino.

PHYSICAL CHARACTERISTICS
Male head and body length is 15.7–18.9 in (400–480 mm); tail length is 15.6–16.1 in (395–410 mm); and weight is 4.8–8.8 lb (2.2–4.0 kg). Female head and body length is 15.0–16.1 in (380–410 mm); tail length is 14.6–16.5 in (370–420 mm); and weight is 4.2–7.3 lb (1.9–3.3 kg). They possess a prominent black beard, temporal swellings, and long, bushy, non-prehensile tail. The coat is black with a brownish red back.

DISTRIBUTION
Guiana Shield forests north of the Amazon River and east of the Rios Negro and Orinoco and south of the Amazon east of the Rio Xingu.

HABITAT
Terra firme forest, igapó, high rainforest, and mountain savanna forest.

BEHAVIOR
Diurnal and arboreal. They live in multimale/multifemale groups of 10–30 individuals, and forages in the middle and upper canopy. The tail is wagged when excited, and they use distinctive, high-pitched whistling vocalization.

FEEDING ECOLOGY AND DIET
Seed predators specializing in large, heavily protected fruit; they also eat fruit pulp and some insects.

REPRODUCTIVE BIOLOGY
Variable mating system. Females exhibit bright red labia during estrus, and give birth to a single offspring from December to April.

CONSERVATION STATUS
The IUCN lists the Uta Hick's bearded saki (*Chiropotes satanas utahicki*) as Vulnerable due to habitat loss and the southern bearded saki (*C. satanas satanas*) as Endangered due to habitat loss and the fragmenting and decline of population sizes.

SIGNIFICANCE TO HUMANS
None known. ◆

Bald uakari
Cacajao calvus

SUBFAMILY
Pitheciinae

TAXONOMY
Cacajao calvus I. Geoffroy, 1847, Brazil.

OTHER COMMON NAMES
English: Bald-headed uakari, red-and-white uakari; Spanish: Huapo colorado, mono ingles.

PHYSICAL CHARACTERISTICS
Male head and body length is 21.3–22.1 in (540–560 mm); tail length is 5.9–6.3 in (150–160 mm); and weight is about 7.6 lb (3.5 kg). Female head and body length is 21.3–22.4 in (540–570 mm); tail length is the same as males; and weight is about 6.3 lb (2.9 kg). They have long, coarse, fluffy hair, white in *Cacajao calvus calvus* to orange-red in *C. c. rubicundus*. The tail is one-third the length of the body. The face and head is bald and pink to scarlet in color.

DISTRIBUTION
Flooded white water (várzea) forests north of the Amazon in Venezuela, Brazil.

HABITAT
Found primarily in flooded white water (várzea) forests north of the Amazon.

BEHAVIOR
Diurnal and arboreal. They forage on the ground during the dry season. The tail is wagged when excited. They have a large repertoire of facial expressions.

FEEDING ECOLOGY AND DIET
Seed predators specializing in large, hard-husked fruits. They also eat fruit pulp, flowers, and insects.

REPRODUCTIVE BIOLOGY
Variable mating system. They live in large multimale/multifemale groups in the wild. Promiscuous mating and seasonal births of single offspring is observed in captivity. Infants are weaned at 15–21 months. Females sexually mature at 43 months, males at 66 months.

CONSERVATION STATUS
IUCN lists the bald uakari (*Cacajao calvus*) as Vulnerable due to over-hunting. The IUCN also lists the Ucayali bald uakari (*Cacajao calvus ucayalii*) as Vulnerable due to a loss of habitat, and lists three other subspecies, the white bald uakari (*C. calvus calvus*), Novae's bald uakari (*C. calvus novaesi*), and the red bald uakari (*C. calvus rubicundus*) as Endangered due to habitat fragmentation and population decline. All *Cacajao* species are CITES Appendix I.

SIGNIFICANCE TO HUMANS
Uakaris are hunted for food and kept as pets. ◆

Dusky titi monkey
Callicebus moloch

SUBFAMILY
Callicebinae

TAXONOMY
Callicebus moloch Hoffmannsegg, 1807, Brazil.

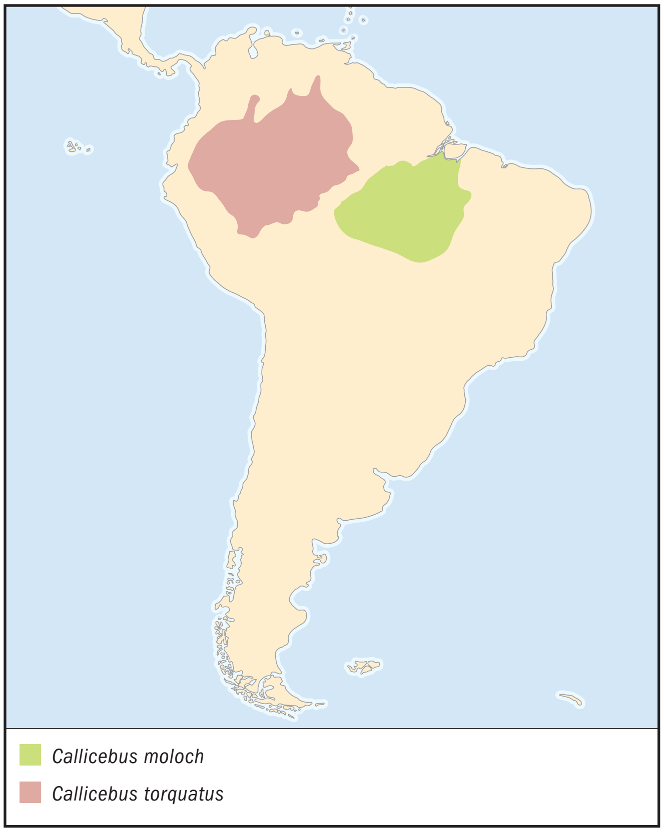
OTHER COMMON NAMES
Spanish: Mono tití, tocón.

PHYSICAL CHARACTERISTICS
Head and body length is 13.6–13.7 in (345–348 mm); tail length is 17.0–17.7 in (432–449 mm); and weight is 24.7–42.3 oz (700–1,200 g). Their coat is buffy or grayish agouti with contrasting reddish brown or orange sideburns and underparts. They possess a long, thickly haired, non-prehensile tail.

DISTRIBUTION
Amazon basin south of the Amazon River in Brazil.

HABITAT
Gallery, swamp, and flooded forests. Lower canopy levels.

BEHAVIOR
Diurnal and arboreal. Small territories are defended by vocal duets of mated pair at daybreak. They forage in dense tangles of vegetation in the lower levels of the canopy, but will forage



higher occasionally. Group members will twine tails together when sleeping, grooming, and dueting.

FEEDING ECOLOGY AND DIET
Fruit, leaves, and insects. They are the only largely folivorous small monkey.

REPRODUCTIVE BIOLOGY
Monogamous. Females gives birth to a single offspring during November–March. Males carry infants the majority of the time, beginning at birth. Infants are weaned at eight months, sexually mature at 30 months, and both sexes leave the group at three years of age.

CONSERVATION STATUS
CITES Appendix II. Common, widespread distribution; not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Collared titi
Callicebus torquatus

SUBFAMILY
Callicebinae

TAXONOMY
Callicebus torquatus Hoffmannsegg, 1807, Brazil.

OTHER COMMON NAMES
English: Widow monkey, yellow-handed titi; Spanish: Cotoncillo, mono viudo, tocón, viduita.

PHYSICAL CHARACTERISTICS
Head and body length is 9.1–14.2 in (232–260 mm); tail length is 16.7–19.3 in (425–493 mm); and weight is 38.8–52.9 oz (1,100–1,500 g). They have a dark brown body, black tail, yellow hands, and a white collar around the neck. The tail is long, thickly haired, and non-prehensile.

DISTRIBUTION
Western Amazon Basin lowlands of Colombia, Venezuela, Peru, and Brazil.

HABITAT
Primary and secondary terre firme forests, forests on white sands and black-water streams.

BEHAVIOR
Diurnal and arboreal; very active. Small territories are defended by vocal duets of mated pair at daybreak. Group members twine tails together when sleeping, grooming, and dueting. They forage in the middle and upper canopy and rest in the lower canopy.

FEEDING ECOLOGY AND DIET
Fruit and seeds, leaves, and insects.

REPRODUCTIVE BIOLOGY
Monogamous. Females give birth to a single offspring at the beginning of the rainy season. Males carry infants the majority of the time, beginning at birth. Infants are weaned at 4–5 months. Females become sexually mature at 24–36 months, males at 24–42 months. Both sexes leave the group at three years of age.

CONSERVATION STATUS
CITES Appendix II. Patchily distributed, locally common; not threatened

SIGNIFICANCE TO HUMANS
None known. ◆

Masked titi
Callicebus personatus

SUBFAMILY
Callicebinae

TAXONOMY
Callicebus personatus E. Geoffroy, 1812.

OTHER COMMON NAMES
Spanish: Guigoacute.

PHYSICAL CHARACTERISTICS
Head and body length is 12.2–16.5 in (310–420 mm); tail length is 16.5–21.7 in (418–550 mm); and weight is 34.2–58.2 oz (970–1,650 g). They have a black face, hands, and feet. The body is grayish to yellowish or orange, with a long, thickly haired, non-prehensile tail.

DISTRIBUTION
Atlantic coastal forest of Brazil.

HABITAT
Primary and secondary forest.

BEHAVIOR
Diurnal and arboreal. Small territories are defended by vocal duets of mated pair at daybreak. Group members twine tails together when sleeping, grooming, and dueting. They feed mainly in small-crowned trees, and spend the majority of the day resting.

FEEDING ECOLOGY AND DIET
Fruit, leaves, and flowers. May eat very small amount of insects.

REPRODUCTIVE BIOLOGY
Monogamous. Females give birth to single offspring during August–October. Males carry infants the majority of the time, beginning at birth.

CONSERVATION STATUS
IUCN Red List lists them as Vulnerable due to habitat loss. Also listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
White-nosed bearded saki *Chiropotes albinasus* English: White-nosed saki	Black body and tail and white nose. Long thickly haired tail. Head and body length 16.2–18.5 in (41.2–47 cm), tail length 15.0–17.7 in (38–45 cm), weight 4.9–7.3 lb (2.2–3.3 kg).	Diurnal and arboreal in groups of 2 to 26. Found in primary forest and igapo.	South America, south of the Amazon River and between the Madiera and Xingu Rivers.	Seed-eaters, specializing in large hard husked fruits.	Not listed by IUCN, but listed as CITES Appendix I
Black uacari *Cacajao melanocephalus* English: Black-headed uacari; Spanish: Uacari-preto, chucuto	Black face and head with brown hind limbs, back, and tail. The tail is thickly haired but short (one-third the body length).	Diurnal and arboreal in large groups. Primarily found in igapo forests but will move to terra firme forest seasonally.	South America, north of the Amazon River in Colombia, Venezuela, and Brazil.	Seed-eaters specializing in large hard husked fruits.	Not listed by IUCN
Monk saki *Pithecia monachus* Spanish: Mico volador, huapo negro, oso mono	Blackish or gray body with reddish beard and underparts and pale hands and feet. White stripe down each side of the nose. Males distinguished by buffy crown hairs. Long thickly haired tail. Head and body length 14.6–18.9 in (37–48 cm), tail length 15.9–19.7 in (40.4–50 cm), weight 2.9–6.8 lb (1.3–3.1 kg).	Diurnal and arboreal in small groups. Primary lowland terra firme forest and some varzea.	Upper Amazon basin of Colombia, Ecuador, Peru, Bolivia, and Brazil west of the Rio Tapajòs.	Eats primarily fruit and seeds, also small amounts of leaves, flowers, insects.	One subspecies Vulnerable due to habitat loss; one subspecies Data Deficient
Red titi *Callicebus cupreus*	Body buffy brown with reddish orange underparts. Long thickly haired tail. Head and body length 12.0–14.2 in (30.4–36 cm), tail length 13.1–17.7 in (33.4–45 cm), weight 2.56–2.60 lb (1.16–1.18 kg).	Monogamous and territorial, found in tropical rainforest in the western Amazon basin.	Peru, Brazil, Ecuador, and Colombia.	Fruit and leaves.	Not listed by IUCN
Brown titi *Callicebus brunneus*	Reddish brown back and sideburns, blackish head, limbs, and tail with pale tip. Tail long and thickly haired. Head and body length 12.3–3.6 in (31.2–34.5 cm), tail length 14.6–17.3 in (37.1–44 cm), weight 29.8–30.0 oz (845–850 g).	Monogamous and territorial, found in riverine, flooded, and bamboo forests.	Amazon basin in Peru, Brazil, and Bolivia.	Fruit, leaves, insects, and flowers.	Not listed by IUCN

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Organizations

Conservation International. 1919 M Street, NW, Suite 600, Washington, DC 20036 United States. Phone: (202) 912-1000; 1 (800) 406-2306. Web site: <http://www.conservation.org>

Primate Center Library, Wisconsin Primate Research Center. 1200 Capitol Court, Madison, WI 53715-1299 United States. Phone: (608) 263-3512. Fax: (608) 263-4031. E-mail: library@primate.wisc.edu Web site: <http://www.primate.wisc.edu/pin/>

World Wildlife Federation (WWF)—The Conservation Organization. 1250 24th Street NW, Washington, DC 20037-1193 United States. Phone: (202) 293-4800. Fax: (202) 293-9211. Web site: <http://www.panda.org>

Brian W. Grafton, PhD

Howler monkeys and spider monkeys
(Atelidae)

Class Mammalia
Order Primates
Suborder Anthropoidea
Family Atelidae

Thumbnail description
The largest New World monkeys, possess prehensile tails; range in color from pale blonde and light gray to black; some have completely black faces, others have pink and white facial mottling

Size
Ateles: head and body length 15–25 in (38–64 cm), tail length 20–35 in (51–89 cm), 13.2 lb (6 kg). *Brachyteles:* head and body length: 18–25 in (46–64 cm), tail length 23–36 in (59–92 cm), 15.4–33 lb (7–15 kg); *Alouatta:* head and body length 22–36 in (56–92 cm), tail length 20–35 in (51–89 cm), 8.8–22 lb (4–10 kg). *Lagothrix:* head and body length: 20–35 in (51–69 cm), tail length 23–28 in (59–72 cm), 12–24 lb (5.5–10.8 kg)

Number of genera, species
5 genera; 22–24 species

Habitat
Gallery forest, deciduous and semi-deciduous rainforest, some species also found in mangrove swamps or secondary forest

Conservation status
Critically Endangered: 3 species; Endangered: 3 species; Vulnerable: 5

Distribution
Mexico through Central and South America

Evolution and systematics

Mid-Miocene deposits of Colombia have yielded material assigned to the fossil genus *Stirtonia*, but there is little else in the way of fossil Atelidae until more recent Pleistocene fossils from caves in eastern Brazil. One of these, *Caipora bambuiorum* is considered to be a large juvenile with a distinctly *Ateles*-like crania. Another, *Paratopithecus brasiliensis*, is an even larger (approximately 55 lb, or 25 kg) adult, whose post-crania resembles extant *Ateles* and *Brachyteles* and some skeletal fragments found in the 1800s in the state of Minas Gerais. The crania of *Paratopithecus* resembles extant *Alouatta*, however, leading to uncertainties in interpreting such a mosaic of traits.

The Atelidae is now widely accepted as a monophyletic family, although some prior classifications included variously Pithecinae, Callicebinae, and Aotinae along with the Alouattinae and Atelinae. *Alouatta* has typically been distinguished from the other genera, but there is still controversy over the phylogenetic relationships among the atelins. Morphological analyses group *Ateles* and *Brachyteles* in a clade separate from *Lagothrix*, while molecular data suggests a *Brachyteles/Lagothrix* clade. Indeed, the karyotypes of these two genera are similar (2n=62 chromosomes), and differ from *Ateles*, which varies from 2n=32 to 2n=34 chromosomes.

Like many other primates, the Atelidae has recently undergone a major taxonomic revision. The result, for the most part, has been the splitting of previously recognized subspecies into distinct species, and in the case of *Lagothrix*, splitting the yellow-tailed woolly monkey, *L. flavicauda*, into a separate genus, *Oreonax flavicauda*. In many cases, the reclassifications have been prompted by new molecular analyses, but re-examinations of museum specimens have also played a role.

Physical characteristics

The Atelidae are the largest New World primates. In *Alouatta* and *Lagothrix*, females are much smaller than males, while in *Ateles* and *Brachyteles*, males and females are more similar to one another in body size. All of the Atelidae possess prehensile tails, which are bare on the distal underside. The tails are very sensitive, and are used for grasping much like an extra hand. All of the atelids also have 36 teeth, with a dental formula of (I2/2 C1/1 P3/3 M3/3). The relative size

A variegated spider monkey (*Ateles belzebuth hybridsus*) surveys the land from above. (Photo by Animals Animals ©Mella Panzella. Reproduced by permission.)

and shapes of their teeth, as well as their jaws and chewing muscles, vary with their respective feeding adaptations.

Atelidae range in color from pale buff or gray (*Brachyteles*) to dark black (some *Alouatta* and *Ateles*). Some species of *Alouatta* are sexually dichromatic in body color. *Alouatta*, *Lagothrix*, and *Brachyteles arachnoides* have completely black faces. *Oreonax* has a lighter muzzle, many species of *Ateles* have distinctly paler eye patches, and *Brachyteles hypoxanthus* has pink and white patches of skin in variable patterns on the face. The latter also exhibit variation in pigment on the scrotum.

In both *Ateles* and *Brachyteles* females, the clitoris is pendulous and elongated. Male *Brachyteles* also have relatively large testes. Both of these genera also have long hooked fingers, and long limbs and tails relative to their bodies. *Lagothrix* and *Alouatta* have more compact bodies and limbs, and relatively shorter tails. *Lagothrix* travels by suspensory locomotion much less than *Ateles* or *Brachyteles*, but is faster and more agile than *Alouatta*. *Alouatta* possesses an enlarged hyoid bone, which contributes to the projection of long distance roars. *Alouatta* also has an elongated hindgut associated with the slow rate of food passage.

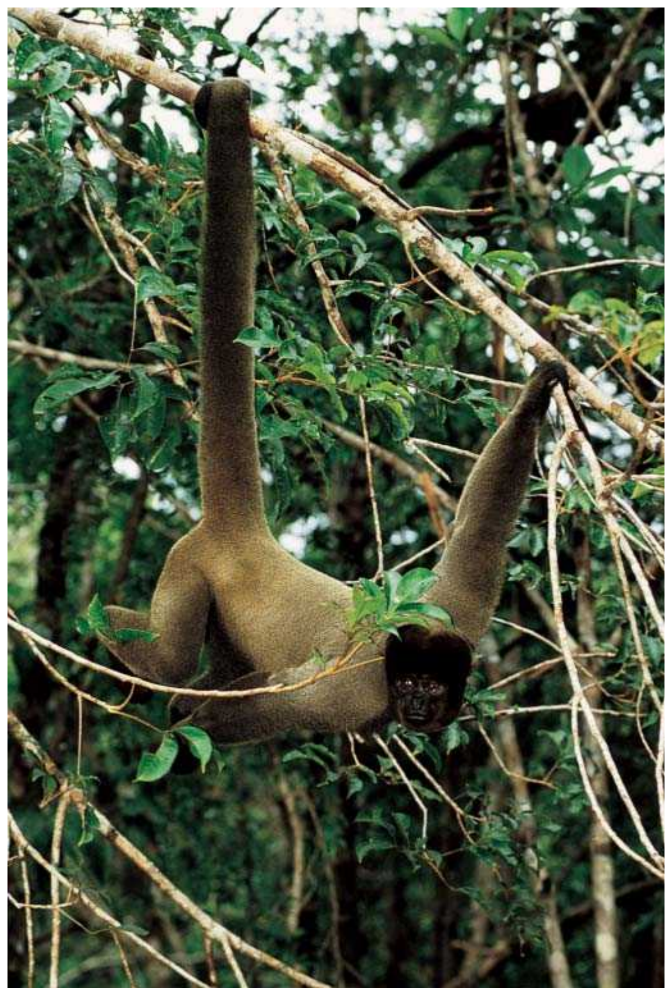
Distribution

The family is found only in Central and South America. Howler monkeys (genus *Alouatta*) have the most extensive distribution, which ranges from southern Mexico in the north to northern Argentina in the south. Spider monkeys (genus *Ateles*) occur from southern Mexico, through Central America and the Amazon. Woolly monkeys (genus *Lagothrix*) are restricted to the Amazon, with the recently recognized genus *Oreonax*, or the yellow-tailed woolly monkey, found only in the northeastern montane cloud forest of Peru. Muriquis (genus *Brachyteles*) are found only in the southeastern Atlantic forest of Brazil.

Howler monkeys occur sympatrically with one, and sometimes two of the other genera. *Alouatta* is the only genus in this family that occurs sympatrically with *Brachyteles*. In some regions in the Amazon, *Alouatta*, *Ateles*, and *Lagothrix* are found together.

Habitat

All species are arboreal, although *Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix* have been observed to descend to the ground to eat, drink, play, and travel for brief periods. With the exception of *Oreonax*, they are found in a wide variety of habitats. *Alouatta* and *Brachyteles* in particular are still found in disturbed and secondary patches of forest, where their ability to consume large quantities of leaves may contribute to their persistence. *Lagothrix* and *Ateles* are more



Humboldt's woolly monkey (*Lagothrix lagotricha*) climbs in the trees in the Amazon. (Photo by John Giustina. Bruce Coleman, Inc. Reproduced by permission.)

The black spider monkey (*Ateles paniscus*) rests for the majority of the day. (Photo by Michael P. Fogden. Bruce Coleman, Inc. Reproduced by permission.)

restricted to primary tropical rainforest, although some species of *Ateles* are also found in semi-deciduous and degraded forest patches.

Atelids appear to prefer the upper canopy, but they also use their tails to exploit foods at lower levels in the forest. They tend to rest on secure branches, but are adept at feeding from terminal branches and lianas.

Behavior

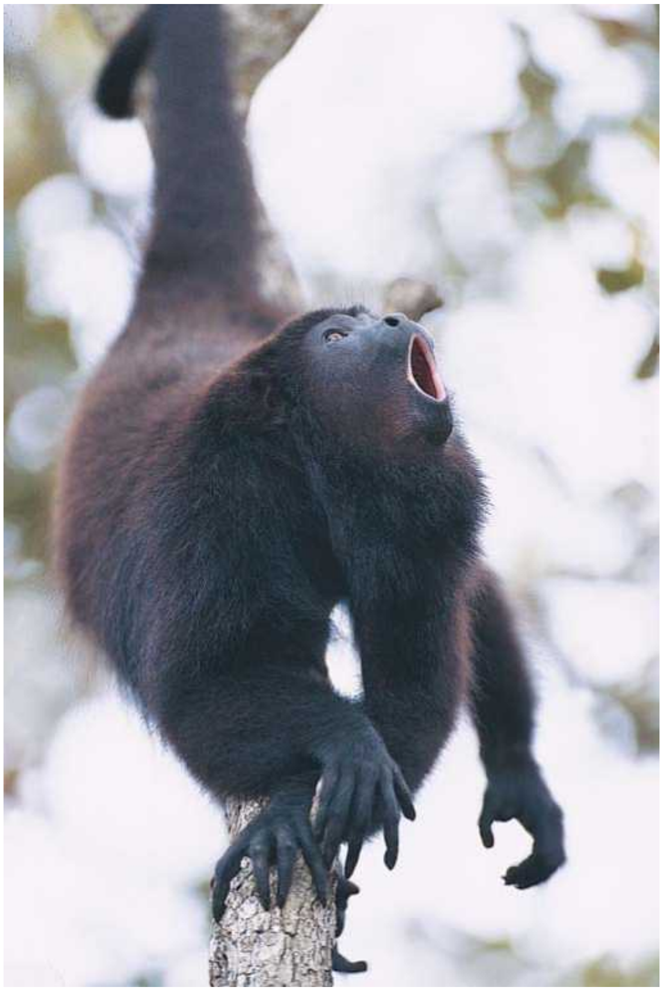
All species live in multimale, multifemale groups, although one-male, multifemale groups of *Alouatta* are also common. In the three well-known atelin genera (*Ateles*, *Brachyteles*, and *Lagothrix*), males are philopatric, while females disperse from their natal groups to join other groups of males. In *Alouatta*, both males and females disperse from their natal groups, usually to establish new troops. Female red howler monkeys (*Alouatta seniculus*) may be retained in their natal troops, while males sometimes disperse in pairs to establish new troops together.

Alouatta are renowned for their loud, long-distance roars. Neighboring troops engage in howling displays, often, but not exclusively, at the boundaries of their ranges. Howler monkey calls can be heard by humans as far as 0.6 mi (2 km) away. *Ateles* and *Brachyteles* have large repertoires of vocalizations, including a long-distance call that resembles a horse's whinny, and an alarm call that resembles a dog's bark. They also have softer, less far ranging "chuckles," which may help them to maintain contact with one another while they are spread out during travel and foraging.

None of the species defend exclusive territories, although encounters between groups, especially of *Alouatta*, can be highly aggressive. In *Lagothrix*, *Ateles*, and *Brachyteles*, large neighboring groups exploit large, overlapping home ranges. Home range overlap is greater at high population densities. Home range sizes vary from 25 acres (10 ha) in *Alouatta* to over 2,220 acres (900 ha) in woolly monkeys and muriquis living in continuous forest in the Amazon and southern Atlantic forest, respectively.

All of the genera are primarily diurnal. Observers that leave the monkeys asleep at dusk often find them in the exact same positions the next morning. Activity patterns differ with climate and season. In general, bouts of morning traveling and feeding are followed by mid-day siestas, and then more traveling and feeding before the groups settle down for the night. Howler monkeys devote up to 70% of their daylight hours to resting, and travel shorter distances each day than the other genera. Spider monkeys and muriquis devote about half of the day to resting, and can travel up to 1.9 mi (3 km) in a day. Woolly monkeys are intermediate in their resting and traveling habitats, at least at the sites where they have been studied to date.

The Venezuelan red howler monkey (*Alouatta seniculus*) lives in groups of about ten. (Photo by Rick Sullivan. Bruce Coleman, Inc. Reproduced by permission.)



The Mexican black howler monkey (*Alouatta pigra*) uses the hyoid bone to amplify its call. (Photo by Tom & Pat Leeson/Photo Researchers, Inc. Reproduced by permission.)

Feeding ecology and diet

All species show clear preferences for ripe fruit when it is available, and supplement their diets with various quantities of leaves. Woolly monkeys at La Macarena, Colombia also consume substantial quantities of insects. Other foods, such as flowers and nectar, and new shoots are eaten when available, while bark and bamboo supplement diets during periods of preferred food scarcity.

Howler monkeys are by far the most folivorous, but the proportion of leaves in their diets varies greatly by habitat. Sympatric species exhibit considerable overlap in diet, feeding on many of the same fruit, leaf, and flower species, sometimes from the same trees or lianas. There are interesting parallels in the proportion of fruits versus leaves in the annual diets of sympatric spider monkeys and howler monkeys, on the one hand, and those of sympatric muriquis and howler monkeys, on the other hand. In each pair, the howler monkeys are substantially more folivorous than either spider monkeys or muriquis.

There is also extensive intraspecific variation in diets. For example, populations of southern muriquis inhabiting disturbed or regenerating forest fragments devote up to 70% of their feeding time to leaves, whereas those inhabiting undisturbed, continuous forest devote up to 70% of their feeding time to fruits. The latter also utilize much larger home ranges, and occur at much lower population densities. Whether low population density permits them to maintain a more frugivorous diet by expanding their home range, or whether undisturbed forests have more abundant fruit is not yet known.

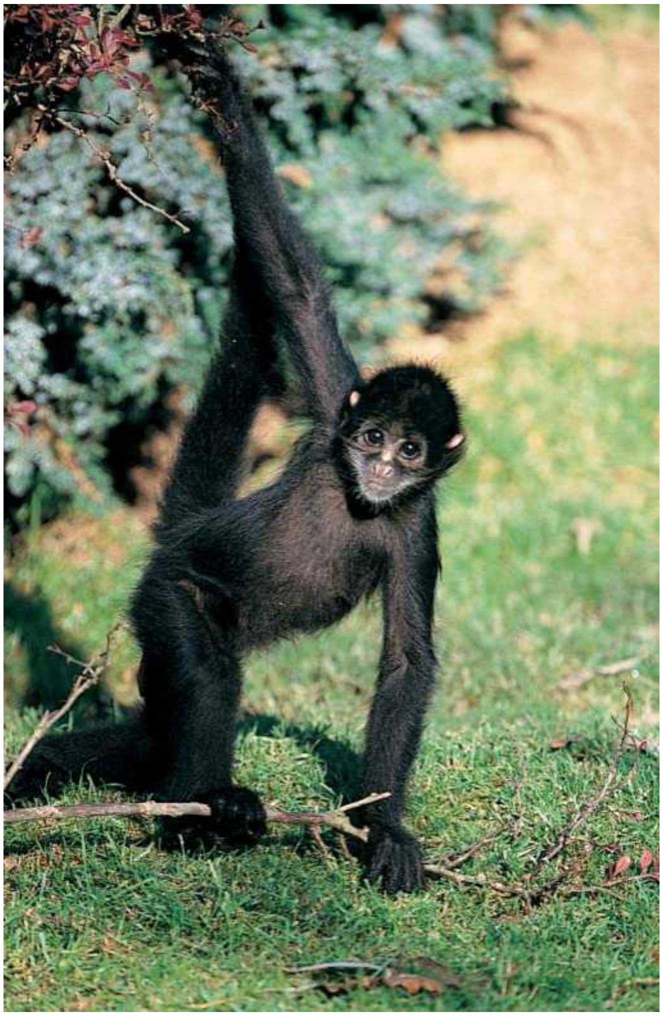
All genera possess prehensile tails, which permit them to feed for long periods of time in suspended postures. Secured by their tails, they can access foods close to the ground or from plants and branches that are too small or flimsy to support their body weights. Their tails also free up their hands, which they can use to sort foods and bring them to their mouths. The atelins also travel by suspensory locomotion, using their arms and tails to swing through the canopy. Suspensory locomotion permits them to travel long distances rapidly, and may contribute to their ability to monitor dispersed patches of preferred fruits. Howler monkeys are quadrupedal, traveling much shorter distances more slowly than the atelins.

Reproductive biology

Females exhibit proceptive behaviors, which in *Brachyteles* and *Ateles* are now known to correspond with their ovarian cycles. Males frequently inspect the genitalia of females by visual and olfactory means. Copulations sometimes occur with the females sitting, instead of standing as occurs in most other primates.

Female atelins typically mate with multiple partners, although the degree to which single males monopolize access to females and exclude other males from mating varies greatly. In multimale troops of red howler monkeys, the alpha male can account for 100% of all fertilizations, resulting in the genetic equivalent of a single-male troop. In woolly monkeys

Venezuelan red howler monkeys (*Alouatta seniculus*) have deep set lower jaws. (Photo by Tom Brakefield/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)



A Colombian black spider monkey (*Ateles fusciceps robustus*) grasps a tree branch. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

and spider monkeys, high-ranking males account for most observed copulations. In muriquis, females mate with multiple partners, often one right after the other, and there is no evidence that males compete overtly with one another for access to mates.

There is no evidence of paternal or allo-parental care among the atelins. However, male howler monkeys will sometimes carry infants or position themselves between infants and extra-troop males, which may threaten infants in their efforts to take over female troops.

Reproductive seasonality varies widely across species and populations of the same species, with a tendency for more seasonal reproduction in more seasonal habitats. It is unclear whether reproductive seasonality reflects maternal condition at the time of conceptions, or the availability of food at the time of weaning. The tendency is for births to occur in the dry season when preferred fruits and new leaves are scarcest, and both conceptions and weaning to occur in the rainy season when preferred foods are most abundant.

Gestation length ranges from 6 months in *Alouatta*, to 7 months in *Ateles*, to 7.2 months in *Brachyteles*. Average interbirth intervals range from 2 years in *Alouatta* to 3 years in the atelins. Age at first reproduction for females ranges from about 4 years in *Alouatta* to at least 9 years in *Brachyteles*.

Conservation status

Both species of *Brachyteles*, along with the recently recognized genus, *Oreonax*, are classified as Critically Endangered based on their highly restricted distributions, small population size, and deteriorating habitats. *Brachyteles* is the only genus of Atelidae endemic to the Brazilian Atlantic forest. The brown howler monkey, *Alouatta guariba*, is also endemic to the Atlantic forest, and is classified as Vulnerable. The status of *Brachyteles hypoxanthus* is probably more critical than that of *B. arachnoides* because the latter still retains relatively large populations in protected forest. Population estimates for *Brachyteles hypoxanthus* are under 500 individuals, with nearly 200 found in one small reserve in Minas Gerais. *Oreonax* population size is estimated at fewer than 300 individuals.

A black howler monkey (*Alouatta caraya*) emits a loud vocalization. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

The female black howler monkey (*Alouatta pigra*), despite what the name implies, is actually tan in color. (Illustration by Jarrod Erdody)

Three species are classified as Endangered (*Alouatta coibensis*, *Ateles marginatus*, and *A. hybridus*) and five species are classified as Vulnerable (*Alouatta guariba*, *Ateles belzebuth*, *Lagothrix cana*, *L. lugens*, and *L. poeppigii*). Local populations of several subspecies are also considered to be Endangered or Vulnerable. In all cases, restricted geographic distributions coupled with habitat destruction and hunting pressures contribute to the precariousness of their futures.

The large body size and large group size of atelid make them attractive prey to hunters. In addition to the toll that hunting takes on local populations, many have suffered due to habitat destruction and fragmentation. The construction of roads increases access for hunters and degrades habitats, while the cutting and burning of forest for pasture and agriculture.

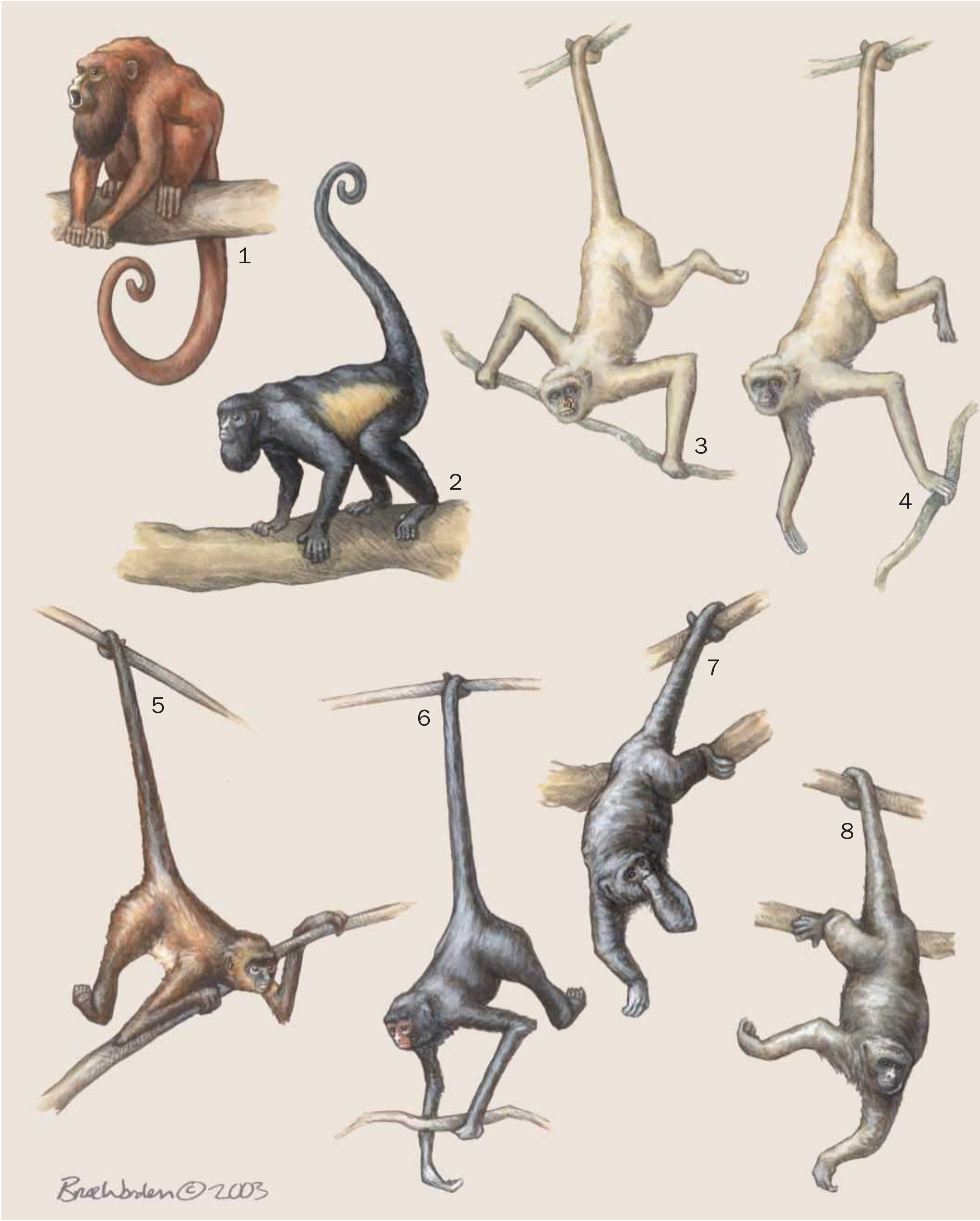
Conservation efforts are widespread, and include the establishment of protected parks and reserves as well as legislation that prohibits hunting. However, enforcement of prohibitions is often impeded by insufficient funds. Conservation education efforts and international collaborations between habitat countries and nongovernmental organizations (NGOs) can be effective, but require long-term commitments at all levels.

Significance to humans

Atelidae are represented in the art and legends of the people they live nearby. Their large body size and social habits have probably always made them a source of prized meat. The large testes of *Brachyteles* were associated with sexual potency, and made into purses by hunters.

None of the Atelidae are considered to be agricultural pests or dangerous to humans. The docile behavior of *Ateles* and *Brachyteles* also contribute to their desirability as pets.

A Geoffroy's spider monkey (*Ateles geoffroyi*) in the trees of Costa Rica. (Photo by Animals Animals ©John Pontier. Reproduced by permission.)



1. Venezuelan red howler monkey (*Alouatta seniculus*); 2. Mantled howler monkey (*Alouatta palliata*); 3. Northern muriqui (*Brachyteles hypoxanthus*); 4. Southern muriqui (*Brachyteles arachnoides*); 5. Geoffroy's spider monkey (*Ateles geoffroyi*); 6. Peruvian spider monkey (*Ateles chamek*); 7. Gray woolly monkey (*Lagothrix cana*); 8. Colombian woolly monkey (*Lagothrix lugens*). (Illustration by Bruce Worden)

Species accounts

Mantled howler monkey
Alouatta palliata

SUBFAMILY
Mycetinae

TAXONOMY
Mycetes palliata (Gray, 1849), Nicaragua.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Black, with a "fringe" on flanks of long gold or brown hair. Backward forehead hair forms a straight crest on crown.

DISTRIBUTION
Mexico through Central America to western Colombia and Ecuador.

HABITAT
Evergreen rainforest, dry decidious forest in lowland and some mangrove forest.

BEHAVIOR
Mantled howler monkeys live in cohesive, multimale, multifemale groups with 4–21 individuals. Both males and females establish dominance hierarchies. Glander found that young females become top ranking when they immigrate into troops, but achieve their highest reproductive success as older, mid-ranking troop members. Males compete aggressively for high rank, and rarely maintain their alpha status for more than a few years. Both sexes disperse from their natal groups. Inter-troop interactions are usually aggressive and occur wherever they are within their overlapping home ranges, which vary from 25 to 148 acres (10–60 ha) in size.

FEEDING ECOLOGY AND DIET
Leaves comprise over 60% of mantled howler monkey diets. They exhibit preferences for young leaves over mature leaves, and eat fruits and flowers whenever they can. Consistent with a heavy dietary reliance on leaves, which are low in energy, mantled howler monkeys spend nearly two-thirds of their days resting, and day ranges are rarely longer than 0.6 mi (1 km).

REPRODUCTIVE BIOLOGY
Polygamous. Alpha males have higher mating success than other males. Births occur throughout the year, but tend to be concentrated in the dry season in more seasonal habitats. Average birth intervals are just under two years, and gestation is about six mos. Females give birth to their first infants at about four years of age, similar to other species of *Alouatta* and younger than the other atelidae genera.

CONSERVATION STATUS
Not listed by the IUCN, although the subspecies *Alouatta palliata mexicana* is classified as Vulnerable.

SIGNIFICANCE TO HUMANS
Hunted for meat. ◆

Venezuelan red howler monkey
Alouatta seniculus

SUBFAMILY
Mycetinae

TAXONOMY
Simia seniculus (Linnaeus, 1766), Colombia.

OTHER COMMON NAMES
English: Red howler monkey.

PHYSICAL CHARACTERISTICS
Dark red-maroon head, back, and limbs, with lighter, more golden sides. Crown hair as runs forward to meet the forehead hair in a concave V.

DISTRIBUTION
South and eastern Venezuela and northwestern Brazil; may also be sympatric with *Alouatta palliata*.

HABITAT
Gallery and semi-deciduous forest, secondary forest.

BEHAVIOR
Both males and females disperse, but over 20% of females may remain and breed in their natal troops. Females that remain in their natal troops reproduce earlier than females that disperse. Recruitment of daughters appears to be constrained by troop

size, with four females being the usual limit. Male red howler monkeys are tolerated in their natal troops longer than male mantled howler monkeys, and may disperse more than once during their lifetimes. Troops may include more than one male, and males sometimes remain together after dispersing from their natal troops. Coalitions of males appear to be more successful at rebuffing threats from extra-troop males, and may therefore hold onto their position in female troops longer than solitary males.

FEEDING ECOLOGY AND DIET
Like other species of howler monkeys, red howler monkey diets are highly folivorous. Their day ranges are similarly short, and their home ranges similarly small compared to other atelidae genera.

REPRODUCTIVE BIOLOGY
Polygamous. Alpha males have higher mating success than other males, and in multimale troops, the alpha male may account for 100% of the fertilizations. Births occur throughout the year, and birth intervals average just under two years. Male red howler monkeys that takeover a troop have been reported to kill infants sired by the males they have ousted.

CONSERVATION STATUS
Not listed by the IUCN, although one subspecies, *Alouatta seniculus insulanus*, is classified as Vulnerable and three subspecies, *A. s. amazonica*, *A. s. juara*, and *A. s. puruensis* are classified as Data Deficient.

SIGNIFICANCE TO HUMANS
Hunted for meat. ◆

Geoffroy's spider monkey
Ateles geoffroyi

SUBFAMILY
Atelinae

TAXONOMY
Ateles geoffroyi Kuhl, 1820, Nicaragua.

OTHER COMMON NAMES
English: Black-handed spider monkey.

PHYSICAL CHARACTERISTICS
Body coat varies in color from yellow, to red, to black, with black hands and feet. Cheek hairs stand out, and that hair on the top of the head forms a cowl that ends in a triangular crest over the brows.

DISTRIBUTION
Northeast and west coast of Mexico to Panama.

HABITAT
Evergreen rainforest, semi-deciduous forest, mangrove forest.

BEHAVIOR
Multimale, multifemales groups with over 40 individuals routinely split up into smaller foraging parties and are rarely observed together. Males remain in their natal groups, and tend to associate more with one another than with females. Males have hierarchical relationships, but also affiliate more closely with one another than with females. At Barro Colorado Island, Panama, males were observed to engage in fur-rubbing behavior more commonly than females.

FEEDING ECOLOGY AND DIET
Geoffroy's spider monkeys at Santa Rosa National Park, Costa Rica prefer fruit, which comprises over 70% of their annual diet. Chapman found that they adjust the size of their feeding parties to the size of fruit patches. Day ranges average about 4,265 ft (1,300 m), within a home range of 420 acres (170 ha). They may be important seed dispersers of the fruit species they eat.

REPRODUCTIVE BIOLOGY
Ovarian cycles last from 20 to 23 days in length. Birth intervals are about three years, and may be concentrated in more seasonal habitats.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Hunted for meat. ◆

Peruvian spider monkey
Ateles chamek

SUBFAMILY
Atelinae

TAXONOMY
Simia chamek (Humbolt, 1812), Peru.

OTHER COMMON NAMES
English: Black-faced black spider monkey.

PHYSICAL CHARACTERISTICS
Pelage and face is black, with a silvery genital patch and sometimes, white facial hairs.

DISTRIBUTION
Peru to the Rio Tapajós in Brazil.

HABITAT
Primary tropical rainforest.

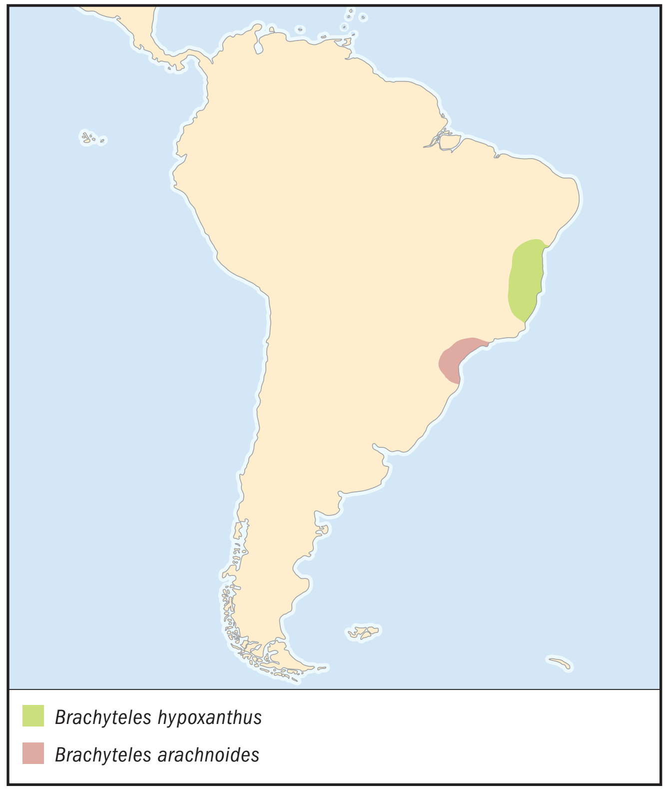
BEHAVIOR
A study of Peruvian spider monkeys (previously, *Ateles paniscus chamek*) at Manu National Park, Peru, emphasized the fluidity of grouping patterns and sex differences in behavior. Males associate and groom with one another more than with females, and maintain hierarchical relationships. Males are dominant over females, and spend more time traveling and less time feeding than females. Encounters between males from different groups are hostile, and involve both vocalizations and chases.

FEEDING ECOLOGY AND DIET
Peruvian spider monkeys devote up to 80% of their feeding time to fruit. They supplement their diets with young leaves and flowers, as well as occasional insects. Like other species of spider monkeys, they adjust their grouping patterns to the size of fruit patches, and travel widely between dispersed patches of fruits. This results in large home ranges, long day ranges, and very fluid grouping patterns.

REPRODUCTIVE BIOLOGY
Polygamous. Birth intervals average about three years.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Like other Atelidae, they are hunted for meat. ◆



Southern muriqui
Brachyteles arachnoides

SUBFAMILY
Atelinae

TAXONOMY
Ateles arachnoides (É. Geoffroy, 1806), Brazil.

OTHER COMMON NAMES
English: Woolly spider monkey; French: Atèle arachnoïde, eroïde, singe-araignèe; Spanish: Mono grande, muriki.

PHYSICAL CHARACTERISTICS
Muriquis are distinguishable by their large body size, light pelage, elongated limbs, and prehensile tails. Southern muriquis have black faces and black genitalia, and are lacking a thumb. The canines of males are larger than those of females.

DISTRIBUTION
Atlantic forest within the states of São Paulo, Paraná, and probably Rio de Janeiro.

HABITAT
Semi-deciduous montane forest.

BEHAVIOR
Behavioral data from two populations in São Paulo indicate substantial variation that is most likely related to ecological differences. At Fazenda Barreiro Rico, Milton (1985) observed a group of 7 individuals, including females and immatures. Females associated only loosely with adult males, except when a female was sexually receptive and mated with multiple males in close succession. At Parque Estadual de Carlos Botelho, Moraes et al. (1998) described a larger group of over 20 individuals including adult males, females, and immatures that usually split up into smaller foraging parties. Low population densities at Carlos Botelho may account for the low frequency at which long-distance vocalizations are heard. Peaceful associations among group members, including adult males, seem to be an unusual behavioral feature of the genus.

FEEDING ECOLOGY AND DIET
Flexible grouping patterns allow southern muriquis to reduce competition over food, which includes primarily fruits, leaves, and flowers. In the large, continuous, more humid forest at the Parque Estadual Carlos Botelho, the majority of the diet is fruit, and home ranges may exceed 1,975 acres (800 ha). By contrast, in the smaller, drier forest at Fazenda Barreiro Rico, the diet is more seasonal and home ranges are much smaller.

REPRODUCTIVE BIOLOGY
Polygamous. Milton (1985) described the mating patterns of one female at Fazenda Barreiro Rico. This female exhibited proceptive behavior, including a distinct "mating twitter" vocalization, and copulated with multiple males in close succession over the course of a few days. Births appear to be concentrated during the dry season months. Milton described the large quantities of ejaculate visible after copulations, which have also been observed in northern muriquis.

CONSERVATION STATUS
Listed as Critically Endangered by the IUCN.

SIGNIFICANCE TO HUMANS
Although they are legally protected, hunters still seek adults for meat and infants as pets. ◆

Northern muriqui
Brachyteles hypoxanthus

SUBFAMILY
Atelinae

TAXONOMY
Brachyteles hypoxanthus Kuhl, 1820, Bahia

OTHER COMMON NAMES
English: Woolly spider monkey.

PHYSICAL CHARACTERISTICS
Northern muriquis are born with black faces, which become dispigmented with pink or white mottling as they mature. Male testes are also variable in color and mottling. Some possess vestigial thumbs, which together with their facial mottling, distinguish the northern species from the southern one.

DISTRIBUTION
Atlantic forest within the states of Minas Gerais, Espírito Santo, and probably still in southern Bahia.

HABITAT
Semi-deciduous montane forest.

BEHAVIOR
Behavioral data are available from two populations in Minas Gerais, including one long-term study initiated in 1982 at Fazenda Montes Claros, now known as the Estação Biológica de Caratinga/Reserva Feliciano Miguel Abdalla (EBC/RFMA). Strier (1999) documented an increase in one group's size from 22 to 70+ individuals over a 20 year period. Grouping patterns became more fluid as the number of group members increased, but adult males, which remain in their natal groups, routinely associate together in the same subgroups. Relationships among group members are strikingly peaceful and egalitarian.

FEEDING ECOLOGY AND DIET
Northern muriquis have highly seasonal diets corresponding to the availability of preferred fruits, flowers, and new leaves. They consume mature leaves, as well as bark and bamboo, primarily in the dry season when their preferred foods are scarce.

REPRODUCTIVE BIOLOGY
Polygamous. Using non-invasive fecal steroid analyses, Strier and Ziegler (1997) found that females at the EBC/RFMA experienced 2–6 ovarian cycles prior to conceiving, intervals between ovulations averaged about 21 days, and gestation lasted 7.2 months. Females routinely mate with multiple partners. The mating season begins at the end of the annual dry season, with the majority of conceptions occuring during the peak of the rainy season. Births are concentrated during the dry season, and interbirth intervals average three years.

CONSERVATION STATUS
Listed as Critically Endangered by the IUCN.

SIGNIFICANCE TO HUMANS
Although they are legally protected, hunters still seek adults for meat and infants as pets. ◆

Gray woolly monkey
Lagothrix cana

SUBFAMILY
Atelinae

TAXONOMY
Simia cana (É. Geoffroy, 1812), Brazil.

OTHER COMMON NAMES
English: Geoffroy's woolly monkey.

PHYSICAL CHARACTERISTICS
Grayer, with an even darker gray head compared to the brown woolly monkey *Lagothrix lagotricha*, whose head is lighter in color than its body. Lowland specimens may be paler gray; in all, hands, feet, and tails are darker than the body.

DISTRIBUTION
Brazil, south of the Amazon and Peru, southern highlands.

HABITAT
Gallery, flooded, and unflooded rainforest.

BEHAVIOR
Peres (1996) studied a group of 39–41 gray woolly monkeys in terre firme forest near the upper Urucu river in Amazonas, Brazil. Altogether, this group included nine adult and subadult males, 12–14 adult females with 5–8 infants, and 15–18 subadult females and juveniles. Group members spent most of their time spread out from one another, but in contrast to the fission-fusion societies of spider monkeys, their movements were not independent of one another and subgroups usually included a combination of adult males, females, and immatures. Gray monkeys use vocalizations, including a "loud neigh" to maintain contact with one another while spread out by more than 1,300 ft (400 m).

FEEDING ECOLOGY AND DIET
Gray woolly monkeys prefer fruits and flowers when these resources are available, but also eat a variety of foliage. They adjust the size of their feeding parties to the size of fruit and flower patches, and the degree to which they spread out while feeding coincides with seasonal variation in the density of fruit patches in their home range, which was estimated to exceed 2,220 acres (900 ha). Within their home range, they preferred unflooded forest to flood forest.

REPRODUCTIVE BIOLOGY
No data are presently available from wild populations.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
A major source of meat in many areas. ◆

Colombian woolly monkey
Lagothrix lugens

SUBFAMILY
Atelinae

TAXONOMY
Lagothrix lugens Elliot, 1907, Colombia.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Highly variable in color and patterns, ranging from brown/black to lighter gray.

DISTRIBUTION
Restricted to the headwaters of the Orinoco tributaries in Colombia and Venezuela.

HABITAT
Lowland tropical forest

BEHAVIOR
In contrast to gray woolly monkeys, the multimale, multifemale groups of Colombia woolly monkeys remain cohesive throughout the year. Males maintain hierarchical relationships, and rarely feed in the same trees with one another. Males are dominant over females, and may exclude non-lactating females and juveniles from feeding trees.

FEEDING ECOLOGY AND DIET
Like other species of woolly monkeys, including the silvery woolly monkey, *Lagothrix poeppigii* in Ecuador, Colombian woolly monkeys prefer fruits more than other food types. Unlike the other species, however, arthropods account for over 20% of Colombian woolly monkey diets. The inclusion of arthropods in their diet may reduce intragroup feeding competition, and therefore permit them to maintain cohesive groups instead of adjusting their grouping patterns to the size of fruit patches. At La Macarena, woolly monkeys occur sympatrically with capuchin monkeys, as well as with spider monkeys and howler monkeys. They compete for many of the same fruit patches used by these other primates, and directed more aggression toward the other species than they received.

REPRODUCTIVE BIOLOGY
Polygamous. Matings occur throughout the year, but births at La Macarena are concentrated between August and December. Like spider monkeys and muriquis, birth intervals are three years. All males copulate with all sexually-receptive females, but high ranking males copulate more frequently than low ranking males.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Hunted, mainly for meat. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Mexican black howler monkey *Alouatta pigra*	Yellowish brown, deep reddish brown, or black in coloration. Coarse hair, naked face. Head and body length 22–36 in (55.9–91.5 cm), tail length 23–36 in (58.5–91.5 cm).	Arboreal, can be found mainly in diurnal forests. Exhibit loud and persistent calls. Breeding season throughout year, one individual per litter.	Yucatán, Guatemala, and Belize.	Leaves, fruit, and other vegetable matter.	Not threatened
Red-handed howler monkey *Alouatta belzebul*	Yellowish brown, deep reddish brown, or black in coloration. Coarse hair, naked face. Head and body length 22.0–36.0 in (55.9–91.5 cm), tail length 23.0–36.0 in (58.5–91.5 cm).	Arboreal, can be found mainly in diurnal forests. Exhibit loud and persistent calls. Breeding season throughout year, one individual per litter. Population density of about 31–39 per mi^2 (12–15 per km^2).	Amazonian Brazil and adjacent regions.	Leaves, fruit, and other vegetable matter.	Not threatened
Brown howler monkey *Alouatta guariba*	Yellowish brown, deep reddish brown, or black in coloration. Coarse hair, naked face. Head and body length 22–36 in (55.9–91.5 cm), tail length 23–36 in (58.5–91.5 cm).	Arboreal, can be found mainly in diurnal forests. Exhibit loud and persistent calls. Breeding season throughout year, one individual per litter.	Bolivia, eastern Brazil, and extreme northeastern Argentina.	Mainly leaves, fruit, and other vegetable matter.	Not threatened
Black howler monkey *Alouatta caraya*	Yellowish brown, deep reddish brown, or black in coloration. Coarse hair, naked face. Head and body length 22–36 in (55.9–91.5 cm), tail length 23–36 in (58.5–91.5 cm).	Arboreal, can be found mainly in diurnal forests. Exhibit loud and persistent calls. Breeding season throughout year, one individual per litter.	Eastern Bolivia, southern Brazil, Paraguay, and northern Argentina.	Mainly leaves, fruits, and other vegetable matter.	Not threatened

[continued]

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Coiba howler monkey *Alouatta coibensis*	Yellowish brown, deep reddish brown, or black in coloration. Coarse hair, naked face. Head and body length 22–36 in (55.9–91.5 cm), tail length 23–36 in (58.5–91.5 cm).	Arboreal, can be found mainly in diurnal forests. Exhibit loud and persistent calls. Breeding season throughout year, one individual per litter	Coiba Island and Azuero Peninsula, Panama.	Mainly leaves, fruit, and other vegetable matter.	Endangered
Bolivian red howler monkey *Alouatta sara*	Yellowish brown, deep reddish brown, or black in coloration. Coarse hair, naked face. Head and body length 22–36 in (55.9–91.5 cm), tail length 23–36 in (58.5–91.5 cm).	Arboreal, can be found mainly in diurnal forests. Exhibit loud and persistent calls. Breeding season throughout year, one individual per litter.	Environs of Rio Paray, Santa Cruz, Bolivia.	Mainly leaves, fruit, and other vegetable matter.	Not threatened
Brown-headed spider monkey *Ateles fusciceps*	Coloration can be yellowish gray, darker gray, reddish brown, dark brown, or almost black. Head and body length 15–25 in (38.2–63.5 cm), tail length 20–35 in (50.8–89.0 cm).	Can be found in rain and montane forests, occupy highest strata of canopy. No set social structure or breeding season.	Eastern Panama, Colombia, and Ecuador west of the Andes.	Consists largely of fruit, but also nuts, seeds, buds, flowers, leaves, insects, arachnids, and bird eggs.	Not threatened
White-bellied spider monkey *Ateles belzebuth*	Coloration can be yellowish gray, darker gray, reddish brown, dark brown, or almost black. Head and body length 15–25 in (38.2–63.5 cm), tail length 20–35 in (50.8–89.0 cm).	Can be found in rain and montane forests, occupy highest strata of canopy. No set social structure or breeding season.	Eastern Columbia and Ecuador, Venezuela, northeastern Peru, and northwestern Brazil.	Consists largely of fruit, but also nuts, seeds, buds, flowers, leaves, insects, arachnids, and bird eggs.	Vulnerable
Black spider monkey *Ateles paniscus*	Coloration can be yellowish gray, darker gray, reddish brown, dark brown, or almost black. Head and body length 15–25 in (38.2–63.5 cm), tail length 20–35 in (50.8–89.0 cm).	Can be found in rain and montane forests, occupy highest strata of canopy. No set social structure or breeding season.	The Guianas, north-eastern and central Brazil to the Mato Grosso, eastern Peru, and northern and central Bolivia.	Consists largely of fruit, but also nuts, seeds, buds, flowers, leaves, insects, arachnids, and bird eggs.	Not threatened
White-whiskered spider monkey *Ateles marginatus*	Coarse, stringy hair, lacking underfur. Coloration above yellowish gray to black. Underparts lighter, whitish, or yellowish. Head and body length 15–25 in (38.2–63.5 cm), tail length 20–35 in (50.8–89.0 cm).	Can be found in rain and montane forests, occupy highest strata of canopy. No set social structure or breeding season.	South of Lower Amazon, Rio Tapajós to Rio Tocantins.	Consists largely of fruit, but also nuts, seeds, buds, flowers, leaves, insects, arachnids, and bird eggs.	Endangered
Yellow-tailed woolly monkey *Lagothrix flavicauda*	Upperparts hoary gray, blue gray, tawny, dark brown, or blackish brown, underparts paler. Head and body length 20–27 in (50.8–68.6 cm), tail length 23.6–28.3 in (60.0–72.0 cm).	Can be found in gallery forests, palm forests, flooded and nonflooded primary forest, and cloud forest up to 9,840 ft (3,000 m). Diurnal and arboreal, walks on hind legs on ground, using tail as brace. Group size of 4–35 individuals.	Eastern slope of Cordillera Central in northern Peru.	Mainly fruit, supplemented by leaves, seeds, and some insects.	Critically Endangered
Humboldt's woolly monkey *Lagothrix lagotricha*	Upperparts hoary gray, blue gray, tawny, dark brown, or blackish brown, underparts paler. Head and body length 20–27 in (50.8–68.6 cm), tail length 23.6–28.3 in (60.0–72.0 cm).	Can be found in gallery forests, palm forests, flooded and nonflooded primary forest, and cloud forest up to 9,840 ft (3,000 m). Diurnal and arboreal, walks on hind legs on ground, using tail as brace. Groups of 4–6 individuals.	Eastern slope of the Andes in Colombia to the Rio Tapajos and Mato Grosso in central Brazil.	Mainly fruit, supplemented by leaves, seeds, and some insects.	Vulnerable

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Karen B. Strier, PhD

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Old World monkeys I

(Colobinae)

Class Mammalia
Order Primates
Family Cercopithecidae
Subfamily Colobinae

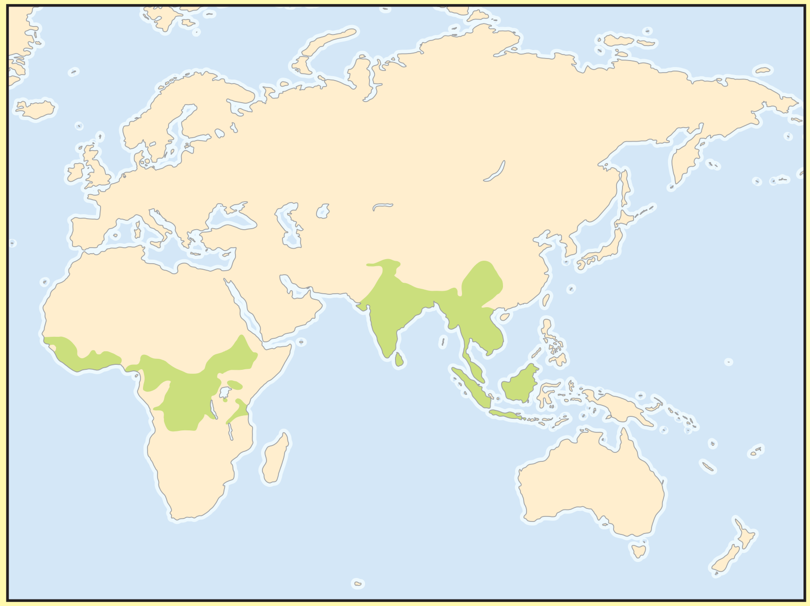
Thumbnail description
Medium-sized, essentially arboreal mammals with forward-facing, quite large eyes, relatively large brains and a quadrupedal pattern of locomotion involving grasping hands and feet

Size
Average body weights range from 9 lb 13 oz (4.45 kg) to 33 lb 5 oz (15.1 kg)

Number of genera, species
10 genera; 59 species

Habitat
Essentially forest-living, but occur in a range of forest types extending from relatively open dry forest to dense evergreen tropical rainforest

Conservation status
Critically Endangered: 4 species; Endangered: 14 species; Vulnerable: 7 species; Near Threatened: 6 species; Data Deficient: 5 species



Distribution
Asia and Southeast Asia, and Africa south of the Sahara

Evolution and systematics

Higher primates (suborder Anthropoidea) include the broad-nosed monkeys of the New World (infraorder Platyrrhini) and the narrow-nosed monkeys and apes of the Old World (infraorder Catarrhini). Old World monkeys and apes, which are widely distributed in Africa, Asia, and Southeast Asia, are uniformly characterized by a dental formula of I2/2 C1/1 P2/2 M3/3. They hence differ from all New World monkeys by reduction in the number of premolars from 3 to 2 in each tooth row. All Old World monkeys and apes have trichromatic color vision comparable to that of humans. Old World monkeys (superfamily Cercopithecoidea) differ from apes (superfamily Hominoidea) in possessing in both upper and lower jaws four-cusped molars with their cusps linked in pairs to form transverse cutting ridges (bilophodonty). Moreover, all Old World monkeys possess prominent hardened sitting pads (ischial callosities) on the buttocks, which are supported by broad, roughened bony flanges (ischial tuberosities) on the pelvis. Apart from gibbons, such a development is lacking in apes. Old World monkeys (family Cercopithecidae) are divided into two main groups, leaf-monkeys (subfamily Colobinae) and cheek-pouched monkeys (subfamily Cercopithecinae). Defining features of these two subfamilies reflect feeding habits. Whereas all cercopithecine monkeys are characterized by possession of cheek pouches for temporary storage of food, all leaf-monkeys have a complex stomach. The complex stomach, which is unique among primates, is subdivided into 4 distinct compartments (cardiac pouch, gastric sac, gastric tube and pyloric chamber). The complex stomach represents an adaptation for housing symbiotic bacteria to permit digestion of plant cell walls in a typically leaf-rich diet. Available evidence indicates that colobine monkeys have somewhat lower basal metabolic rates than cercopithecine monkeys, and this may be connected with their leaf-eating specialization. Leaf-monkeys also differ consistently and obviously from cheek-pouched monkeys in skull morphology: the distance between the eye sockets (interorbital distance) is large in colobines and small in cercopithecines.

Although there seems to be a fairly clear distinction between leaf-monkeys living in Asia and Southeast Asia and those living in sub-Saharan Africa, this is not recognized in any formal subdivision (e.g., as tribes) in current classifications.

Numerous Old World monkeys show some form of sexual dimorphism, in which males and females differ in features not directly related to reproduction. Males and females of a species can differ markedly in general appearance, in overall body size and/or in the size of the canine teeth, although these features can vary somewhat independently. As a general rule, sexual dimorphism is less pronounced in leaf-monkeys than in cheek-pouched monkeys. Nevertheless, there are some quite striking examples of dimorphism in leaf-monkeys as well. The most outstanding example of sexual dimorphism in all three aspects is provided by the proboscis monkey (*Nasalis larvatus*), in which males weigh more than twice as much as females, have significantly bigger canine teeth and exhibit

The proboscis monkey (*Nasalis larvatus*) is found in mangrove and lowland forests in Borneo. (Photo by Aaron Ferster/Photo Researchers, Inc. Reproduced by permission.)

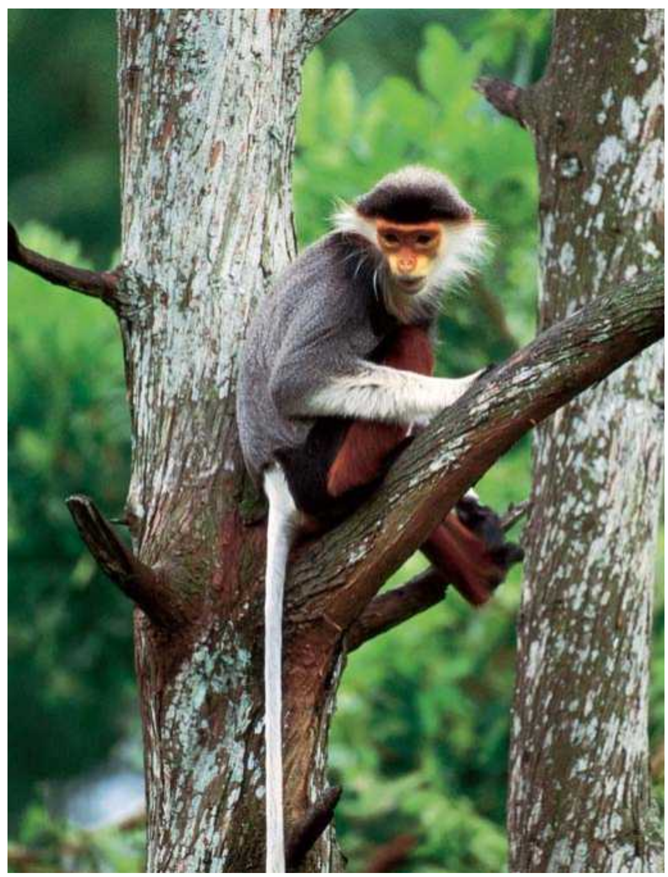
more extreme development of the prominent nose that characterizes this species.

Although morphological evidence is equivocal, chromosomal and molecular evidence indicates that the African and Asian groups of leaf-monkeys are both monophyletic, each being derived from a separate common ancestor after the leaf-monkeys diverged from the cheek-pouched monkeys. The African leaf-monkeys, which can be referred to collectively as colobus monkeys, include 15 species belonging to 3 genera (*Colobus*, *Piliocolobus*, and *Procolobus*). All of these monkeys were originally included in the single genus *Colobus*, but it is now recognized that their diversity merits separation at the generic level. Nevertheless, the Asian leaf-monkeys are undoubtedly more diverse both numerically and morphologically, and the 44 species are allocated to 7 different genera. Some of the Asian leaf-monkeys are generally labeled langurs and can be allocated to 3 genera (*Presbytis*, *Semnopithecus*, and *Trachypithecus*). The remaining Asian leaf-monkeys all show some kind of special modification of the nose and can be collectively labeled "odd-nosed leaf-monkeys." They can be allocated to four different genera: *Nasalis*, *Pygathrix*, *Rhinopithecus* and *Simias*.

The early fossil history of the Old World monkeys is poorly known. Early Miocene deposits of Africa, dated at about 20 million years ago (mya), have yielded *Prohylobates* and *Victoriapithecus*, both possessing bilophodont molar teeth. These early fossil forms were originally known exclusively from isolated teeth and jaw fragments. This is still the case for *Prohylobates*, but a fairly complete skull and parts of the postcranial skeleton are known for *Victoriapithecus*. As a result, it is known that this genus was characterized by possession of ischial tuberosities on the pelvis and by a short interorbital distance. It is unclear whether *Victoriapithecus* is specifically related to modern cheek-pouched monkeys, as might be suggested by the small interorbital distance, but there is certainly no trace as yet of an early relative of leaf-monkeys. It is not until the late Miocene and the Pliocene (less than 10 mya) that Old World monkeys become relatively well documented in the fossil record. By that stage, it is certainly possible to distinguish between colobines (relatives of leaf-monkeys) and cercopithecines (relatives of cheek-pouched monkeys). Skulls of colobine monkeys are comparatively common in Pliocene and Pleistocene deposits of northern and sub-Saharan Africa (e.g., *Libypithecus*, *Paracolobus*, and *Cercopithecoides*). In southern Europe the late Miocene leaf monkey *Mesopithecus* is documented by several skulls and almost all elements of the skeleton, and the Pliocene genus *Dolichopithecus* is also well documented. Furthermore, partial jaws and isolated teeth from late Miocene deposits in Pakistan have been allocated to the modern genus *Presbytis* as the species *Presbytis sivalensis*.

Physical characteristics

In the head, the eyes are always directed directly forwards and the snout is typically relatively short. As is the rule for higher primates, a rhinarium (a naked, moist area of skin around the nostrils that is present in most mammals) is al-



Red-shanked douc langurs (*Pygathrix nemaeus*) reside primarily in Cambodia, Laos, and Vietnam. (Photo by Art Wolfe, Inc./Photo Researchers, Inc. Reproduced by permission.)

A banded leaf-monkey (*Presbytis melalophos*) on the island of Sumatra consuming fruit. (Photo by Art Wolfe, Inc./Photo Researchers, Inc. Reproduced by permission.)

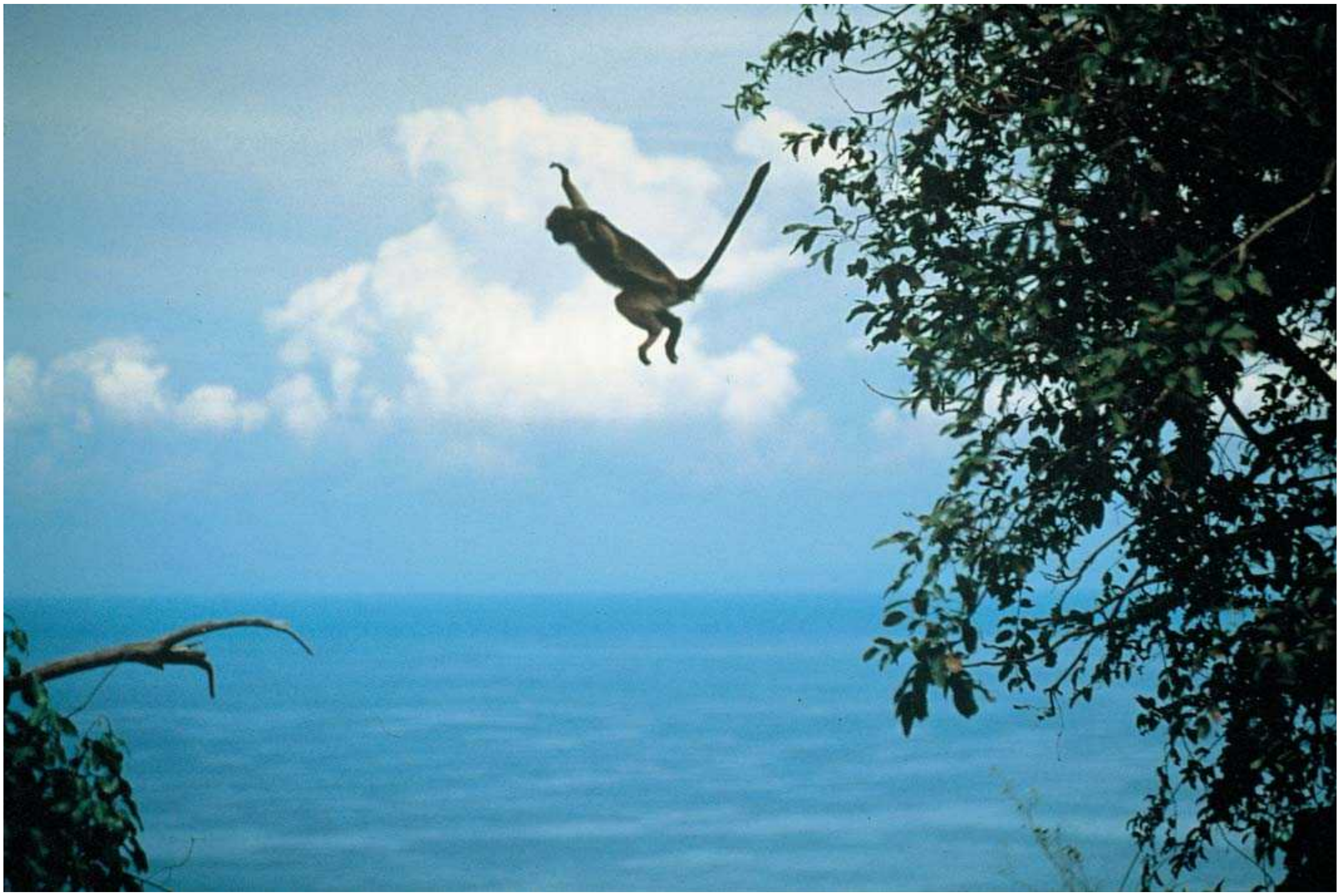
ways completely absent. The nostrils are relatively close-set and typically downward-pointing (with the notable exception of the Mentawai Islands snub-nosed leaf-monkey *Simias concolor*), and in some species the nose is prominently developed. Cheek pouches are never present. As in all other Old World monkeys and apes, the dental formula is I2/2 C1/1 P2/2 M3/3. The canine teeth are typically large, stabbing teeth (although generally less prominent than in cheek-pouched monkeys), and the rear edges of the upper canines are honed against the leading edges of the anterior premolars in the lower jaw. In both upper and lower jaws, all molar teeth are bilophodont. Colobine monkeys typically walk and run quadrupedally in the trees and, in some cases, on the ground. In the trees, they are typically agile climbers. In contrast to cheek-pouched monkeys, the legs are typically somewhat longer than the arms. In the hand, the thumb is generally reduced, and in the colobus monkeys it is virtually vestigial. Fine manipulative actions of the hand are thus largely precluded. Well-developed hardened sitting pads (ischial callosities) are present on the buttocks, and these are supported by broad, roughened bony flanges (ischial tuberosities) on the pelvis. Reflecting the predominance of arboreal habits, the tail is usually relatively long, although it is reduced to a short appendage in some species, for example in the snub-nosed leaf-monkey.

In many species, coloration of the body fur is relatively inconspicuous or even cryptic, generally being darker dorsally and paler ventrally. In several species, infants have a distinctive coloration. The face is usually virtually naked, although there is occasionally tufts of hair on the cheeks and/or chin. Body size ranges from the olive colobus (*Procolobus verus*), with a head and body length a 19.0 in (48.0 cm) for males and 18.5 in (46.5 cm) for females, and a tail length of 22.5 in (56.0 cm) for males and 23 in (57.5 cm) for females, to the proboscis monkey (*Nasalis larvatus*), with a head and body length of 30 in (74.5 cm) for males and 25 in (62.0 cm) for females, and a tail length of 26.5 in (66.5 cm) for males and 23 in (57.5 cm) for females. Body mass ranges from 10 lb 6 oz (4.7 kg) for males and 9 lb 4 oz (4.2 kg) for females in the olive colobus (*Procolobus verus*) to 45 lb (20.4 kg) for males and 21 lb 10 oz (9.8 kg) for females in the proboscis monkey (*Nasalis larvatus*).

Distribution

In contrast to cheek-pouched monkeys of the subfamily Cercopithecinae, the leaf-monkeys predominantly occur in Southeast Asia, where they are very widely distributed. The only colobine monkeys to occur in Africa are the colobus monkeys (genera *Colobus*, *Piliocolobus*, and *Procolobus*), although they are quite widely distributed south of the Sahara. The remaining seven genera (*Nasalis*, *Presbytis*, *Pygathrix*, *Rhinopithecus*, *Semnopithecus*, *Simias*, and *Trachypithecus*) are restricted to Asia and Southeast Asia.

Northern plains gray langurs (*Semnopithecus entellus*) play in Jodphur, India. (Photo by K & K Ammann. Bruce Coleman, Inc. Reproduced by permission.)



A western red colobus (*Procolobus badius*) escapes from chimpanzees. (Photo by K & K Ammann. Bruce Coleman, Inc. Reproduced by permission.)

Habitat

Leaf-monkeys are essentially forest-living, but they occur in a wide range of forest types, including relatively open dry forest, bamboo jungle, gallery forest, swamp forest, mangrove forest, and dense evergreen tropical rainforest.

Behavior

All members of the subfamily Colobinae are diurnal and most species are arboreal in habits. In all cases, locomotion is typically quadrupedal, although suspensory behavior is also quite common during arboreal feeding. Gregarious social groups that move around and feed as relatively cohesive units are formed by all species, but these vary from multi-male troops through one-male troops to a few rare cases of monogamy. In some species that exhibit one-male groups, surplus males form bachelor male groups. Moreover, there are certain species in which individual groups temporarily combine to form larger bands. In most species, females tend to stay in their natal groups, whereas males migrate at round the time of sexual maturity. However, there are exceptions. For example, in guerezas (genus *Colobus*), males migrate between groups, whereas in red colobus (genus *Piliocolobus*) it is the females that migrate.

Feeding ecology and diet

As is indicated by their name, leaf-monkeys feed predominantly on relatively low-energy leaves and other plant parts, although many species show a preference for relatively nutritious young leaves. The bilophodont teeth that characterize all Old World monkeys probably represent an adaptation for mastication of resistant material such as leaves, so it seems likely that the common Old World ancestor of both cheek-pouched monkeys (subfamily Cercopithecinae) and leaf-monkeys (subfamily Colobinae) was at least to some extent folivorous. However, uniquely among primates, colobine monkeys also possess a complex, four-chambered stomach that permits them to digest plant cell wall material with the aid of symbiotic bacteria. Despite this fundamental adaptation for digestion of resistant plant parts, there is considerable variation in diet among colobine monkeys, and some of them have become specialized for feeding on seeds rather than leaves (e.g., *Colobus satanas*).

Reproductive biology

Generally polygynous. Single births are typical, although twins are born very occasionally, and two teats (mammae) are consistently present in the chest region. All species have a

A mantled guereza (*Colobus guereza*) troop in Kenya. (Photo by Norman Owen Tomalin. Bruce Coleman, Inc. Reproduced by permission.)

menstrual cycle lasting approximately a month and marked by externally visible menstrual bleeding. In contrast to cheek-pouched monkeys, females generally lack a conspicous sex skin in the genital region that changes in coloration and size over the course of the ovarian cycle. The only exceptions are the olive colobus monkey (*Procolobus verus*), in which females have a moderately developed sex swelling, and some species of red colobus (*Procolobus preussi*), in which the sex swelling is enormous. Subadult red and olive colobus males also have a "perineal organ," which mimics the female's sexual swelling. Placentation is of a highly invasive hemochorial type. The gestation period is even longer than in cheek-pouched monkeys, varying between 195 days and 212 days for few species for which data are available.

Conservation status

Four species are Critically Endangered (*Piliocolobus rufomitratus*, *Rhinopithecus avunculus*, *Trachypithecus delacouri*, and *Trachypithecus poliocephalus*), 14 are Endangered (*Nasalis larvatus*, *Presbytis comata*, *Piliocolobus badius*, *Piliocolobus kirkii*, *Piliocolobus pennantii*, *Pygathrix nemaeus*, *Pygathrix nigripes*, *Rhinopithecus bieti*, *Rhinopithecus brelichi*, *Simias concolor*, *Trachypithecus auratus*, *Trachypithecus geei*, *Trachypithecus pileatus*, and *Trachypithecus vetulus*), seven are Vulnerable (*Colobus satanas*, *Colobus vellerosus*, *Presbytis potenziani*, *Piliocolobus gordonorum*, *Rhinopithecus roxellana*, *Trachypithecus francoisi*, and *Trachypithecus johnii*), and six are Near Threatened (*Colobus polykomos*, *Presbytis femoralis*, *Presbytis melalophos*, *Presbytis thomasi*, *Procolobus verus* and *Semnopithecus entellus*). Five species are listed as Data Deficient (*Presbytis fredericae*, *Presbytis frontata*, *Presbytis hosei*, *Trachypithecus laotum*, and *Trachypithecus villosus*).

Significance to humans

Leaf-monkeys are commonly hunted for food (bushmeat) in Asia, Southeast Asia, and Africa, although they are sometimes protected by local taboos in parts of Southeast Asia, as is the case with the northern plains gray langur (*Semnopithecus entellus*) in India. Despite the fact that they are just as closely related to humans as the cheek-pouched monkeys (subfamily Cercopithecinae), monkeys in the subfamily Colobinae have rarely been used in biomedical research because they are relatively difficult to maintain in captivity.

Trachypithecus auratus auratus, a subspecies of Javan langur (*Trachypithecus auratus*). (Photo by Art Wolfe, Inc./Photo Researchers, Inc. Reproduced by permission.)

1. Northern plains gray langur (*Semnopithecus entellus*); 2. Western red colobus (*Piliocolobus badius*); 3. Mantled guereza (*Colobus guereza*); 4. Banded leaf-monkey (*Presbytis melalophos*); 5. Olive colobus (*Procolobus verus*). (Illustration by Wendy Baker)

1. Golden snub-nosed monkey (*Rhinopithecus roxellana*); 2. Proboscis monkey (*Nasalis larvatus*); 3. Mentawai Island langur (*Simias concolor*); 4. Juvenile silvery leaf-monkey (*Trachypithecus cristatus*); 5. Adult female silvery leaf-monkey (*T. cristatus*); 6. Red-shanked douc langur (*Pygathrix nemaeus*). (Illustration by Wendy Baker)

Species accounts

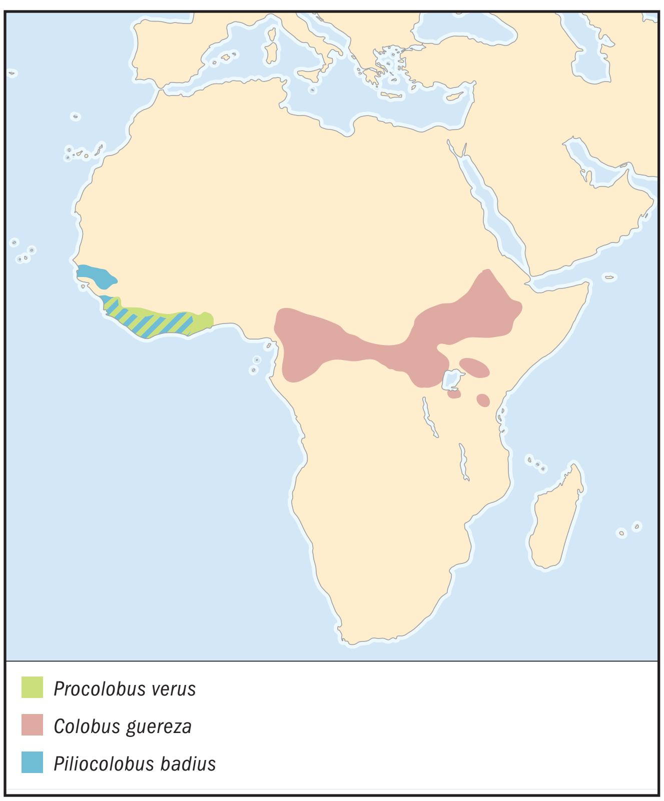
Mantled guereza
Colobus guereza

SUBFAMILY
Colobinae

TAXONOMY
Colobus guereza Rüppell, 1835, Ethiopia. The genus *Colobus* originally contained all colobus monkeys, but it is now restricted to the black-and-white colobus monkeys, some of which are known as guerezas. Eight subspecies of the mantled guereza can be recognized.

OTHER COMMON NAMES
English: Mantled black-and-white colobus; French: Guéréza; German: Guereza.

PHYSICAL CHARACTERISTICS
Fur black dorsally and ventrally, with a starkly contrasting U-shaped mantle of white fur descending from the shoulders and running across the lower back. The face is black and framed with a fringe of white hair. The end of the tail is white, with the length of the white region varying between subspecies. There is moderate sexual dimorphism in body size. Head and body length: 24.5 in (61.5 cm) for males and 23 in (57.5 cm) for females; tail length: 26.5 in (66.5 cm) for males and 27.5 in (68.5 cm) for females. Body mass: 29 lb 12 oz (13.5 kg) for males and 20 lb 5 oz (9.2 kg) for females.



DISTRIBUTION
Extensive range from Nigeria and Cameroon in the west, eastwards through the northern Democratic Republic of Congo into southern Sudan and Ethiopia, western Uganda and isolated areas in Kenya and northern Tanzania.

HABITAT
Inhabits primary and secondary rainforest, gallery forest and wooded grassland, including some forested areas with a prolonged dry season.

BEHAVIOR
Diurnal and arboreal. Typically live in relatively small one-male social groups containing less than a dozen individuals, but some multimale groups have been reported. Groups show conspicuous territorial behavior. Males migrate from the natal group on reaching maturity.

FEEDING ECOLOGY AND DIET
Primarily eats leaves, but supplements its diet with fruits. Diet includes a large proportion of mature leaves, and there is commonly heavy concentration on a few tree species as sources of leaves.

REPRODUCTIVE BIOLOGY
Polygynous. Births are typically single and occur year-round. Young infants are commonly passed around among females other than the mother, and also carried by them, even quite soon after birth. This species has been little studied in captivity, so basic reproductive features such as the gestation period remain unknown.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Frequently hunted for bushmeat. ◆

Western red colobus
Piliocolobus badius

SUBFAMILY
Colobinae

TAXONOMY
Piliocolobus badius (Kerr, 1792), Sierra Leone. Red colobus monkeys were long included in the genus *Colobus*, but they are sufficiently distinctive to merit the separate genus *Piliocolobus*. Three subspecies of the western red colobus can be recognized.

OTHER COMMON NAMES
French: Colobe bai, colobe ferrugineux; German: Roter Stummelaffe; Spanish: Colobo herrumbroso occidental.

PHYSICAL CHARACTERISTICS
Fur black or dark gray dorsally and contrastingly bright red ventrally. The cheeks and the lower parts of the limbs are also bright red. There is relatively little sexual dimorphism in body size; males are only marginally bigger than females. Head and body length: 23 in (57.0 cm) for males and 21 in (53.0 cm) for females; tail length: 26.5 in (66.5 cm) for males and 26.5 in

(66.5 cm) for females. Body mass: 18 lb 7 oz (8.36 kg) for males and 18 lb 2 oz (8.21 kg) for females.

DISTRIBUTION
Originally widely distributed in West Africa, from the coast of Senegal to Ghana.

HABITAT
Inhabits primary and secondary rainforest, gallery forest and wooded grassland, often occurring together with mantled guerezas. Prefers rainforest providing young leaves throughout the year.

BEHAVIOR
Diurnal and arboreal. Typically live in moderately sized multimale groups. Groups lack conspicuous territorial behavior. Unusually among Old World monkeys, females migrate from the natal group on reaching maturity.

FEEDING ECOLOGY AND DIET
Predominantly eat leaves, but also consume appreciable quantities of flowers, shoots and fruits. Feed selectively, exhibiting a marked preference for young leaves.

REPRODUCTIVE BIOLOGY
Polygynous. Births are typically single and occur year-round. In contrast to guerezas, young infants are never held or carried by females other than the mother. Little-studied in captivity, but the gestation period has been reported to be 198 days.

CONSERVATION STATUS
Listed as Endangered; one subspecies, *P. b. waldronae* is believed extinct.

SIGNIFICANCE TO HUMANS
Frequently hunted for bushmeat. ◆

Olive colobus
Procolobus verus

SUBFAMILY
Colobinae

TAXONOMY
Procolobus verus (van Beneden, 1838), Africa. This is the only species in the genus *Procolobus* and no subspecies are recognized. The olive colobus was originally included in the genus *Colobus* along with all other colobus monkeys, but several distinctive features (such as the sexual swelling of females) justify its classification in a separate genus.

OTHER COMMON NAMES
English: Green colobus; French: Colobe vert, colobe de van Beneden; German: Grüner Stummelaffe; Spanish: Colobo verde.

PHYSICAL CHARACTERISTICS
This is the smallest species in the subfamily Colobinae. Fur dull olive-brown dorsally and light gray to white ventrally. The face is framed with gray hair and there is a low crest of hair along the midline of the head. There is only mild sexual dimorphism in body size. Head and body length: 19.0 in (48.0 cm) for males and 18.5 in (46.5 cm) for females; tail length: 22.5 in (56.0 cm) for males and 23 in (57.5 cm) for females. Body mass: 10 lb 6 oz (4.7 kg) for males and 9 lb 4 oz (4.2 kg) for females.

DISTRIBUTION
Range extends from Sierra Leone to eastern Nigeria, with some intervening gaps.

HABITAT
Occupies a range of habitats, including evergreen rainforest, swamp forest and even dry deciduous forest.

BEHAVIOR
Diurnal and arboreal. Typically live in small uni-male groups with less than a dozen members. It is possible that females migrate from the natal group on reaching maturity, which would make this species another exception among Old World monkeys.

FEEDING ECOLOGY AND DIET
Food is taken from a large number of different tree species. Approximately two thirds of the diet consists of young leaves, but mature leaves, seeds, flowers and fruits together make up the rest.

REPRODUCTIVE BIOLOGY
Generally polygynous. Births are typically single. There are restricted mating and birth seasons. The species is unique among higher primates in that infants are carried in the mother's mouth. Olive and red colobus are also unusual among colobine monkeys in that females exhibit a moderate-sized sexual swelling around the time of ovulation. The species has been little studied in captivity, so basic reproductive features such as the gestation period are unknown.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Frequently hunted for bushmeat. ◆

Banded leaf-monkey
Presbytis melalophos

SUBFAMILY
Colobinae

TAXONOMY
Presbytis melalophos (Raffles, 1821), Sumatra, Indonesia. This species was originally combined with two forms that are now regarded as separate species: *Presbytis femoralis* and *Presbytis siamensis*. Following separation from these two species, the more narrowly defined *Presbytis melalophos* includes three subspecies.

OTHER COMMON NAMES
English: Mitered leaf-monkey, Sumatran surili; French: Semnopithèque mélalophe; German: Roter Langur; Spanish: Langur de cresta.

PHYSICAL CHARACTERISTICS
There is considerable variation in coat coloration between subspecies. Fur ranges from off-white/gray through reddish orange to chocolate dorsally and from white through cream to pale orange ventrally. There is relatively little sexual dimorphism in body size, with males being only slightly bigger than females. Head and body length: 19.5 in (49.0 cm) for males and 20 in (49.5 cm) for females; tail length: 28.5 in (71.0 cm) for males and 28.5 in (71.0 cm) for females. Body mass: 14 lb 8 oz (6.59 kg) for males and 14lb 4 oz (6.47 kg) for females.

DISTRIBUTION
Restricted to the southern part of Sumatra.

HABITAT
Primarily inhabits primary lowland rainforest, but also occurs in plantations and forest subject to logging.

BEHAVIOR
Diurnal and arboreal. Social groups are variable in composition. The species commonly lives in relatively small one-male groups, but larger multi-male groups also occur. Home ranges overlap and no overt territorial behavior is shown. As is typical for most Old World monkeys, males migrate from the natal group at maturity, but some females also migrate.

FEEDING ECOLOGY AND DIET
Feed on items from a wide range of tree species, consuming young leaves, mature leaves, flowers, seeds and fruits. This is one of the exceptional leaf-monkey species that includes less than 50% of leaves in its diet and therefore does not fit the standard definition of "folivory."

REPRODUCTIVE BIOLOGY
Polygynous. Births are typically single. This species has scarcely been studied in captivity, so little is known about its reproduction and the gestation period is unknown.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Occurs quite frequently in plantations. Frequently hunted for bushmeat. ◆

Northern plains gray langur
Semnopithecus entellus

SUBFAMILY
Colobinae

TAXONOMY
Semnopithecus entellus (Dufresne, 1797), Bengal, India. This species was previously included in the genus *Presbytis*, but there are enough distinctive characters to justify a separate genus. Furthermore, several of the original subspecies included in the species *Semnopithecus entellus* are now regarded as separate species.

OTHER COMMON NAMES
English: Hanuman langur, sacred langur, common langur; French: Houleman; German: Hanuman; Spanish: Langur hanuman.

PHYSICAL CHARACTERISTICS
Fur gray to brownish gray dorsally and white to creamy white ventrally. The face and ears are black, and the face is framed by long white or pale gray hairs. Long, stiff hairs point forward from the brow ridge. Limbs are slightly darker than the rest of the body; the hands and feet are black. There is moderate sexual dimorphism in body size. Head and body length: 25.5 in (64.0 cm) for males and 23.5 in (58.5 cm) for females; tail length: 36.5 in (91.0 cm) for males and 34.5 in (86.0 cm) for females. Body mass: 28 lb 11 oz (13.0 kg) for males and 21 lb 13 oz (9.9 kg) for females.

DISTRIBUTION
Pakistan and India, between the Godavari and Krishna Rivers in the south and the Ganges River in the north.

HABITAT
Occurs in a wide range of forest types, from dry, thorny scrub forest to evergreen tropical rainforest.

BEHAVIOR
Diurnal and semi-arboreal. Although arboreal activity is common, much time is spent on the ground, and this is one of the most terrestrial species among the leaf-monkeys. Patterns of social organization are notably variable. In some areas, northern plains gray langurs live in one-male groups, with surplus males forming bachelor groups. Violent takeovers of one-male groups by males from bachelor groups are quite common. In other cases, however, multi-male social groups are formed and such violent upheavals are lacking. This langur species is renowned for the occurrence of infanticide, which has been observed quite frequently in association with male takeovers. Typically, males emigrate from their natal groups on reaching maturity.

FEEDING ECOLOGY AND DIET
Leaves (particularly mature leaves) form the largest component in the diet, but buds, flowers and fruits are also eaten. In addition, animal prey, plant exudates and various other items are also consumed occasionally. As leaves make up less than 50% of the diet, this species does not in fact meet the standard definition of "folivory."

REPRODUCTIVE BIOLOGY
Variable mating system (polygyny, promiscuity). Single births are typical. Births often occur throughout the year, but there is a confined birth season in areas with marked seasonality in rainfall. Females do not have sexual swellings, but they display receptivity around the time of ovulation by means of behavioral signals (behavioral estrus). Gestation period 212 days.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
In many regions, this species is protected from harm by local custom, and food is often provided, particularly in the form of offerings at temple sites. One of the common names of this species is derived from the Hindu monkey-god Hanuman. ◆

Silvery leaf-monkey

Trachypithecus cristatus

SUBFAMILY
Colobinae

TAXONOMY
Trachypithecus cristatus (Raffles, 1821), Sumatra, Indonesia. Originally included in the genus *Presbytis* as the species *Presbytis cristata*. Two subspecies can be recognized.

OTHER COMMON NAMES
English: Silvery lutung, silvered langur; German: Haubenlangur.

PHYSICAL CHARACTERISTICS
Fur brownish gray to black dorsally and pale gray ventrally. A silvery appearance results from the fact that the hairs on the back have gray or yellowish tips. There is a crest of long hairs down the midline of the head, although its prominence differs between the two subspecies. There is mild sexual dimorphism in body size. Head and body length: 22 in (55.5 cm) for males and 20 in (50.5 cm) for females; tail length: 29.5 in (73.5 cm) for males and 28 in (70.0 cm) for females. Body mass: 14 lb 9 oz (6.61 kg) for males and 12 lb 11 oz (5.76 kg) for females.

DISTRIBUTION
Widely distributed in Southeast Asia, occurring along the west coast of the Malayan peninsula as well as on Borneo, Sumatra, the Natuna Islands, Bangka, Belitung, and various islands in the Riau Archipelago.

HABITAT
Occurs in a wide range of forest types, including primary and secondary rainforest, gallery forest and mangrove forest.

BEHAVIOR
Diurnal and arboreal. Live in one-male groups. There is no clear-cut territorial behavior. All males and some females migrate from their natal groups on reaching maturity.

FEEDING ECOLOGY AND DIET
Diet consists predominantly of leaves, supplemented by shoots and fruits. Food items are taken from a wide range of tree species.

REPRODUCTIVE BIOLOGY
Polygynous. Typically gives birth to a single infant. The infant is bright orange in color for the first 3 months of life and is passed among, and carried by, adult females other than the mother. The species has rarely been kept in captivity, so basic reproductive features such as the gestation period remain unknown.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Often found in plantations. Frequently hunted for bushmeat. ◆

Proboscis monkey

Nasalis larvatus

SUBFAMILY
Colobinae

TAXONOMY
Nasalis larvatus (Wurmb, 1787), Indonesia. This is now the only species in the genus *Nasalis*, and no subspecies are recognized. The species *Simias concolor* has sometimes been included in the genus *Nasalis*, but it is sufficiently distinctive to deserve its own genus.

OTHER COMMON NAMES
French: Nasique; German: Nasenaffe; Spanish: Mono narigudo.

PHYSICAL CHARACTERISTICS
This is the largest species in the subfamily Colobinae. Fur reddish orange on the crown and back and grayish white ventrally. The fur on the shoulders, neck and cheeks is pale orange. The legs and the tail are grayish white. In males, the penis is bright red in color, contrasting with the black scrotum. Both sexes have a prominent nose, but there is marked sexual dimorphism in that the nose is particularly long and drooping in males, whereas it is shorter and forward-pointing in females. Sexual dimorphism in body size is also very pronounced, with adult males weighing more than twice as much as adult females. Head and body length: 30 in (74.5 cm) for males and 25 in (62.0 cm) for females; tail length: 26.5 in (66.5 cm) for males and 23 in (57.5 cm) for females. Body mass: 45 lb (20.4 kg) for males and 21 lb 10 oz (9.8 kg) for females.

DISTRIBUTION
Occurs throughout Borneo, wherever suitable forest habitat is available.

HABITAT
Occurs in a variety of habits, including lowland rainforest, gallery forest, peat swamp forest and mangrove forest.

BEHAVIOR
Diurnal and essentially arboreal. Individuals and groups have been observed swimming across rivers and even in the sea near the coast. Typically form one-male social groups, with surplus males living in bachelor groups. Individual one-male groups sometimes combine with other groups temporarily. Groups do not show clear-cut territorial behavior.

FEEDING ECOLOGY AND DIET
Feeds predominantly on leaves, but also eats flowers, fruits (mostly unripe), seeds and a small amount of animal prey.

REPRODUCTIVE BIOLOGY
Polygynous. Typically gives birth to a single infant. The species has rarely been kept in captivity and reproductive features such as the gestation period are hence unknown.

CONSERVATION STATUS
Listed as Endangered.

SIGNIFICANCE TO HUMANS
Quite often hunted for bushmeat. ◆

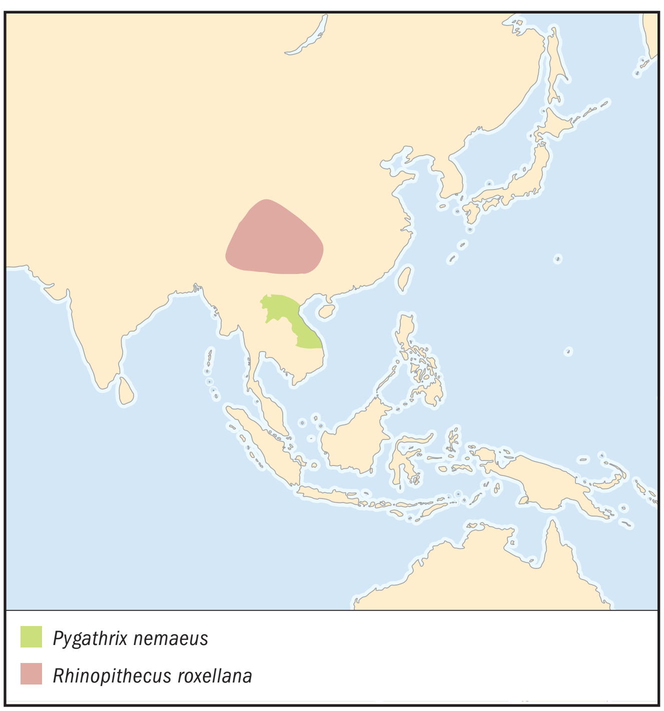
Red-shanked douc langur
Pygathrix nemaeus

SUBFAMILY
Colobinae

TAXONOMY
Pygathrix nemaeus (Linnaeus, 1771), Cochin-China (Indochina). Two subspecies were originally recognized in this species, but they have been raised to the rank of separate species, the other being *Pygathrix nigripes*. A third species, *Pygathrix cinerea*, was described only in 1997.

OTHER COMMON NAMES
French: Rhinopithèque douc du nord; German: Nördlicher Kleideraffe; Spanish: Mono pigatrix.

PHYSICAL CHARACTERISTICS
The douc langurs are probably the most colorful leaf-monkey species. In the red-shanked douc langur, the fur is grizzled medium gray dorsally and lighter gray ventrally. There is a fringe of black hair across the crown, and there are long, white cheek whiskers. The eyes slant downwards towards the nose. Around the eyes and nose, the face is yellow-brown, contrasting with a distinctive white muzzle. The hands and feet are black, whereas the forearms and wrists are covered with white hair. The thighs are black, while the lower parts of the legs are reddish-brown. There is moderate sexual dimorphism in body size. Head and body length: 23.5 in (58.5 cm) for males and 24 in (60 cm) for females; tail length: 27 in (68 cm) for males and 24 in (60 cm) for females. Body mass: 24 lb 4 oz (11.0 kg) for males and 18 lb 10 oz (8.45 kg) for females.



DISTRIBUTION
Occurs throughout Laos and in the northern part of Vietnam.

HABITAT
Inhabits primary and secondary evergreen rainforest.

BEHAVIOR
Diurnal and essentially arboreal. Lives in multimale groups containing up to two dozen individuals. Individuals of both sexes migrate from the natal group on reaching maturity.

FEEDING ECOLOGY AND DIET
Eats leaves, buds, flowers, fruits, and seeds from a wide variety of tree species.

REPRODUCTIVE BIOLOGY
Polygynous. Typically have single births. Gestation period 210 days.

CONSERVATION STATUS
Listed as Endangered.

SIGNIFICANCE TO HUMANS
Often hunted for bushmeat. ◆

Golden snub-nosed monkey
Rhinopithecus roxellana

SUBFAMILY
Colobinae

TAXONOMY
Rhinopithecus roxellana (Milne-Edwards 1870), Sichuan, China. Some authors include snub-nosed monkeys in the genus *Pygathrix*, rather than recognizing the separate genus *Rhinopithecus*. Three subspecies can be recognized for the golden snub-nosed monkey.

OTHER COMMON NAMES
English: Sichuan golden snub-nosed monkey; French: Rhinopithèque doré; German: Goldener Stumpfnasenaffe.

PHYSICAL CHARACTERISTICS
This is one of the largest leaf-monkey species, second only to the proboscis monkey. Fur grayish brown with distinctive golden strands dorsally and yellowish to golden white ventrally. Crown of head dark, with a crest of short hairs. Around the eyes, the face is pale blue. The upturned nose with forward-facing nostrils, from which this species derives its common name, is located well back relative to the inflated white muzzle. Hands and feet yellowish. Males are more brightly colored than females. There is also marked sexual dimorphism in body size. Head and body length: 23.5 in (59 cm) for males and 20.5 in (51.5 cm) for females; tail length: 35 in (87.0 cm) for males and 28 in (69.5 cm) for females. Body mass: 39 lb 7 oz (17.9 kg) for males and 25 lb 9 oz (11.6 kg) for females.

DISTRIBUTION
Mountainous areas of central and western China, including parts of the provinces of Sichuan, Hubei, Ganssu and Shaanxi.

HABITAT
Lives in bamboo jungles, coniferous forests and deciduous forests up to altitudes exceeding 10,000 ft (over 3,000 m). In areas inhabited by golden snub-nosed monkeys, there is snow cover on the ground for about half the year.

BEHAVIOR
Diurnal and semi-arboreal. Although these monkeys commonly feed in trees, they travel predominantly on the ground. Seasonally shifting ranges are characteristic for this species. Golden snub-nosed monkeys live in one-male social groups, with surplus males forming bachelor groups. Several groups may aggregate to form a band containing more than 200 individuals, and 2–3 such bands may temporarily join up.

FEEDING ECOLOGY AND DIET
Feed on leaves, buds, fruits and lichens.

REPRODUCTIVE BIOLOGY
Polygynous. Single births are typical. Infants may be carried by adult females other than the mother. Gestation period 195 days.

CONSERVATION STATUS
Listed as Vulnerable.

SIGNIFICANCE TO HUMANS
These monkeys are sometimes hunted for food. ◆

Mentawai Island langur
Simias concolor

SUBFAMILY
Colobinae

TAXONOMY
Simias concolor (Miller, 1903), western Sumatra, Indonesia. This is the only species in the genus *Simias*. The species has sometimes been included in the genus *Nasalis*, but it is sufficiently distinctive to deserve its own genus. Two subspecies can be recognized.

OTHER COMMON NAMES
English: Mentawai Islands snub-nosed leaf-monkey, pig-tailed snub-nosed langur, simakobu; German: Pagehstumpfnasenaffe.

PHYSICAL CHARACTERISTICS
Fur is black or creamy buff dorsally, irrespective of species, and paler ventrally. The nose is prominently developed, but far less so than in the proboscis monkey. This species derives one of its common names from the fact that (uniquely among leaf-monkeys) the tail is very short, almost hairless and curled upwards. There is moderate sexual dimorphism in body size. Head and body length: 20.5 in (51.5 cm) for males and 20 in (50.0 cm) for females; tail length: 6 in (15.5 cm) for males and 5.5 in (14.0 cm) for females. Body mass known only for single individuals, 19 lb 5 oz (8.75 kg) for a female and 15 lb 12 oz (7.15 kg) for a female.

DISTRIBUTION
Restricted to the Mentawai Islands, occurring on Siberut, Sipura and the Pagai Islands, along with a few smaller islands.

HABITAT
Inland evergreen rainforest and swamp forest.

BEHAVIOR
Diurnal and arboreal. Social organization is variable, sometimes as one-male groups (perhaps with just a single female) and sometimes as multimale groups.

FEEDING ECOLOGY AND DIET
Diet consists mainly of leaves and fruit, in a ratio of 2:1.

REPRODUCTIVE BIOLOGY
Variable mating system (polygny, monogamy). Single births are typical. Breeding may be seasonal. No studies have been conducted in captivity, so reproductive features such as the gestation period are unknown.

CONSERVATION STATUS
Listed as Endangered.

SIGNIFICANCE TO HUMANS
Frequently hunted for bushmeat. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Angolan colobus *Colobus angolensis* German: Angola-Stummelaffe, Angola-Guereza; Spanish: Colobo angoleño	Black and white coloration on sides of face, throat, and tip of tail. Adult body mass 13.2–25.1 lb (6.0–11.4 kg).	Found in gallery, montane, lowland, and alpine bamboo forests, savannas, and swamp lands. Diurnal, arboreal species. Group sizes range from about 10 to 15 individuals.	Angola, southern Zaire, Tanzania, and Kenya.	Eats mainly leaves, but also termite clay, fruits, and flowers.	Not threatened
King colobus *Colobus polykomos* French: Colobe à longs poils; German: Bärenstummelaffe, Südlicher Guereza; Spanish: Colobo de cola blanca	Chest and whiskers are white while the rest of the body is black. Slender body with long, white tail. Head and body length 17.7–28.3 in (45–72 cm), tail length 20.5–39.4 in (52–100 cm), body mass 11–30.9 lb (5–14 kg).	Found in tropical rainforest (lowland and montane types). Females produce one young every 20 months. Social groups consist of 3–4 adult females and 1–3 adult males.	Gambia to Benin.	Mainly leaves, but also fruits and flowers.	Lower Risk/Near Threatened
Black colobus *Colobus satanas* German: Schwarzer Stummelaffe, Schwarzer Guereza; Spanish: Colobo negro	Coloration is entirely black. Long fingers, back and limbs, and a heavy body. Head and body length 19.7–27.6 in (50–70 cm), tail length 24.6–34.6 in (62.5–88 cm), weight 8.8–30.9 lb (4–14 kg).	Found in high canopy of forest. Birth season extends from December to early April.	Southwest Cameroon, Bioko Island, and the Zaire River.	Seeds and unripe fruits, with special preference for the leaves of lianas.	Vulnerable
Pig-tailed langur *Nasalis concolor* French: Rhinopitheque des iles Pagai; German: Pageh-Stumpfnasenaffe; Spanish: Langur cola de cerdo	The two color types are a dark gray color and a light buff color, regardless of sex. Black face, hairless tail.	Found primarily in primary forests on hillsides of the interior region of the islands. Also lives in freshwater and brackish water swamp forest and lowland rainforest. Monogamous or polygynous mating system. Females give birth to a single young. Group sizes range from 1 to 5 individuals.	Mentawai Islands (Indonesia).	Mainly leaves, but also fruits and berries.	Endangered
Hose's leaf-monkey *Presbytis hosei* German: Mentawailangur; Spanish: Langur gris	Coloration is gray on dorsal side, white on ventral side. Hands and feet are black. Adult male mass 13.7 lb (6.2 kg), adult females 12.3 lb (5.6 kg).	Found in tall and secondary forests, occasionally plantations between 3,280 and 4,270 ft (1,000–1,300 m). Unimale social system, polygynous mating system.	Borneo.	Mainly leaves, but also fruits and seeds.	Data Deficient
Mentawai Island leaf-monkey *Presbytis potenziani* French: Semnopithèque de Mentawei; German: Mentawailangur; Spanish: Langur de Mentawai	Long slender body, deep jaw, short and broad face. Mean male body mass 14.3 lb (6.5 kg), adult females 14.1 lb (6.4 kg).	Can be found in lowland forests.	Found on Mentawai Island off the west coast of Sumatra.	Leaves, fruits, seeds, and flowers.	Vulnerable
Nilgiri langur *Presbytis johni* English: Lion-tailed macaque	Smooth, black hair, distinctive gray mane frames face. Head and body length usually 24 in (61 cm), tail length 18 in (46 cm), males usually larger than females.	Found in upland forests between 3,000 and 7,000 ft (910–2,130 m). Move in groups of 3 to 25 individuals. Strong dominance hierarchy among females. Loud, distinctive whooping cry. No particular season for mating.	Southern India.	Leaves, fruits, seeds, and flowers.	Vulnerable

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Penant's red colobus *Procolobus pennantii*	Black, slaty, or brownish upperparts, red or chestnut brown arms, legs, and head. Slender body, long tail, prominent rump callosities.	Stable groups ranging from 12 to 82 individuals. Most mating done by highest-ranking male. Little to no reproductive seasonality.	Lower Congo River region in Congo and Zaire; Bioko Island.	Leaves, fruits, flowers, and seeds.	Endangered
Tonkin snub-nosed monkey *Rhinopithecus avunculus* German: Tokin-Goldaffe	Coloration is black on inner limbs, thighs, and face. Head is creamy white, tail is dorsally black and ventrally white, orange patch on throat and around eyes. Skin around mouth is bluish black. Head and body length 20.5 in (52 cm), tail length 26 in (66 cm).	Found in steep karst mountains in northern Vietnam. Unimale groups normal, except for feeding. Moves quadrupedally.	Northern Vietnam.	Young leaves, buds, bamboo shoots, seeds, and unripe fruit.	Critically Endangered
Gray snub-nosed monkey *Rhinopithecus brelichi*	Long, black tail tipped white on end. Limbs, sides of neck, top of head, and hands and feet are black. Ears tipped white, face is bare and white. Average body mass male 30.9 lb (14 kg), female 17.6 lb (8 kg).	Found in forests of mixed deciduous and evergreen broadleaf trees and deciduous broadleaf trees between 4,920 and 7,220 ft (1,500–2,200 m).	Known from two species from Van Gin Shan Range south of Middle Yangtze in China.	Leaf buds, flower buds, fruits, seeds, bark, and insect larvae.	Endangered

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Robert D. Martin, PhD

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Old World monkeys II

(Cercopithecinae)

Class Mammalia
Order Primates
Family Cercopithecidae
Subfamily Cercopithecinae

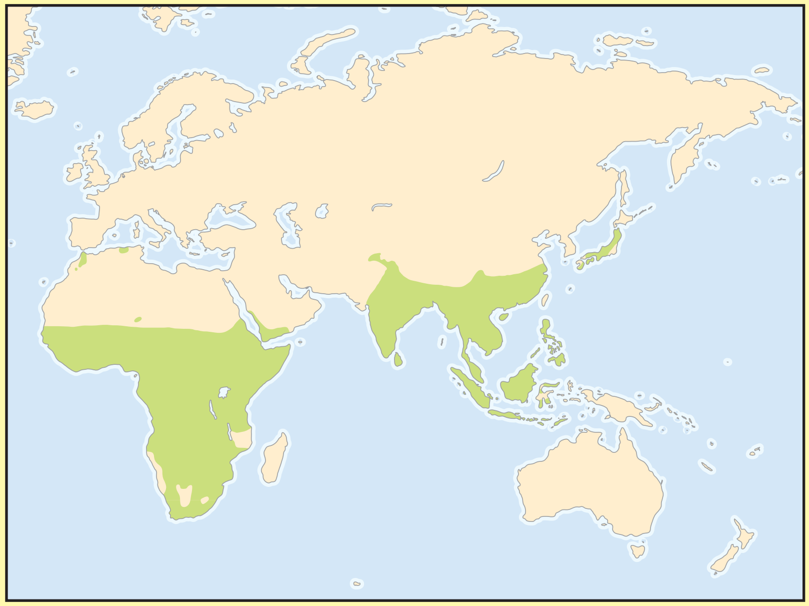
Thumbnail description
Medium-sized mammals with forward-facing, quite large eyes, relatively large brains and a quadrupedal pattern of locomotion involving grasping hands and feet

Size
2 lb 12 oz (1.25 kg) to 48 lb (21.7 kg)

Number of genera, species
11 genera; 72 species

Habitat
Wide range of habitats, ranging from semi-arid scrub with only sparse vegetation to dense evergreen tropical rainforest

Conservation status
Critically Endangered: 1 species; Endangered: 8 species; Vulnerable: 10 species; Near Threatened: 16 species; Data Deficient: 3 species



Distribution
Predominantly occur in Africa south of the Sahara; macaques occur outside Africa, having a wide distribution throughout Asia and Southeast Asia

Evolution and systematics

The higher primates (suborder Anthropoidea) are divided into the broad-nosed monkeys of the New World (infraorder Platyrrhini) and the narrow-nosed monkeys and apes of the Old World (infraorder Catarrhini). The Old World monkeys and apes, which occur in Africa, Asia and Southeast Asia, are uniformly characterized by a dental formula of (I2/2 C1/1 P2/2 M3/3) $\times$ 2 = 32, differing from all New World monkeys by reduction in the number of premolars from three to two in each tooth row. All Old World monkeys and apes have trichromatic color vision comparable to that of humans. As a group, the Old World monkeys are distinguished from the apes by the presence in both upper and lower jaws of four-cusped molars with the cusps linked in pairs to form transverse cutting ridges (bilophodonty). Furthermore, all Old World monkeys possess well-developed hardened sitting pads (ischial callosities) on the buttocks, supported by broad, roughened bony flanges (ischial tuberosities) on the pelvis. Among the apes, only the gibbons show a similar development. The Old World monkeys are divided into two main groups, the cheek-pouched monkeys (subfamily Cercopithecinae) and the leaf-monkeys (subfamily Colobinae). Defining features of these two groups are related to their feeding habits. Whereas all cercopithecine monkeys possess cheek pouches for the temporary storage of food, leaf-monkeys have a complex, multi-chambered stomach as an adaptation for digestion of plant cell walls in their leaf-rich diet with the aid of symbiotic bacteria. There is also a consistent and immediately obvious difference in skull morphology, in that the dis-

A grivet (*Chlorocebus aethiops*) probes for insects in bark. (Photo by David M. Maylen, III. Reproduced by permission.)

A Guinea baboon (*Papio papio*) nurses her baby. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

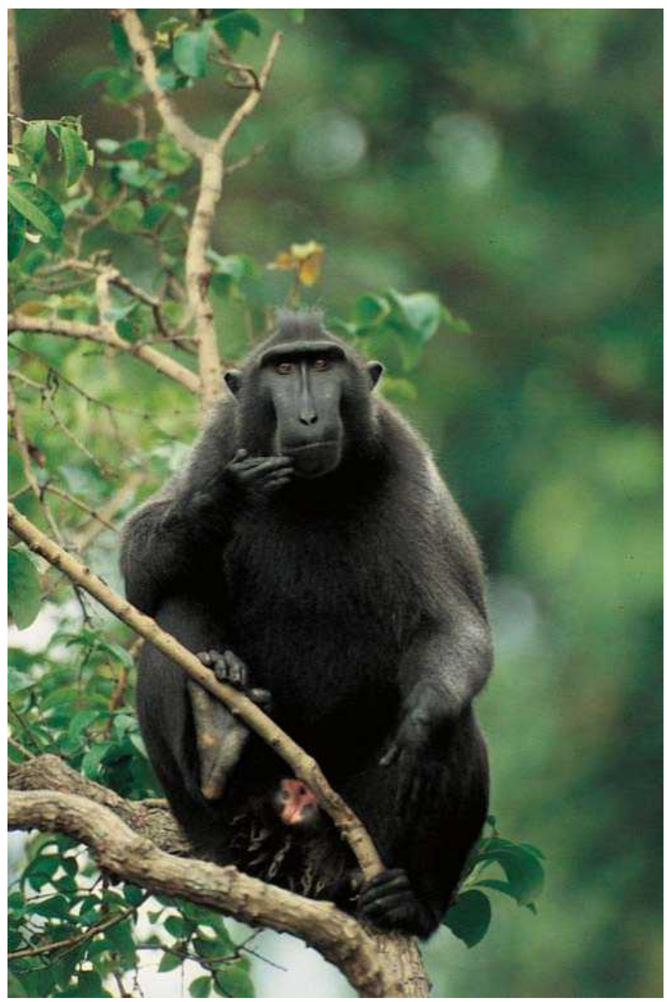
tance between the eye sockets (interorbital distance) is small in cheek-pouched monkeys and large in leaf-monkeys.

Two tribes can be recognized among the cercopithecine monkeys: the Cercopithecini (guenons) and the Papionini (baboons, geladas, mangabeys, drill, mandrill, and macaques). The guenons are generally smaller and more arboreal than the baboons and their relatives, which tend to be large-bodied and at least partially terrestrial; but there is some degree of overlap in these features. For instance, the patas monkey (*Erythrocebus patas*) is a member of the guenon tribe but is quite large-bodied and predominantly terrestrial.

Old World monkeys commonly show some degree of sexual dimorphism, in which males and females differ in features other than those directly related to reproduction. Males and females of a species can differ markedly in fur coloration, in overall body size and in the size of the canine teeth, although these features can vary to some extent independently. The most striking example of sexual dimorphism in all three aspects is provided by the mandrill (*Mandrillus sphinx*), in which males weigh more than twice as much as females, have strikingly large canine teeth and are more brightly colored.

Chromosomal and molecular evidence indicates that the two tribes Cercopithecini and Papioni are both monophyletic, each being derived from a separate common ancestor after the cheek-pouched monkeys diverged from the leaf-monkeys. Within the Cercopithecini, there appear to be two main clusters, one formed by most of the forest-living guenons (*Cercopithecus* species) and the other containing the talapoins (*Miopithecus*), the vervets or grivets (*Chlorocebus*), l'Hoest's guenon (*Cercopithecus lhoesti*), and the patas monkey (*Erythrocebus patas*). Within the Papionini, there is a basic division between the baboons, macaques, and geladas on one branch and the mandrills on another. Unexpectedly, the Old World monkeys known as mangabeys, which were all originally classified as species of the genus *Cercocebus*, turned out to belong to two distinct lineages. The genus name *Cercocebus* is now reserved for more terrestrial species related to the mandrill, whereas the genus name *Lophocebus* is used for more arboreal species related to baboons.

The early fossil history of the Old World monkeys is still poorly documented. Two early Miocene forms from Africa, from deposits dated at about 20 million years ago (mya) are



The Celebes macaque (*Macaca nigra*) is native to Sulawesi, part of Indonesia. (Photo by Art Wolfe, Inc./Photo Researchers, Inc. Reproduced by permission.)

A mandrill (*Mandrillus sphinx*) baring its teeth as a threat. (Photo by C. K. Lorenz/Photo Researchers, Inc. Reproduced by permission.)

Prohylobates and *Victoriapithecus*, both of which have bilophodont (two-ridged) molar teeth. These early fossil forms were originally known only from isolated teeth and jaw fragments, and this is still the case for *Prohylobates*. However, a fairly complete skull and parts of the postcranial skeleton have been reported for *Victoriapithecus*, and as a result it is known that this genus was characterized by a short interorbital distance and by possession of ischial tuberosities on the pelvis. But it is unclear whether *Victoriapithecus* is specifically related to modern cheek-pouched monkeys, as the small interorbital distance suggests. It is not until the late Miocene and the Pliocene, less than 10 mya, that fossil remains of Old World monkeys become relatively well documented, and by that stage it is certainly possible to distinguish between cercopithecines (relatives of cheek-pouched monkeys) and colobines (relatives of leaf-monkeys). Cercopithecine monkeys are comparatively common in Pliocene deposits of Africa. Many of them resemble modern baboons (e.g. *Dinopithecus*, *Dolichopithecus* and *Gorgopithecus*), and there are also relatives of the modern gelada, some of them almost as big as a female gorilla, which are placed in the same genus *Theropithecus*. During warm interglacial periods of the middle Pleistocene, macaques related to the modern Barbary macaque (*Macaca sylvanus*) were present in central Europe, but they subsequently became restricted to North Africa.

Physical characteristics

Coloration of the body fur is often relatively inconspicuous and occasionally cryptic, generally being darker dorsally and paler ventrally. The face is usually virtually naked, although in some species there is a beard-like tuft of hair on the chin. However, in many cases the fur and skin on the face and sometimes on other areas of the body are conspicuously patterned, notably in various guenons, where species-specific coloration patterns on the head are commonly emphasized by characteristic head movements. Striking color contrasts are also frequently present in the genital region. In males, the scrotum and/or penis are often distinctively colored, while in females of some species there is often a conspicuous sex skin

An olive baboon (*Papio anubis*) troop feeding in sausage tree in Masai Mara, Kenya. (Photo by John Shaw. Bruce Coleman, Inc. Reproduced by permission.)

that changes in color and size over the course of the ovarian cycle. The most colorful species is undoubtedly the mandrill (*Mandrillus sphinx*). In this species, the faces of males have a bright red nose flanked by blue, ridged paranasal bulges along with white whiskers, and there is a large, orange-yellow beard, while the rump is also colored red and blue and the penis is bright red. Females are similarly, although less brightly, colored; but they also have prominent sexual swellings that are bright red at peak inflation.

In the head, the eyes are always directed directly forwards and the snout is mildly to strongly elongated. In common with other higher primates, a rhinarium (a naked, moist area of skin around the nostrils present in most mammals) is always completely lacking. The nostrils are relatively close-set and point downward. Cheek pouches are consistently present, but the degree of development varies from species to species. The dental formula, which is the same in all Old World monkeys and apes, is (I2/2 C1/1 P2/2 M3/3) $\times$ 2 = 32. The canine teeth are typically large, stabbing teeth, and the rear edges of the upper canines are honed against the leading edges of the anterior premolars in the lower jaw. The molars in both upper and lower jaws are bilophodont. Cercopithecine monkeys typically walk and run quadrupedally both in the trees and on the ground, and the arms and legs are of approximately equal length. In the trees, they are agile climbers. On the hand, the thumb is always well developed, and fine manipulative actions are particularly prevalent in terrestrial species. In all Old World monkeys, including leaf-monkeys (colobines), well-developed hardened sitting pads (ischial callosities) are present

A chacma baboon (*Papio ursinus*) female carries her infant. (Photo by Martin Grosnick. Bruce Coleman, Inc. Reproduced by permission.)

Japanese macaque (*Macaca fuscata*) mother and young in a steamy thermal pool in Japan. (Photo by Tom Brakefield/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)

on the buttocks, and these are supported by broad, roughened bony flanges (ischial tuberosities) on the pelvis. The tail is very variable in length, being very long in some species and reduced to a small stump in others. As a rule, arboreal species tend to have a relatively long tail, whereas marked reduction of the tail is found in species that spend much of their time on the ground. Head and body length varies from 14 in (35 cm) to 30 in (75 cm), while tail length varies from practically zero to 34 in (86 cm), according to species. Body mass ranges from 2 lb 12 oz (1.25 kg) for the diminutive talapoin (*Miopithecus talapoin*) to 48 lb (31.6 kg) for a male mandrill (*Mandrillus sphinx*).

Distribution

Cheek-pouched monkeys of the subfamily Cercopithecinae are largely confined to Africa south of the Sahara, where they are very widely distributed. The only cercopithecine monkeys to occur outside Africa are the macaques (genus *Macaca*), which occur widely in Southeast Asia. Just one macaque species, the Barbary macaque (*Macaca sylvanus*) is found in Africa, occurring north of the Sahara in Algeria and Morocco.

Habitat

Cheek-pouched monkeys occur in a remarkably wide range of habitats, spanning the spectrum from semi-arid scrub vegetation marked by strictly seasonal rainfall to highly humid evergreen tropical rainforest with year-round rainfall. Most species depend upon trees to some extent, at least for sleeping sites during the night. Most species typically inhabit evergreen tropical rainforest. This applies to most guenons (genera *Allenopithecus* and *Cercopithecus*), talapoins (genus *Miopithecus*), mangabeys (genera *Cercocebus* and *Lophocebus*), drills and mandrills (genus *Mandrillus*) and many Asiatic macaque species (genus *Macaca*). By contrast, baboons (genus *Papio*), geladas (genus *Theropithecus*), a few guenons (genera *Chlorocebus* and *Erythrocebus*), and some macaque species (e.g. the Barbary macaque, *Macaca sylvanus*) commonly live in relatively open, dry-country habitats. The most extreme example of the latter is probably provided by the chacma baboon (*Papio ursinus*), which lives under extremely dry, almost desert-like conditions in some parts of southern Africa.

Behavior

All members of the subfamily Cercopithecinae are diurnal. Most species are essentially arboreal, but there are also

The gelada (*Theropithecus gelada*) is native to the grasslands of Ethiopia. (Photo by Aaron Ferster/Photo Researchers, Inc. Reproduced by permission.)

The lesser white-nosed monkey (*Cercopithecus petaurista*) is diurnal and arboreal. (Photo by Art Wolfe/Photo Researchers, Inc. Reproduced by permission.)

The stump-tailed macaque (*Macaca arctoides*) carries food in its cheek pouches. (Photo by Renee Lynn/Photo Researchers, Inc. Reproduced by permission.)

numerous species that have become adapted for terrestrial activity. In all cases, locomotion is typically quadrupedal. All cheek-pouched monkeys live in gregarious social groups that move around and feed as relatively cohesive units, organized in some cases as harem groups with a single adult male (one-male groups) and in others as groups containing several adult males (multimale groups). Monogamy is extremely rare as a social system in cercopithecine monkeys. Forest-living guenons of the genus *Cercopithecus*, patas monkeys (*Erythrocebus*), hamadryas baboons (*Papio hamadryas*), and geladas (*Theropithecus*) all form one-male groups. In some species that exhibit one-male groups, surplus males form bachelor male groups, and it is possible for several harem groups and bachelor male groups to live in large herds, as is the case with hamadryas baboons and geladas. As a general rule, females tend to stay in their natal groups, whereas males migrate at round the time of sexual maturity.

Feeding ecology and diet

As a rule, cheek-pouched monkeys feed predominantly on relatively high-energy foods such as fruits, seeds, insects, and

The savanna or yellow baboon (*Papio cynocephalus*) with young. (Photo by Tom & Pat Leeson/Photo Researchers, Inc. Reproduced by permission.)

(occasionally) other vertebrates. Although many species also eat leaves, these typically represent a minor part of the diet and relatively nutritious young leaves are generally preferred. However, the bilophodont teeth that characterize all Old World monkeys probably represents an adaptation for mastication of resistant material such as leaves, so it seems likely that the common Old World ancestor of both cheek-pouched monkeys (subfamily Cercopithecinae) and leaf-monkeys (subfamily Colobinae) was folivorous at least to some extent. On the other hand, the cheek pouches that characterize all cercopithecine monkeys probably constitute an adaptation for temporary storage of small, easily collected food items such as fruits and seeds, so their development in the common ancestor of Cercopithecinae probably presumably a shift towards increased consumption of such food items. With respect to diet, the most aberrant species among the cheek-pouched monkeys is the gelada (*Theropithecus gelada*), which feeds extensively on grass shoots, seeds and roots and shuffles along on its hindquarters much of the day while foraging.

Reproductive biology

Monogamy is rare in cercopithecine monkeys; most are polygamous.

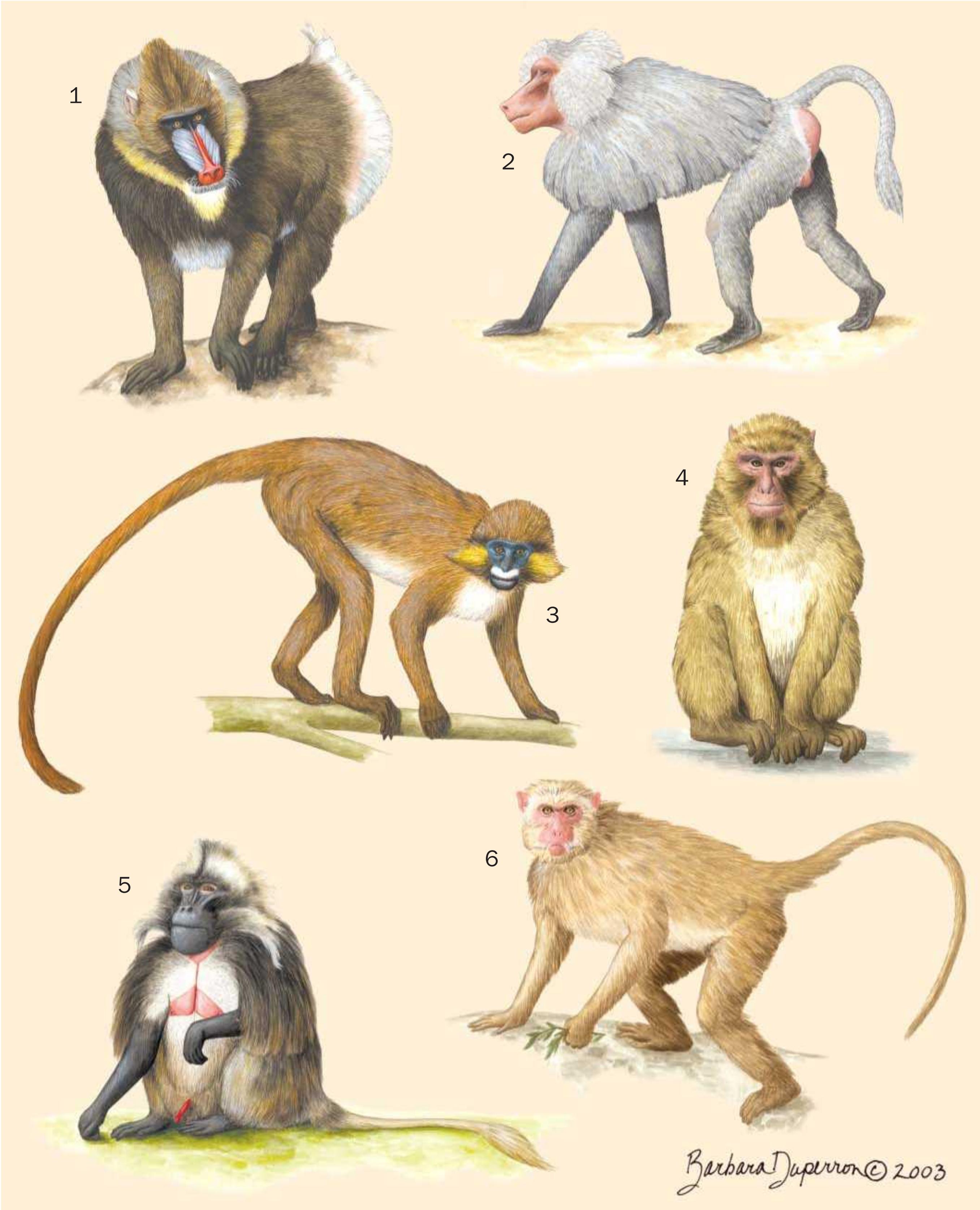
Single births are typical, although twins are born very occasionally, and two teats (mammae) are consistently present in the chest region. All species have a menstrual cycle lasting approximately a month and marked by externally visible menstrual bleeding. In many species, females have a conspicuous sex skin in the genital region that changes in coloration and size over the course of the ovarian cycle. Maximum swelling and the most prominent degree of coloration (commonly bright red) occur around the time of ovulation, approximately halfway between menstrual episodes. Conspicuous sex swellings are found in baboons, mandrills, some mangabeys, short-tailed macaques, swamp monkeys and talapoins, but they are less prominent or virtually absent in long-tailed macaques and forest-living guenons and other mangabeys. Geladas are highly unusual in that the sex skin is located on the chest, as a patch bordered by vesicles that varies in color and prominence over the ovarian cycle. This special development is undoubtedly linked to the fact that geladas spend much of the day shuffling along on their hindquarters while foraging. Placentation is of a highly invasive hemochorial type. The gestation period is long, varying between 162 days for the smallest species, the talapoin (*Miopithecus talapoin*), and 187 days for one of the largest, the chacma baboon (*Papio ursinus*).

Conservation status

One species is Critically Endangered (*Macaca pagensis*), eight species are Endangered (*Cercopithecus diana*, *Cercopithecus erythrogaster*, *Cercopithecus preussi*, *Cercopithecus sclateri*, *Macaca maurus*, *Macaca nigra*, *Macaca silenus*, and *Mandrillus leucophaeus*), 10 are Vulnerable (*Cercopithecus erythrotis*, *Cercopithecus solatus*, *Macaca arctoides*, *Macaca assamensis*, *Macaca cyclopis*, *Macaca leonina*, *Macaca nemestrina*, *Macaca sinica*, *Macaca sylvanus*, and *Mandrillus sphinx*), and 16 are Near Threatened (*Allenopithecus nigroviridis*, *Cercocebus atys*, *Cercocebus galeritus*, *Cercocebus torquatus*, *Cercopithecus hamlyni*, *Cercopithecus lhoesti*, *Lophocebus aterrimus*, *Macaca fascicularis*, *Macaca hecki*, *Macaca mulatta*, *Macaca nigrescens*, *Macaca thibetana*, *Macaca tonkeana*, *Papio hamadryas*, *Papio papio*, and *Theropithecus gelada*). Three species are listed as Data Deficient (*Cercopithecus dryas*, *Macaca fuscata*, and *Macaca ochreata*).

Significance to humans

Cheek-pouched monkeys are commonly hunted for food (bushmeat) in Africa, Asia and Southeast Asia, although they are often protected at least to some extent by local customs in Asia and parts of Southeast Asia, as is the case with rhesus macaques (*Macaca mulatta*) and bonnet macaques (*Macaca radiata*) in India. Monkeys of the subfamily Cercopithecinae have also been used extensively in biomedical research because they are relatively closely related to humans. The rhesus macaque has long been established as a standard laboratory species and, among other things, served as a basic model for the study of reproductive processes and maternal behavior. Other macaque species, various baboons and some guenon species have also been widely used in biomedical research.



1. Mandrill (*Mandrillus sphinx*); 2. Hamadryas baboon (*Papio hamadryas*); 3. Moustached guenon (*Cercopithecus cephus*); 4. Barbary macaque (*Macaca sylvanus*); 5. Gelada (*Theropithecus gelada*); 6. Rhesus macaque (*Macaca mulatta*). (Illustration by Barbara Duperron)

1. Allen's swamp monkey (*Allenopithecus nigroviridis*); 2. Gray-cheeked mangabey (*Lophocebus albigena*); 3. Patas monkey (*Erythrocebus patas*); 4. Angolan talapoin (*Miopithecus talapoin*); 5. Collared mangabey (*Cercocebus torquatus*); 6. Grivet (*Chlorocebus aethiops*). (Illustration by Barbara Duperron)

Species accounts

Allen's swamp monkey
Allenopithecus nigroviridis

SUBFAMILY
Cercopithecinae

TRIBE
Cercopithecini

TAXONOMY
Allenopithecus nigroviridis (Pocock, 1907), upper Congo River, Zaire. This species was originally included in the genus *Cercopithecus*, but it resembles members of the tribe Papionini in a number of features and is best allocated to the separate genus *Allenopithecus*.

OTHER COMMON NAMES
English: Allen's swamp guenon; French: Cercopithèque d'Allen; German: Schwarzgrüne Meerkatze.

PHYSICAL CHARACTERISTICS
Fur greenish gray dorsally and pale gray (sometimes with an orange tinge) ventrally. Webbing is present between the fingers and toes. The ischial callosities are fused across the midline in adult males. In males, the scrotum is pale blue. Average head and body length: 18 in (45 cm); average tail length: 17.5 in (43.5 cm). There is marked sexual dimorphism in body size. Body mass: 13 lb 9 oz (6.15 kg) for males and 7 lb (3.20 kg) for females.

DISTRIBUTION
Central Congo basin in eastern Congo-Brazzaville and western Democratic Republic of the Congo (Zaïre).

HABITAT
Swampy forest areas and regularly flooded parts of riverine forests.

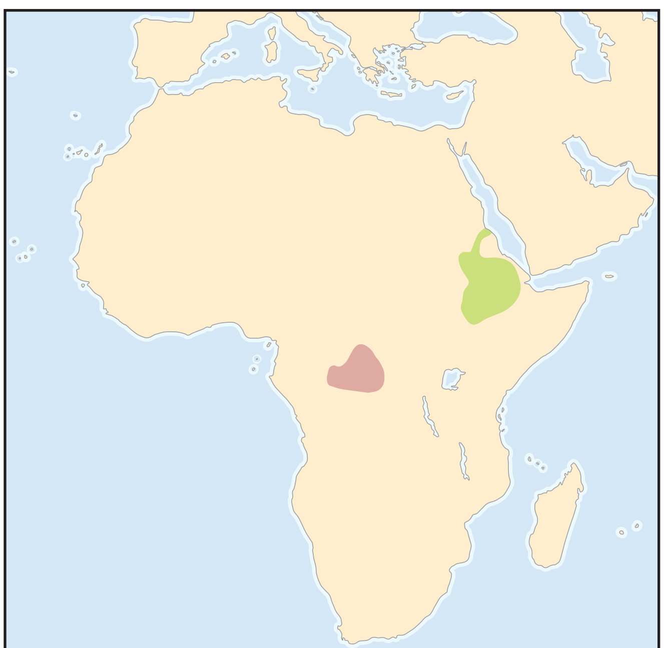
BEHAVIOR
Diurnal and semi-arboreal, typically occurring relatively low down in the forest. Swim well and may dive into rivers to escape from predators. Live in multimale groups of moderate size, 23 to 57, with very few rules.

FEEDING ECOLOGY AND DIET
Often forage on the ground. Diet primarily consists of fruit, supplemented by flowers, nectar, roots and animal prey (e.g., insects and, reputedly, fish).

REPRODUCTIVE BIOLOGY
Polygamous. Single births are typical. Females have a prominent sexual swelling that varies in size and coloration across the cycle. Little-studied in captivity, so reproductive characteristics such as the gestation period are unknown.

CONSERVATION STATUS
Listed as Near Threatened.

SIGNIFICANCE TO HUMANS
Hunted for bushmeat, particularly by hunters operating from boats. ◆



Chlorocebus aethiops
Allenopithecus nigroviridis

Patas monkey
Erythrocebus patas

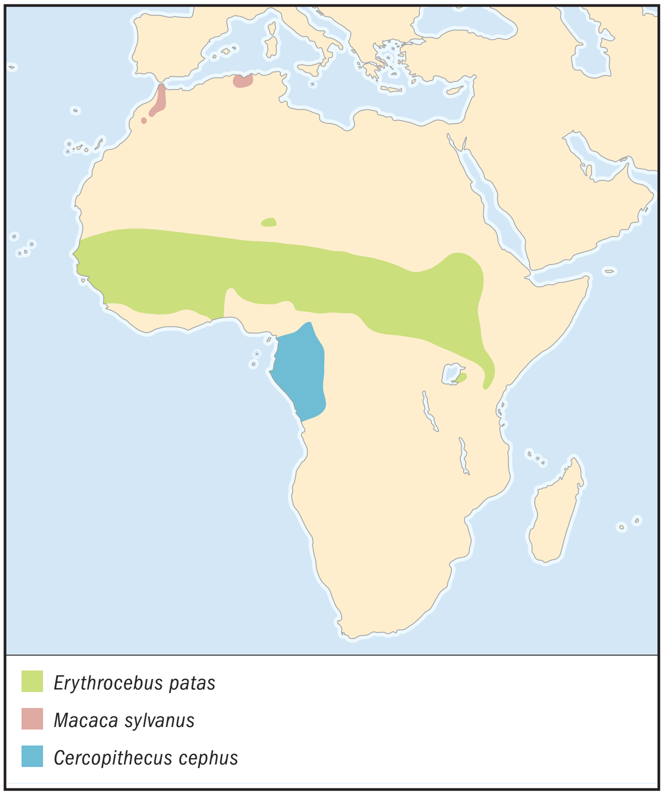
SUBFAMILY
Cercopithecinae

TRIBE
Cercopithecini

TAXONOMY
Erythrocebus patas (Schreber, 1775), Senegal. The patas monkey is sometimes included in the genus *Cercopithecus*, but it is so distinctive in many features that recognition of the separate genus *Erythrocebus* is surely justified. Four subspecies have been recognized.

OTHER COMMON NAMES
English: Hussar monkey, red monkey; French: Patas; German: Husarenaffe.

PHYSICAL CHARACTERISTICS
This is the largest species in the guenon tribe Cercopithecini and there is pronounced sexual dimorphism in body size, with males weighing almost twice as much as females. The body fur is bright reddish orange dorsally and white ventrally. Both sexes have a conspicuous white mustache. In non-pregnant females, the nose is black and there is a black band across the temples and above the eyes. In males, the scrotum is bright blue. The limbs are long and slender, and the patas monkey is



the only species that shows locomotion using the tips of the fingers (digitigrady) rather than the palms of the hand (palmigrady) as in other primates. Head and body length: 26 in (65.5 cm) for males and 19.5 in (49.0 cm) for females; tail length: 27.5 in (68.5 cm) for males and 20.5 in (51.0 cm) for females. Body mass: 27 lb 5 oz (12.4 kg) for males and 14 lb oz (6.5 kg) for females.

DISTRIBUTION
Very large range in sub-Saharan Africa, extending from Senegal in the west to the borders of Ethiopia in the east and southward in East Africa down to Serengeti and Mount Kilimanjaro.

HABITAT
Semi-desert, grassland, and woodland savanna characterized by a pronounced dry season.

BEHAVIOR
Diurnal and predominantly terrestrial, although they occasionally climb trees while foraging and sleep in trees at night. Typically form one-male groups of moderate size, with surplus males forming bachelor groups. However, extra-group males commonly invade harem groups and mate with the females during the breeding season.

FEEDING ECOLOGY AND DIET
Feeds on fruits, seeds, gums, grasses, and a variety of animal prey, including insects, lizards, and birds' eggs.

REPRODUCTIVE BIOLOGY
Polygamous. Single births are typical. Females do not have a sexual swelling. There are well-defined mating and birth seasons. Gestation period 167 days. Unusually, there is a change in facial color in females during late pregnancy: the black coloration is lost from the nose and from the band across the temples and above the eyes, and does not reappear until about six weeks after birth.

CONSERVATION STATUS
Not currently regarded as threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Angolan talapoin
Miopithecus talapoin

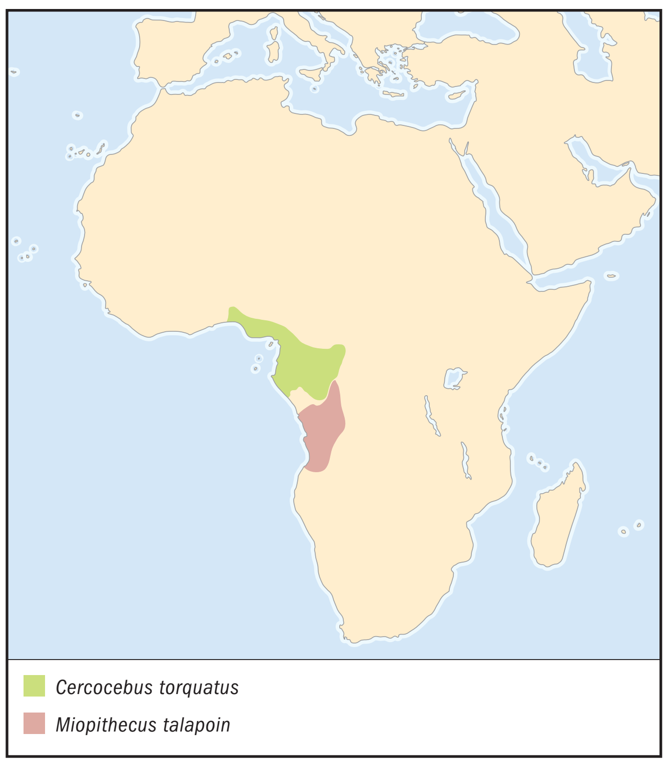
SUBFAMILY
Cercopithecinae

TRIBE
Cercopithecini

TAXONOMY
Miopithecus talapoin (Schreber, 1774), Angola. It has been customary to recognize only a single species in the genus *Miopithecus talapoin*, but the population in Cameroon (south of the River Sanaga), Río Muni and Gabon can be distinguished as a separate species, *Miopithecus ogouensis*.

OTHER COMMON NAMES
English: Angolan dwarf guenon; French: Talapoin d'Angola; German: Zwergmeerkatze.

PHYSICAL CHARACTERISTICS
Talapoins are the smallest Old World monkeys and almost certainly evolved from a larger-bodied ancestor by dwarfing. The fur is coarsely banded yellow-and-black dorsally and white or grayish white ventrally. The nose is back and the skin bordering the face is also black. In males, the scrotum is colored pink medially and blue laterally. There is mild sexual dimorphism in body size. Average head and body length: 16 in (40



cm); average tail length: 21 in (52.5 cm). Body mass: 3 lb 1 oz (1380 g) for males and 2 1b 10 oz (1120 g) for females.

DISTRIBUTION
Equatorial West Africa in western Democratic Republic of the Congo and the coastal region of Angola.

HABITAT
Occur in both primary and secondary gallery, mangrove, and swamp forests.

BEHAVIOR
Diurnal and predominantly arboreal, although they may occasionally descend to the ground while foraging. Talapoins are good swimmers and commonly sleep on branches overhanging rivers so that they can dive to escape from predators. Live in multimale groups usually of moderate size, but that can reach 100 or more individuals.

FEEDING ECOLOGY AND DIET
Diet consists of approximately equal proportions of fruits and animal prey, including various arthropods (mainly insects), small vertebrates, and eggs.

REPRODUCTIVE BIOLOGY
Polygamous. Single births are typical. Females have a prominent sexual swelling that varies in size and coloration across the cycle. Gestation period 162 days.

CONSERVATION STATUS
Not currently regarded as threatened.

SIGNIFICANCE TO HUMANS
Occasionally hunted as a source of bushmeat, although the small body size makes this relatively unprofitable. ◆

Grivet
Chlorocebus aethiops

SUBFAMILY
Cercopithecinae

TRIBE
Cercopithecini

TAXONOMY
Chlorocebus aethiops (Linnaeus, 1758), Sennaar, Sudan. It has been customary to include the grivet in the genus *Cercopithecus* along with other guenons, but grivets and their close relatives are sufficiently distinctive to warrant the separate genus name *Chlorocebus*. Molecular studies indicate that there was a relatively early separation between the grivet lineage and typical forest-living guenons in the genus *Cercopithecus*.

OTHER COMMON NAMES
English: Vervet monkey, green monkey; French: Grivet, cercopithèque vert; German: Graugrüne Meerkatze.

PHYSICAL CHARACTERISTICS
Fur grizzled olive agouti dorsally and white ventrally. The skin on the abdomen has a blue hue. The facial skin is black. Conspicuous long white whiskers are present on the cheeks, and there is a narrow white band above the eyes. There is a tuft of white hair at the base of the tail, and in males the scrotum is bright blue, contrasting with the bright red coloration of the penis. This pattern provides the basis for the "red, white, and blue display" of males. There is mild sexual dimorphism in body size. Head and body length: 19.5 in (49.0 cm) in males and 17 in (42.5 cm) in females; tail length: 25 in (63.0 cm) in males and 22 in (56.0 cm) in females. Body mass: 9 lb 6 oz (4.25 kg) for males and 6 lb 10 oz (3.00 kg) for females.

DISTRIBUTION
Occurs east of the White Nile in Sudan, Eritrea, and through Ethiopia as far as the Rift Valley.

HABITAT
Savanna woodland and riverine forest characterized by a pronounced dry season.

BEHAVIOR
Diurnal and semi-arboreal, feeding both in the trees and on the ground. Sleeps in trees at night. Lives in multimale groups of moderate size.

FEEDING ECOLOGY AND DIET
Broad diet including fruits, seeds, some leaves and animal prey (insects, reptiles, birds and small mammals).

REPRODUCTIVE BIOLOGY
Polygamous. Single births are typical. Females do not have a sexual swelling, but the perineal skin changes from white to pink around the time of ovulation. Gestation period 163 days.

CONSERVATION STATUS
Not currently regarded as threatened.

SIGNIFICANCE TO HUMANS
Grivets are occasionally hunted as a source of bushmeat. ◆

Moustached guenon
Cercopithecus cephus

SUBFAMILY
Cercopithecinae

TRIBE
Cercopithecini

TAXONOMY
Cercopithecus cephus (Linnaeus, 1758), Africa. The genus *Cercopithecus* is the most species-rich among the cheek-pouched monkeys, with a total of at least 26 species. Three subspecies have been recognized within the species *Cercopithecus cephus*.

OTHER COMMON NAMES
English: Moustached monkey; French: Cercopithèque moustachu; German: Blaumaulmeerkatze.

PHYSICAL CHARACTERISTICS
Fur brown with rufous tint dorsally and gray-white ventrally. The face is mainly black, with blue skin surrounding the eyes. There is a conspicuous white bar (moustache) across the upper lip. There is mild sexual dimorphism in body size. Head and body length: 23 in (58.0 cm) in males and 19.5 in (49.0 cm) in females; tail length: 31 in (78.0 cm) in males and 28 in (69.5 cm) in females. Body mass: 9 lb 8 oz (4.30 kg) for males and 6 lb 6 oz (2.90 kg) for females.

DISTRIBUTION
In equatorial West Africa, between the Sanaga River in southern Cameroon and the lower reaches of the Congo River in Angola.

HABITAT
Primary and secondary rainforest, gallery forest, and flooded forest.

BEHAVIOR
Diurnal and essentially arboreal, preferring the middle strata of trees. Forms relatively small one-male groups. Notable for forming mixed species groups (polyspecific associations) with certain other guenons and sometimes mangabeys.

FEEDING ECOLOGY AND DIET
Diet consists primarily of fruits and seeds, with a complement of animal prey (mainly insects, but also birds' eggs and nestlings).

REPRODUCTIVE BIOLOGY
Polygamous. Single births are typical. Females do not have sexual swellings. Little-studied in captivity, so gestation period unknown.

CONSERVATION STATUS
Not currently regarded as threatened.

SIGNIFICANCE TO HUMANS
Commonly hunted for bushmeat. ◆

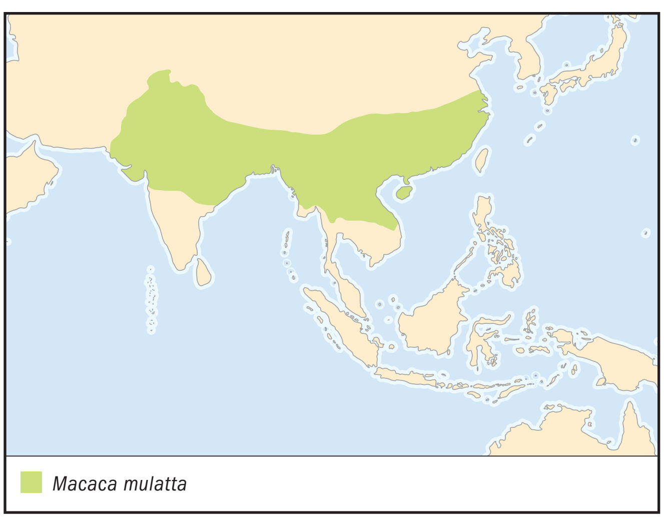
Rhesus macaque
Macaca mulatta

SUBFAMILY
Cercopithecinae

TRIBE
Papionini

TAXONOMY
Macaca mulatta (Zimmermann, 1780), Nepal Terai, India. The genus *Macaca* is the second most species-rich among the cheek-pouched monkeys, with at least 20 species. Within the species *Macaca mulatta*, six subspecies can be distinguished.

OTHER COMMON NAMES
English: Rhesus monkey; French: Macaque rhésus; German: Rhesusaffe; Spanish: Mono resus.



PHYSICAL CHARACTERISTICS
Fur medium brown dorsally, with a reddish tone on the hindquarters, and pale brown ventrally. The skin on the face and rump is red and in adult males the scrotum is also red. The tail is relatively short and there is moderate sexual dimorphism in body size. Head and body length: 21 in (53.0 cm) in males and 18 in (45.0 cm) in females; tail length: 10 in (24.5 cm) in males and 9 in (22.0 cm) in females. Body mass: 17 lb (7.70 kg) for males and 11 lb 13 oz (5.35 kg) for females.

DISTRIBUTION
Extremely wide geographical distribution, extending from eastern Afghanistan and northern India in the west to China and southern Vietnam in the east. In India, the southern limit lies some distance south of the River Godavari. The distribution of rhesus monkeys thus includes Afghanistan, Pakistan, India, Nepal, Bhutan, Bangladesh, Myanmar, China, Thailand, Laos, and Vietnam.

HABITAT
Live in a very wide spectrum of habitats, ranging from semi-desert scrub through dry deciduous and mixed deciduous forests and temperate cedar-oak forests to tropical forest and swamps.

BEHAVIOR
Diurnal and semi-terrestrial. Typically sleep in trees at night.

FEEDING ECOLOGY AND DIET
Broad diet includes fruits, seeds, gums, leaves, grasses, roots and invertebrates (mainly insects).

REPRODUCTIVE BIOLOGY
Polygamous. Single births are typical, although twinning occurs very occasionally. Females have no sexual swelling, but the perineal area shows cylical variation in color, becoming bright red around the time of ovulation. The average length of the ovarian cycle is 29 days and the gestation period is 167 days.

CONSERVATION STATUS
Listed as Near Threatened.

SIGNIFICANCE TO HUMANS
Rhesus macaques are protected by local custom in certain parts of their range, for example in much of northern India, and they play an important part in mythology. This species has become the standard laboratory primate for biomedical investigations and has hence been intensively studied in captivity. ◆

Barbary macaque
Macaca sylvanus

SUBFAMILY
Cercopithecinae

TRIBE
Papionini

TAXONOMY
Macaca sylvanus (Linnaeus, 1758), "Barbary Coast," north Africa. This is the only one of 20 species of the genus *Macaca* that occurs in Africa. All other species are confined to Asia and Southeast Asia.

OTHER COMMON NAMES
English: Barbary ape; French: Magot; German: Berberaffe; Spanish: Mono de Berberea.

PHYSICAL CHARACTERISTICS
Fur coarse; grayish yellow agouti dorsally and gray-white ventrally. Eyelids pale. Face pink in juveniles but becoming progressively mottled with dark freckles with increasing maturity. There is moderate sexual dimorphism in body size. Head and body length for males: 25.5 in (64.0 cm); tail length: 1 in (2.5 cm). Body mass: 31 lb 15 oz (14.5 kg) for males and 21 1b 13 oz (9.9 kg) for females.

DISTRIBUTION
Originally occurred widely in north Africa and even in southern Europe. Disappeared from Tunisia in relatively recent times and now restricted to isolated forest regions in Algeria and northeastern Morocco. There is a relatively large, artificially provisioned (fed) but otherwise free-ranging colony on Gibraltar.

HABITAT
Deciduous mixed oak and cedar forests with a pronounced dry season.

BEHAVIOR
Diurnal and predominantly terrestrial when moving and feeding. Typically sleep in trees at night. Live in moderate-sized multimale social groups that undergo fission when they become too large. Mating is promiscuous and paternity is widespread among group males. Infant carriage by males is particularly prevalent.

FEEDING ECOLOGY AND DIET
Feed predominantly on the ground but sometimes in trees, eating acorns in addition to cones, needles and bark of cedar trees. Also eat mushrooms and bulbs dug from the ground, along with various invertebrates (particularly insects and scorpions) and occasionally other animal prey.

REPRODUCTIVE BIOLOGY
Polygamous and promiscuous. Single births are typical, although twinning occurs very occasionally. Females have a prominent sexual swelling, but this is often gray-red rather than bright red when maximally inflated. Gestation period 164 days.

CONSERVATION STATUS
Listed as Vulnerable.

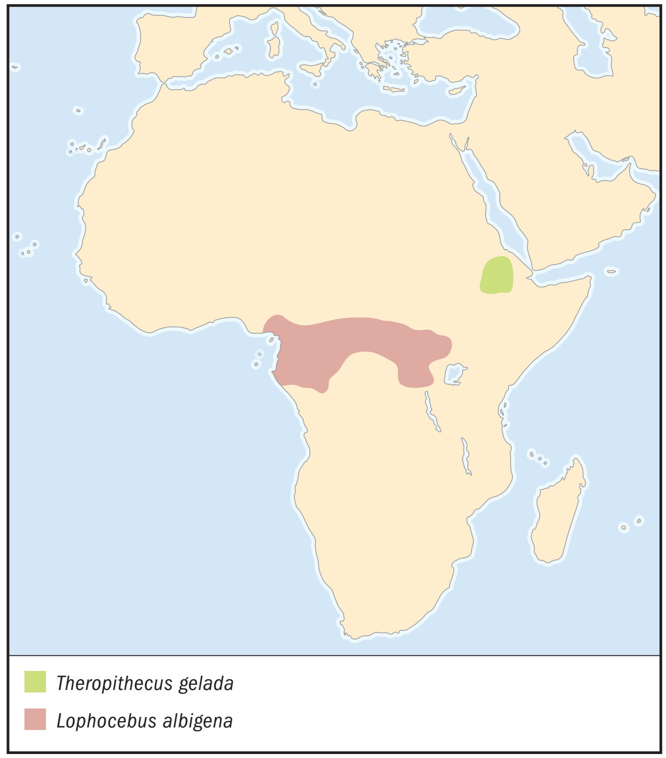
SIGNIFICANCE TO HUMANS
Barbary macaques are regarded as pests in Morocco because they eat the growing tips of trees. ◆

Gray-cheeked mangabey
Lophocebus albigena

SUBFAMILY
Cercopithecinae

TRIBE
Papionini

TAXONOMY
Lophocebus albigena (Gray, 1850), Mayombe, Zaire. Traditionally, all mangabeys were included in the genus *Cercocebus*. However, morphological evidence that was subsequently confirmed by molecular data indicated that there are, in fact, two distinct groups that have independently undergone shortening of the face, such that a pronounced hollow (fossa) has developed below each eye socket. Predominantly arboreal mangabeys that are more closely allied to baboons are now allocated to the separate genus *Lophocebus*.



OTHER COMMON NAMES
English: Mantled mangabey; French: Mangabé à gorge blanche; German: Mantelmangabe.

PHYSICAL CHARACTERISTICS
Long fur, blackish brown dorsally and dark gray ventrally. There is a single or paired tuft of hair on the head and there are long, pale whiskers on the cheeks. A cape of longer hair covers the shoulders, more prominently in males. There is moderate sexual dimorphism in body size. Head and body length: 22.5 in (56.0 cm) for males and 21 in (52.0 cm) for females; tail length: 32 in (80.0 cm) for males and 28.5 in (71.5 cm) for females. Body mass: 18 lb 3 oz (8.25 kg) for males and 13 lb 4 oz (6.00 kg) for females.

DISTRIBUTION
Range extends across tropical Africa from the Cross River in Nigeria eastwards into Uganda and Burundi and southwards to the coast of Gabon and the Alima River in Congo-Brazzaville.

HABITAT
Primary evergreen tropical rainforest, swamp forest, flooded forest, and semi-deciduous forest in some areas.

BEHAVIOR
Diurnal and essentially arboreal. Sleeps in trees at night. Lives in multimale groups of moderate size.

FEEDING ECOLOGY AND DIET
Predominantly eats fruit, but also feeds on animal prey (both invertebrates and vertebrates), leaves, and flowers.

REPRODUCTIVE BIOLOGY
Polygamous. Single births are typical. Females do not have a sexual swelling. Gestation period 176 days.

CONSERVATION STATUS
Not currently regarded as threatened.

SIGNIFICANCE TO HUMANS
Frequently hunted as a source of bushmeat. ◆

Collared mangabey
Cercocebus torquatus

SUBFAMILY
Cercopithecinae

TRIBE
Papionini

TAXONOMY
Cercocebus torquatus (Kerr, 1792), west Africa. All mangabeys were included in the single genus *Cercobecus* until it was realized that they fall into two distinct groups that have independently undergone facial shortening. Predominantly arboreal mangabeys that are more closely allied to baboons (*Papio*) are now allocated to the separate genus *Lophocebus*. More terrestrial mangabeys of the genus *Cercobecus* are instead related to *Mandrillus*.

OTHER COMMON NAMES
English: Red-capped mangabey, white-collared mangabey; French: Mangabé à collier blanc; German: Halsbandmangabe; Spanish: Mangabey de collar blanco.

PHYSICAL CHARACTERISTICS
Fur dark gray dorsally and contrastingly white ventrally. The hair on the crown is dark red, while the chin, cheeks and sides of the neck are white. Eyelids white, contrasting starkly with the black skin of the face. The tail has a distinctive white tip. Sexual dimorphism in body size is pronounced. For males, head and body length is 24 in (60 cm) and tail length is 27.5 in (68.5 cm). Body mass: 20 lb 15 oz (9.50 kg) for males and 12 lb 2 oz (5.50 kg) for females.

DISTRIBUTION
Tropical west Africa, from western Nigeria eastwards through Cameroon and southwards to Río Muni and Gabon.

HABITAT
Specifically associated with moist forest areas, occurring in primary and secondary swamp, mangrove, and riverine forest.

BEHAVIOR
Diurnal and largely terrestrial, using vegetation in the understory when in trees. Live in multimale groups of moderate size. Often form mixed groups (polyspecific associations) with various guenon species.

FEEDING ECOLOGY AND DIET
Fruits, leaves, flowers, and a variety of animal prey.

REPRODUCTIVE BIOLOGY
Polygamous. Single births are typical. Females have a pronounced sexual swelling. Gestation period 171 days.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Frequently hunted as a source of bushmeat. ◆

Hamadryas baboon
Papio hamadryas

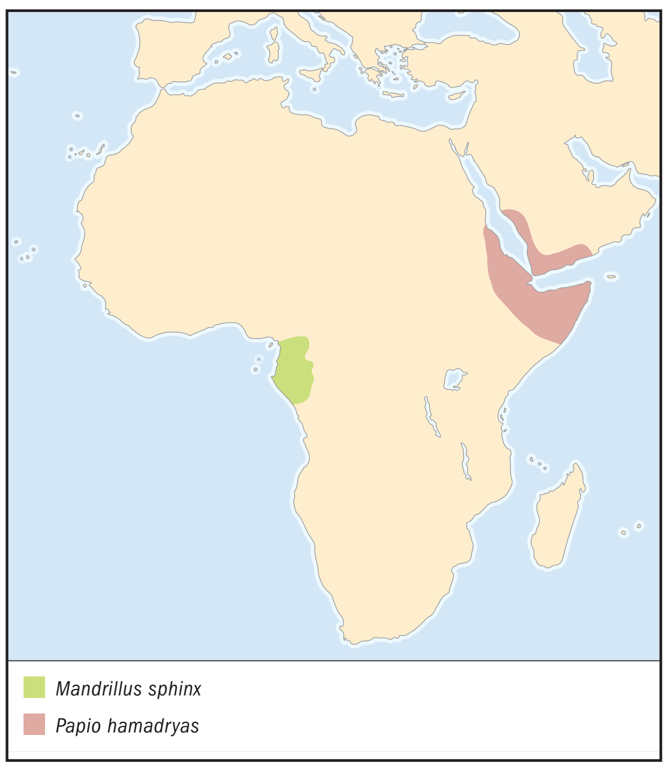
SUBFAMILY
Cercopithecinae

TRIBE
Papionini

TAXONOMY
Papio hamadryas (Linnaeus, 1758), Egypt. There has been considerable discussion about the taxonomy of baboons in the genus *Papio* because of the existence of hybrid zones between at least some of the main populations. One approach has been to recognize five different species, one being *Papio hamadryas* and the others being *Papio anubis*, *Papio cynocephalus*, *Papio papio*, and *Papio ursinus*. At the other extreme, it has been suggested that it would be appropriate to recognize only the single "superspecies" *Papio hamadryas*, as this name has priority, and to regard the five populations as subspecies. Molecular evidence indicates that *Papio ursinus* and *Papio papio*, at least, are distinct, and that *Papio cynocephalus* is probably distinct, whereas the separation between *Papio anubis* and *Papio hamadryas* is unclear.

OTHER COMMON NAMES
English: Sacred baboon, mantled baboon; French: Babouin hamadryas; German: Mantelpavian; Spanish: Papión negro.

PHYSICAL CHARACTERISTICS
There is marked sexual dimorphism in the pelage. In males, the fur is silvery gray dorsally, forming an extensive mane, and pale gray ventrally. Females lack a mane and the fur is olive



brown dorsally and pale gray ventrally. Males have much larger canine teeth than females. There is also pronounced sexual dimorphism in body size. For males, head and body length: 30 in (75.0 cm); tail length: 22 in (55.0 cm). Body mass: 46 lb 5 oz (21.0 kg) for males and 25 lb 2 oz (11.4 kg) for females.

DISTRIBUTION
Distributed on either side of the Red Sea, inhabiting northeastern Somalia, Ethiopia, and a small part of Sudan on the western side and Yemen and part of Saudia Arabia on the eastern side.

HABITAT
Semi-arid, sparsely wooded savanna, dry short-grass plains and alpine meadows.

BEHAVIOR
Diurnal and essentially terrestrial, sleeping on steep rock faces at night. Live in large troops in which the basic units are one-male groups (harem groups) and bachelor male groups organized first into clans and then into bands. Unusual among cheek-pouched monkeys in that males remain in their natal clans, whereas females migrate.

FEEDING ECOLOGY AND DIET
Forage primarily on the ground for grass seed, roots, tubers, and animal prey, including arthropods (particularly termites) and small vertebrates. Also eat leaves.

REPRODUCTIVE BIOLOGY
Polygamous. Single births are typical. Females have a prominent sexual swelling, which becomes bright red, along with adjacent areas of skin, around the time of ovulation. Gestation period 187 days.

CONSERVATION STATUS
Listed as Near Threatened.

SIGNIFICANCE TO HUMANS
Known as the sacred baboon because of its significance in Egyptian mythology. ◆

Gelada
Theropithecus gelada

SUBFAMILY
Cercopithecinae

TRIBE
Papionini

TAXONOMY
Theropithecus gelada (Rüppel, 1835), Semyen (Simien), Ethiopia. This is the only extant species in this genus, but several recent fossil relatives are known, some of them very large-bodied.

OTHER COMMON NAMES
English: Gelada baboon; French: Gelada; German: Dschelada.

PHYSICAL CHARACTERISTICS
There is marked sexual dimorphism in the pelage. In males, the fur is yellow-brown dorsally, with a long cape of darker hair, and dark grayish brown ventrally. There is a prominent tuft of pale whiskers on each cheek. Females lack a cape and the fur is yellow brown dorsally and dark grayish brown ventrally. The eyelids are very pale, contrasting with the dark facial skin. Males have much larger canine teeth than females. In both sexes, there is a large, hourglass-shaped patch of red skin on the chest. There is also pronounced sexual dimorphism in body size. Head and body length: 28.5 in (71.5 cm) for males and 23 in (57.5 cm) for females; tail length: 19 in (48.0 cm) for males and 15 in (37.0 cm) for females. Body mass: 41 lb 14 oz (19 kg) for males and 25 1b 13 oz (11.7 kg) for females.

DISTRIBUTION
Very limited range in the northern and central highlands of Ethiopia.

HABITAT
Inhabits montane grassland interspersed with dense thickets, but lacking tall trees and characterized by a pronounced dry season.

BEHAVIOR
Diurnal and essentially terrestrial. The basic social units are one-male groups and bachelor male groups, which are organized into bands and then into herds that may contain hundreds of members.

FEEDING ECOLOGY AND DIET
Specialized grass-feeder, foraging by shuffling along on the ischial callosities on the buttocks and plucking grass with the hands. Eats seeds, leaves, and bulbs, along with some animal prey.

REPRODUCTIVE BIOLOGY
Polygamous. Single births are typical. In females, which lack a sexual swelling in the perineal area, the coloration of the red chest patch changes over the ovarian cycle, reaching maximum intensity around the time of ovulation, when pale, bead-like vesicles bordering the chest patch are also most prominent. Gestation period approximately 170 days.

CONSERVATION STATUS
Listed as Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Mandrill
Mandrillus sphinx

SUBFAMILY
Cercopithecinae

TRIBE
Papionini

TAXONOMY
Mandrillus sphinx (Linnaeus, 1758), Bitye, Ja River, Cameroon. This is one of only two species in the genus *Mandrillus*.

OTHER COMMON NAMES
French: Mandrill; German: Mandrill; Spanish: Mandril.

PHYSICAL CHARACTERISTICS
Body fur is grizzled light brown dorsally and gray-white ventrally. There is pronounced sexual dimorphism in coloration of the face and rump, with males being more brightly colored than females. In males, the nose is bright red and flanked by blue, ridged paranasal bulges along with white whiskers. There is an orange-yellow beard in both sexes, larger in males. In males, the rump is also colored red and blue and the penis is bright red. The coloration of females is similar but less striking. Males also have much larger canine teeth than females. The tail is

markedly reduced. There is also a striking degree of sexual dimorphism in body size, with males weighing more that twice as much as females. For females, head and body length: 22 in (54.5 cm); tail length: 3 in (7.5 cm). Body mass: 69 lb 11 oz (31.6 kg) for males and 28 lb 7 oz (12.9 kg) for females.

DISTRIBUTION
Confined to equatorial tropical rainforest of west Africa in southern Cameroon, Río Muni, Gabon, and Congo.

HABITAT
Primary and secondary evergreen tropical rainforest, gallery forest, and coastal forest.

BEHAVIOR
Diurnal and semi-arboreal, sleeping in trees at night. Move around in large multimale troops that may be aggregates of individual one-male groups; it has recently been claimed that males are solitary and occupy territories through which females and young move.

FEEDING ECOLOGY AND DIET
Primarily feeds on fruits and seeds. Also eats leaves, bark, stems, and some animal prey, including both invertebrates (e.g., ants and termites) and vertebrates.

REPRODUCTIVE BIOLOGY
Polygamous. Single births are typical. Females have small but prominent sexual swellings that are bright red when maximally swollen around the time of ovulation. Gestation period 175 days.

CONSERVATION STATUS
Listed as Vulnerable.

SIGNIFICANCE TO HUMANS
Frequently hunted as a source of bushmeat. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Gray-cheeked mangabey *Cercocebus albigena*	Dark pelage and long, ruffled tail. Gray cheeks, long limbs, and long tail. Average body mass 19.8–22 lb (9–10 kg) for males, 14.12–15.4 lb (6.4–7.0 kg) for females.	Found in swamp, flooded, and primary evergreen forests, as well as secondary forests with evergreen forests nearby. Species is arboreal, diurnal. Group size is 14 to 17 individuals. Social system is either single male or multi-male.	Cameroon, Central African Republic, Congo, Equatorial Guinea, Gabon, Uganda, and Zaire.	Fruits, mainly figs, and seeds, but also eats leaves, foliage, flowers, and animal prey (arthropods).	Not threatened
Sooty mangabey *Cercocebus atys*	Dark gray to black pelage, giving sooty or dirty color. Long limbs and tail. Average body mass 18.7 lb (8.5 kg).	Found mainly in primary and secondary forests and in flooded, dry, swamp, mangrove, and gallery forests. Species is arboreal and diurnal. Group size can consist of up to 95 individuals. Moves quadrupedally.	Sierra Leone to Ghana.	Mainly fruits and seeds, but also eats leaves, foliage, flowers, animal prey, and gum.	Lower Risk/Near Threatened
Agile mangabey *Cercocebus galeritus* Spanish: Mangabeye del Río Tana	Upperparts are golden brown with black, or dark brown with gold. Underparts are orange or whitish. Long limbs and long tail. Whorl or parting of hair on top of head. Average male body mass 22.5 lb (10.2 kg), female 11.9 lb (5.4 kg).	Found mainly in forests that are seasonally flooded, and will also live in open-canopied gallery forests and in areas near rivers. Species is arboreal and diurnal. Group size ranges from 7 to 36 individuals. Moves quadrupedally. Main core of group is adult female and offspring. Social system is led by single male or is multi-male.	Cameroon, Central African Republic, Congo, Equatorial Guinea, Gabon, and Zaire.	Mainly fruits and seeds, but also eats leaves, foliage, flowers, animal prey, and gum.	Lower Risk/Near Threatened
Campbell's monkey *Cercopithecus campbelli* Spanish: Cercopiteco de Campbell	Coloration on upperparts ranges from greenish gray or black to greenish yellow or buff. Underparts are white or gray. Face is naked. Considerable color variation. Head and body length 12.8–27.6 in (32.5–70 cm), tail length 19.7–39.4 lb (50–100 cm).	Found in various habitats, including primary lowland rainforest, secondary forest, riverine forest, and drier woodland. Group size ranges from 8 to 13 individuals. Diurnal species that moves quadrupedally. Very territorial and there are two types of groups; ones with one male and a number of females, and male-only groups.	Gambia to Ghana.	Mainly fruits, leaves, and gums.	Not threatened
Diana monkey *Cercopithecus diana* Spanish: Cercopiteco diana	Pelage is black and surrounded by white beard. Large cheek pouches to carry food while foraging. Average male body mass 11 lb (5 kg), female 8.8 lb (4 kg).	Found mainly in primary and. secondary forests in upper canopy. Group size ranges from 14 to 50 individuals. Species is arboreal and diurnal. Moves quadrupedally. Species has unimale social structure.	Ghana, Guinea, Ivory Coast, Liberia, and Sierra Leone.	Mainly and primarily fruits and seeds, but also eats leaves and arthropods.	Endangered

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Blue monkey *Cercopithecus mitis* Spanish: Cercopiteco azul	Blue, reddish brown, or grayish brown. Large cheeks. Average male body mass 15.2 lb (6.9 kg), female 9.3 lb (4.2 kg).	Found in a variety of habitats, but never very far away from a water source. Group size ranges from 10 to 40 individuals. Species is highly arboreal and diurnal. Moves quadrupedally. Uni-male social system with polygynous mating system.	Angola, Burundi, Congo, Ethiopia, Kenya, Malawi, Mozambique, Rwanda, Somalia, South Africa, Sudan, Tanzania, Uganda, Zaire, Zambia, and Zimbabwe.	Mainly fruits, but also seeds, arthropods, and leaves.	Not threatened
Black mangabey *Lophocebus aterrimus* German: Schopfmangaben	Coarse and glossy black hairs, long brown whiskers, high conical crest. Head and body length 15–35 in (38.2–88.8 cm), tail length 17.1–30.1 in (43.4–76.4 cm), weight 6.6–26.5 lb (3–12 kg).	Found in primary and secondary forests, as well as flooded areas. Species is arboreal and diurnal. Group size ranges from 11 to 20 individuals. Moves quadrupedally. Females form linear hierarchy, main core of groups is females and offspring.	Central Zaire.	Mainly fruits and seeds, but also eats leaves, foliage, flowers, animal prey, and gum.	Lower Risk/Near Threatened
Toque macaque *Macaca sinica* French: Macaque couronné, macaque toque; Spanish: Macaca de Sri Lanka	Orange to red, female may have red face. Long limbs and long tail. Average male body mass 12.6 lb (5.7 kg), female 7.9 lb (3.6 kg).	Found in a variety of forest types, generally those that are located near water. This species does not live near humans. Average group size is 20.6 individuals. Species is diurnal, travels quadrupedally, has a multimale-multifemale social system. Less dominant individuals are forced to feed in areas with less food.	Sri Lanka.	Mainly fruits, but also eats flowers, insects, food from crops, and garbage.	Vulnerable
Drill *Mandrillus leucophaeus* Spanish: Dril	Olive-green, face and ears are black. Region around anus is colored red, which is more pronounced when excited. Swells exist on sides of nasal area. Infants born with light-colored face that darkens to black at 8 months of age. Average male body mass 44.1 lb (20 kg), female 27.6 lb (12.5 kg).	Found in mature primary forests that are lowland, riverine, or coastal. Sometimes also found in secondary forests. On Bioko Island, they can be found in altitudes from sea level to 3,940 ft (1,200 m). Group size ranges from 14 to 200 individuals. Species is diurnal, moves quadrupedally, and has a uni-male social system. Infanticide may occur in the wild.	Southeastern Nigeria; Cameroon, north of the Sanaga River and just south of it; and Bioko Island, Equatorial Guinea.	Mostly fruits, but also insects, leaves, roots, ground plants, cultivated crops, snails, turtle eggs, and coconuts.	Endangered
Guinea baboon *Papio papio*	Coloration has red tone to it. Hindquarters lack hair and are red in color. Males have mantle of fur around head. Head and body length 20–45 in (50.8–114.3 cm), tail length 18–28 in (45.6–71.1 cm).	Found in savanna, woodland, steppe, and gallery forests. Group size ranges from 40 to 200 individuals. Species has a multimale-multifemale social system, moves quadrupedally on the ground, is highly competitive (internally), and there is a matrilineal hierarchy.	Guinea, Liberia, Mali, Mauritania, Senegal, and Sierra Leone.	Mainly fruits, but also flowers, roots, grasses, bark, twigs, sap, tubers, bulbs, mushrooms, lichens, aquatic plants, seeds, shoots, buds, invertebrates, and small vertebrates, such as gazelle.	Lower Risk/Near Threatened

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Robert D. Martin, PhD

Gibbons

(Hylobatidae)

Class Mammalia

Order Primates

Family Hylobatidae

Thumbnail description
Small apes, with very long arms, gracile bodies, and no tail; upright body posture; monogamous, territorial, acrobatic suspensory, frugivorous, elaborate song duets; species distinguished by song especially female great call, and pelage color and markings, especially on head; the most diverse of living apes

Size
16.5–35.0 in (42–89 cm); 9.7–32.6 lb (4.4–14.8 kg)

Number of genera, species
4 genera; 10–12 species

Habitat
Tropical evergreen rainforest, as well as semi-evergreen forest

Conservation status
Critically Endangered: 1 species; Endangered: 2 species; Vulnerable: 3 species; Low risk: 4 species; Data Deficient: 1 species

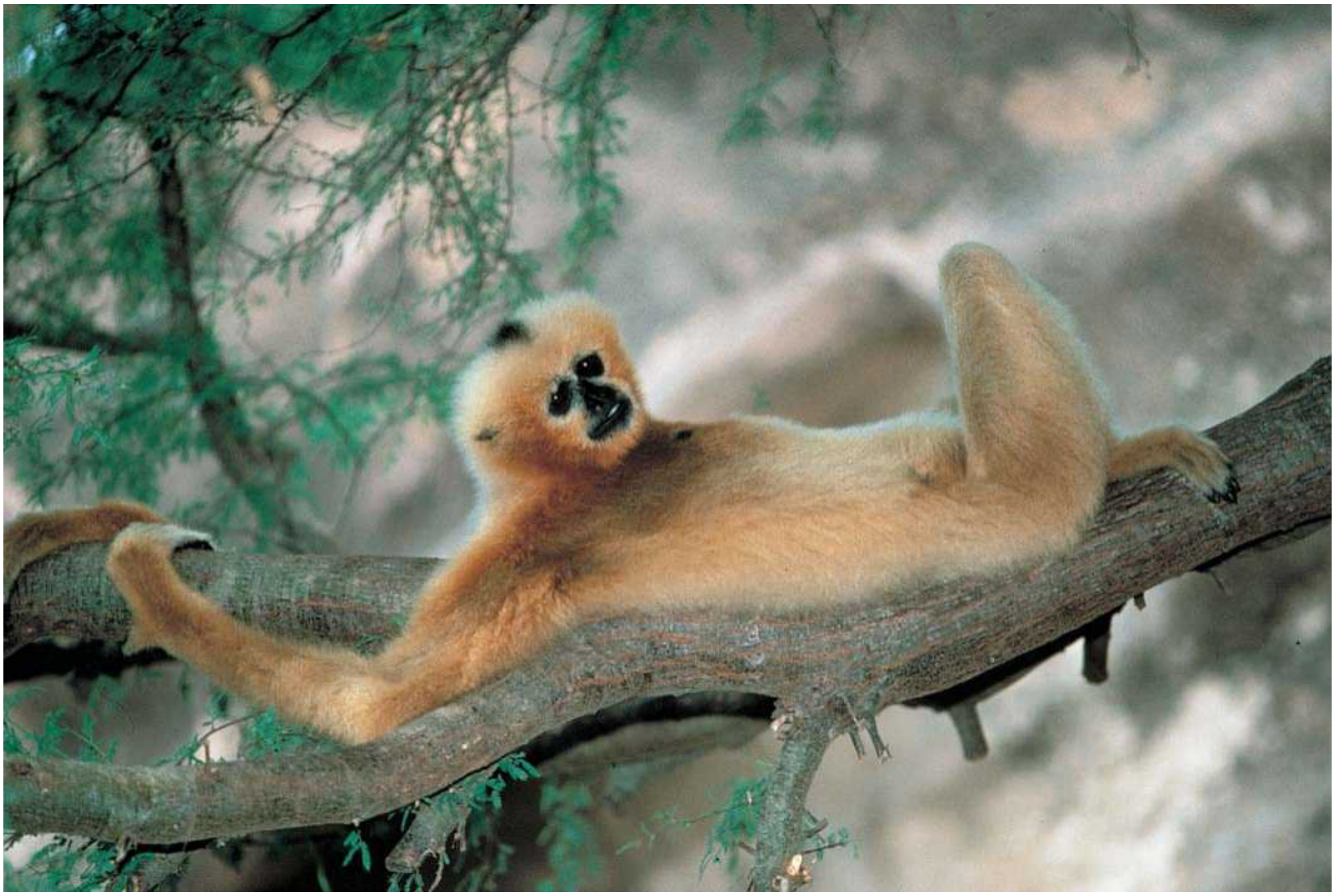
Distribution
Southeast Asia, from the Brahmaputra in the northwest, to southern China in the northeast, Sumatra in the southwest, and Borneo and Java in the southeast

Evolution and systematics

The Sunda Shelf emerged out of the sea as a consequence of volcanic activity about 12 million years ago (mya). It owes its uniquely rich fauna and flora to an admixture of immigrants, first from the Indian subcontinent, the Siva-Malayan fauna, and then later from China, the Sino-Malayan fauna. The frequent changes of sea level during the latter part of the Pleistocene alternately exposed the Sunda Shelf as one landmass, and then flooded it, leaving numerous islands. The gibbon populations so isolated speciated and then migrated when land bridges were restored. After the initial spread of three of the genera into different parts of the Sunda Shelf, gibbon speciation occurred within the Shelf (not on mainland Asia), followed by subsequent, sequential spread back to the mainland, with the hoolock (fourth genus in the van). The pileated and lar gibbons followed, and the Kloss, Bornean, and Javan gibbons originated on the edges of the Shelf, with agile and lar gibbons in the center. During the dry periods, the key rainforest relicts, into which gibbons and other forest animals retreated and out of which they spread when sea level rose, were in eastern Indochina and southern China, northeast Borneo, west Java, north Sumatra, and southern Myanmar, as well as the Mentawai Islands.

To determine the pattern of speciation from the ancestral gibbon, there has been thorough reanalysis of all morphological and behavioral characters by multivariate techniques. It had been difficult to resolve whether siamang, concolor, or hoolock gibbon is the most primitive, but the most prudent picture has the hoolock gibbon evolving first, followed by concolor, and then siamang; Kloss follows, and then Mueller's, moloch, pileated, lar, and agile. Patterns vary according to whether one uses cranial and dental, pelage, song, or all variables. There are still burning issues to be resolved concerning the validity of species and subspecies, especially in the northeast. Apart from clarifying distribution and abundance from lesser-known areas, DNA analysis is the best way to resolve disputes.

The genus *Hylobates* has now been divided into four genera: *Symphalangus*, the siamang (*H. syndactylus*) of Sumatra and Peninsular Malaysia; *Nomascus* comprises at least three species of crested gibbons, each with several subspecies, from southern China, Vietnam, east Cambodia, and Laos, including *H. concolor* in the north; *H. leucogenys* in the center; and *H. gabriellae* in the south; *Bunopithecus*, the hoolock gibbon (*H. hoolock*) of Assam, Bangladesh, and Myanmar, extending across northern



A white-cheeked gibbon (*Nomascus leucogenys*) on a tree branch in Southeast Asia. (Photo by Animals Animals ©Michael Dick. Reproduced by permission.)

Thailand into the southwest corner of China; and *Hylobates* comprises five to six allopatric species, extending from Thailand through the islands of the Sunda Shelf, including *H. klossi*, confined to the Mentawai Islands off the west coast of Sumatra; *H. pileatus* of southeast Thailand and west Cambodia; *H. moloch* of Java, now confined to the west; *H. lar*, with two or three subspecies in Thailand and Yunnan, China, one in the Malay Peninsula, and one in north Sumatra; *H. agilis*, with one subspecies between two lar subspecies in the Malay Peninsula, one over all of Sumatra south of Lake Toba, and one in the southwest of Borneo, west and central Kalimantan, bounded by the Kapuas and Barito rivers); and *H. muelleri*, with three subspecies radiating around the rest of Borneo.

In view of the extensive hybridization between the last two species in the center of the island, it may be necessary to sink *H. muelleri* into *H. agilis*, as a fourth subspecies of the latter, but it has been argued that the agile is more similar to the lar gibbon. The four genera are partly justified by molecular data indicating a split as long ago as 8 mya. It is argued that male and female solos were ancestral, but another more persuasive claim is that solos are derived from an ancestor that dueted, that dueting occurred early in gibbon ancestry. In most species, the song is split into the distinctive male and female parts of the duet.

Two populations of hybrid gibbons have been well known for many years: between *H. lar* and *H. pileatus* in Thailand and between *H. lar* and *H. agilis* in west Malaysia. The former results from a lar gibbon isolate pushed up against the pileated population in the Khao Yai National Park in Thailand; the hybrid zone is narrow, mixed social groups unstable, and gene exchange limited. A small hybrid population was discovered in the northwest of Peninsular Malaysia between *H. lar* and *H. agilis*, where a dam built in 1968 had created a lake, so that males wandering across the Mudah River and its tributaries where they were narrow were trapped on the wrong side of the lake, and they mated with females of the other species. Given the distinctive appearance and songs of the taxa, it is agreed that they are not conspecific. For conservation purposes in particular, it is vital to promote such taxa, especially as gene exchange is so limited.

The third population of hybrid gibbons, between *H. agilis albibarbis* and *H. muelleri* in the Barito watershed in the center of Borneo, now presents a very different problem. When discovered in 1979, it seemed little different from the other two restricted populations, and to be of recent origin. The agile gibbon had supposedly entered Borneo from Sumatra during a glacial period, when the sea level was low, with the Bornean (or Mueller's) gibbon having retreated to the warmer

A lar gibbon (*Hylobates lar*) grooming session. (Photo by Animals Animals ©Michael Dick. Reproduced by permission.)

and moister maritime influence of northeast Borneo (around present-day Sabah). When they spread toward each other they were separated by the Barito and Kapuas Rivers, except in the headwaters where tree crowns intermingled across the narrower rivers. It was concluded that there has been large-scale gene flow among hybrids for about 5,000–10,000 years over at least 1,930 mi^2 (5,000 km^2), so that agile and Bornean gibbons should be regarded as conspecific.

Physical characteristics

Hominoids share truncal erectness, for posture more than for locomotion, that seems to have evolved for climbing and sitting or hanging to feed, with their very long and mobile arms. The thorax is dorso-ventrally (antero-posteriorly) compressed, so that the scapula is dorsal and the shoulder joint projects laterally; hence, the great mobility in all directions, especially in the upper cone. The myth that all hominoids evolved from a brachiating ancestor has finally been put to rest. What the hominoids share is the ability to climb, pulling up with the strong and mobile arms, rather than the "rear-wheel drive" of monkeys that use their better developed legs.

Gibbons occupy a niche where suspensory behavior of all kinds, and the related functional anatomy, are of paramount importance. This is especially important for brachiating out under the more flexible branches and for suspending to feed in the terminal branches, where the more nutritious plant foods such as flowers and fruit are most abundant.

Those who group most *Hylobates* forms into two species, *H. klossi* and *H. lar*, argue that the cranial features of gibbons are very similar, making it difficult to separate them into species. The field workers respond that once theories have evolved an animal to fill this particular suspensory niche, such anatomical differences are unlikely. It is calls and pelage color and markings that are so distinctive. Females have the most readily diagnostic call, the "great call," and species are either monochromatic (black in the west and gray in the southeast) or polychromatic (in the center), and asexually or sexually dichromatic (in the north in the more open semi-evergreen habitat)—an intriguing geographical pattern. Since they both have a genetic basis, such features, with profound behavioral significance for reproduction, should be taken seriously in classifying gibbons.

Siamang emit harsh barking and booming notes—a staccato song, with the resonating boom produced by air passing across the entrance to an inflated lateral laryngeal ventricle. The hoolock gibbon also has a hooting call, but not so harsh to the ear. By contrast, the other gibbons are much more

A siamang (*Symphalangus syndactylus*) calling. (Photo by R. Van Nostrand/Photo Researchers, Inc. Reproduced by permission.)

melodic, with long pure notes rising and falling during the great call.

Distribution

Current range is essentially Southeast Asia, from the Brahmaputra River in the northwest, encompassing Bangladesh, most of the northeastern states of India, and Burma, across the Salween and Mekong Rivers through Thailand to Indochina (Cambodia, Laos, and Vietnam), and then up across the Red River into southern China. The rest of the range is the islands of the Sunda Shelf, down the Malay Peninsula (west Malaysia) to Sumatra and the Mentawai Islands, to Java and to the large island of Borneo (east Malaysia, Brunei, and Kalimantan).

Historically, concolor gibbons were distributed far more widely through China, occurring just north of the Yellow River, far north from the Yangtze a thousand years ago, with a steady contraction ever since, down to the far south of China.

Habitat

Gibbons span the semi-evergreen rainforests of mainland Asia north of the isthmus of Kra and the evergreen rainforests of the islands of the Sunda Shelf. The latter comprise the main gibbon habitat, but significant numbers of taxa and individuals occur in the more seasonal forests of mainland Asia, concentrated in pockets of evergreen forest, surviving in the moister areas under maritime influence, including Indochina, Thailand, Myanmar, and Bangladesh. The evergreen rainforest zone in the wet humid tropics is characterized by the main northeast monsoon early in the year, with a milder southwest monsoon in April or May, and an annual rainfall of 200 in (5,000 mm). Trees of the family Dipterocarpaceae are typical of most gibbon habitats, ranging from 1% to 43% of forest composition; there are in total about 400 trees per 2.5 ac (1 ha). Moraceae (figs) and Euphorbiaceae are the most common tree families used as food sources in gibbon habitats.

The siamang occurs more frequently in higher altitude forests. Otherwise, gibbons prefer the lowland forests, where diversity and density of fruit trees is greatest. The main features of increasing altitude are a decrease in the size of trees and in species diversity. Those smaller species that are common at higher altitude clearly provide sufficient food for siamang, in terms of leaves if not fruit. Altitudinal zonation is more compressed in isolated massifs such as the Malay Peninsula. At lower altitudes, there is a greater biomass and diversity of trees and, hence, of animals.

Sadly, lowland forests are the first to be cleared, as they are more accessible and have better soils. Nevertheless, gibbons can live in surprisingly small patches of surviving forest, and they cope very well (albeit at half the density initially in some areas) with selectively logged forest, since the colonizing tree species in the gaps and the proliferation of lianas provide abundant food. In a more detailed study before, during, and after selective logging in Sungai Tekam, west Malaysia, it was found that gibbon density was much less reduced than that of langurs.

Behavior

Information comes from nine field studies of eight gibbon species (omitting *H. concolor*), with the most detailed on the siamang (in Malaya), lar, agile, and Kloss gibbons, the sketchiest on the hoolock (now remedied in a Bangladesh study), and the most important on the pileated, moloch, and Mueller's gibbons. A 1992 study of the siamang and lar gibbon in the very rich forests of north Sumatra, and a 1999 study of the hybrid (agile with Mueller's) gibbon in Kalimantan and concolor gibbons have been investigated in Yunnan and on Hainan Island by Chinese primatologists, but have yet to be fully published or reviewed.

Group size averages 3.8, including an adult pair and two young, but range from two to seven; there may often be three to four young. Only the concolor gibbon has been recorded as living in polygynous groups, with two to three adult females and young, and an average group size of 7.2 in Yunnan, although this requires confirmation. Infants are up to two to three years old before are wholly capable of independent travel; juveniles up to five to six years; and subadults, physically adult-like, to eight years or so, when they leave the natal group.

Social interactions within groups are relatively infrequent, because the family group is so cohesive. Overt signals are rare, since the young watch and follow their parents. The only sounds heard, apart from the resounding group calls and the movement of branches and foliage, are squeals from an immature animal, usually the subadult, who has come too close to a parent, usually the male, and the bleats of an infant in distress as it is encouraged to move independently. Overt facial expressions are limited to open-mouth threats in aggressive/submissive interactions.

Only in the siamang does the male carry the infant during its second year of life, when weaned from the female (although it may still suckle at night as it sleeps with her). In this way, it learns first to recognize those animals on whom it is most dependent for its survival, the female and the male, and then the subadult with whom it plays while the adults groom. It interacts least with the juvenile. The adult female usually leads the group around the home range; hence, the need to shed the growing infant at the earliest opportunity. The juvenile follows the female, while the subadult lags behind in the rear. It is clear, however, that the adult male, from its central position, is influencing the direction of travel. The smaller gibbons separate more often, to forage on a broad front, as they move between the main food trees.

Grooming involves either adults and subadults during rest periods, or adults and young as they settle for the night (the juvenile tends to sleep with the male, the infant with the female). Play is the other main social activity, recorded in up to 4% of the active day in some studies (siamang, lar, pileated, and hoolock). While the infant (and juvenile) spend much time playing alone—swinging, jumping, manipulating tree parts—they do swing from, grapple with, and bite at adults and sub-adults, and sometimes the juvenile.

Song is a key diagnostic parameter for species and sexes. Gibbon family groups tend to sing daily to advertise their territory and strength of their pair bond. Male and female have distinctive parts; it is a true duet in most species, though most unusual among primates, and more common in birds. There is an introductory sequence, similar to the tuning up of an orchestra, which then leads into an organizing sequence for the great-call sequence of the female, often followed by a male coda; these two sequences then alternate for about three-minute intervals for the rest of the 15-minute bout. Group songs/duets may, of course, be much longer or shorter than this. In some species, male solos occur at dawn, and the duets follow after the first feed of the day. Kloss and moloch gibbon males in an area chorus before dawn, and females chorus after dawn; there is no duet.

The duet in all gibbon species serves to maintain mate and territory, especially to advertise availability and to attract a mate, to develop the pair bond as well as cement other bonds within the group, and to defend the mate and the territory. It seems that the female defends her mate and the male defends the forest space. These functions have been best clarified by playback experiments on Mueller's and agile gibbons in Borneo and on lar gibbons in Thailand. The resident pair has been shown to respond differently to the songs of neighbors than to those of strangers; the former they expect, the latter cause much agitation. The female reacts strongly to a strange female, as a threat to her pair-mate. Groups duet in response to a lone female calling, but silently approach a lone male that is calling.

A male pileated gibbon (*Hylobates pileatus*) calling in Thailand. (Photo by Terry Whittaker/Photo Researchers, Inc. Reproduced by permission.)

Feeding ecology and diet

Gibbons (*Hylobates* spp.) are monogamous, territorial, frugivorous, and suspensory with elaborate duets. The nine species studied have all been shown to conform to this pattern; they live at low-biomass density in small territories, because of their focus on small, scattered but predictable sources of ripe fruit. It is for these dietary reasons, in competition with the opportunistic, frugivorous macaques (*Macaca* spp.) living in large social groups and with the one-male groups of langurs (*Presbytis* and *Trachypithecus* spp.) eating leaves and seeds, that they have opted for monogamous family groups defending the area containing the necessary resources.

Gibbons are fruit-pulp specialists, like the spider monkeys (*Ateles* spp.) of the Neotropics, and the chimpanzee (*Pan* spp.)

Female pileated gibbon (*Hylobates pileatus*) in Thailand. (Photo by Terry Whittaker/Photo Researchers, Inc. Reproduced by permission.)

of Africa. But, unlike most primates, especially cercopithecids (*Macaca* spp. of Asia), gibbons compete more with large birds such as pigeons and hornbills for the small, colorful, sugary fruit. The monogamous family groups focus on small fruiting trees to avoid competition with the large multimale, multifemale groups of macaques and the large orangutan (*Pongo pygmaeus* in Borneo and north Sumatra in Indonesia).

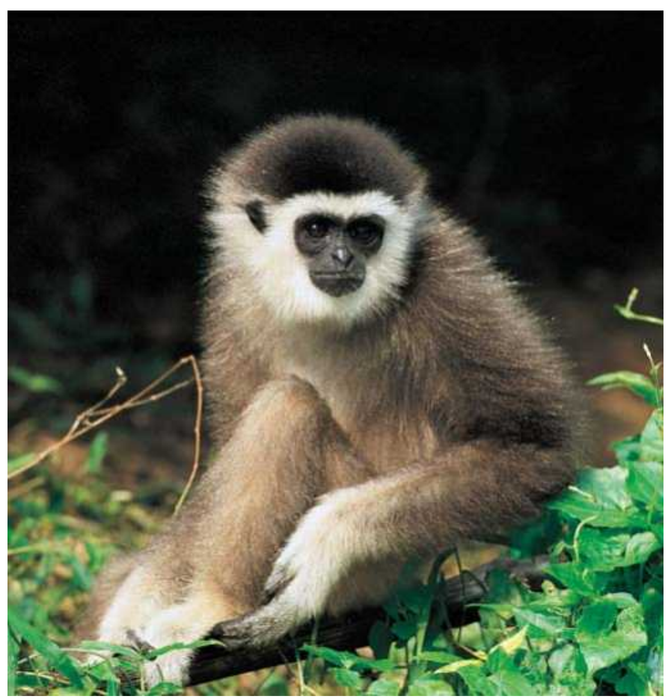
Gibbons differ from other primates in not having a markedly bimodal pattern of daily activity, with feeding peaks early and late in the day, and a long mid-day siesta. After active bouts of feeding, gibbons continue foraging in the cooler lower levels of the canopy through the heat of the day; they retire early for the night, usually several hours before sunset.

Gibbons are active for 9–10 hours each day on average in the evergreen rainforest, but for only 8–9 hours in Bangladesh. Lar gibbons tend to be active for a shorter time than siamang, with a 40–50% activity period for siamang compared to 30–40% for lar gibbons. Hoolock gibbons actually feed for about 40% of the active period.

Between 57% and 72% of feeding time is spent eating the reproductive parts of plants, such as fruit and flowers, except for the larger siamang (44%). About 25% of the fruit intake is figs (nearly 40% in siamang). Young leaves are important for most gibbons, especially the siamang, but not for the Kloss gibbon (where the soils are poor and the leaves are better defended chemically). Animal matter, mostly invertebrate, provides an important source of animal protein (about 10% of feeding time). More recent studies have confirmed that the gibbons of the more seasonal forests are finding as much, if not more, of such fruit, compared with those in the evergreen forests. Hoolock gibbons spend 79% of their feeding time on fruit.

Ketambe (Sumatra), unusually rich in fruit, has a very high biomass of primates. It was found that figs predominated in the diets of siamang and lar gibbons (44%). With 61% of the diet being fruit, the siamang had an intake of only 17% leaves, whereas the lar gibbon ate 71% fruit and only 4% leaves. Both fed on small fruit patches (the lar gibbon finding more of them) that were seasonally variable. There was more feeding competition in the lar group, hence its greater dispersion, lower cohesiveness. Tree fruit were more abundant than liana fruit, but only 37% of trees fruited annually, compared with 58% of lianas. Trees produced more young leaves seasonally, whereas lianas provided a more continuous supply. Both species consumed more than 20% animal matter.

The consumption of fruits and dispersal of seeds is a key feature of the coevolution of animals and plants in the natural regeneration of forests. Different animals remove seeds of different sizes, which can be related to a suite of characters that distinguish fruit whose seeds are dispersed by primate or bird or rodent. For some plant species, gibbons are key seed dispersers; for others, especially those dispersed by several bird species, gibbons are less important dispersers.



Mueller's gibbon (*Hylobates muelleri*) is found only in Borneo. (Photo by Tom & Pat Leeson/Photo Researchers, Inc. Reproduced by permission.)

The density of monogamous family groups of gibbons (usually four individuals) varies from 1.5 (two species in Malaya) to 6.5 (Thailand) groups/mi^2 (km^2); the combined biomass of siamang and lar gibbons in Malaya was 278 lb/mi^2 (l26 kg/km^2), with 75 lb/mi^2 (34 kg/km^2) for Mueller's gibbon in Kalimantan, and 229 lb/mi^2 (l04 kg/km^2) for lar gibbons in Thailand. Thus, there are not fewer gibbons in the more seasonal forests further north. Biomass density relates more closely to food availability, presumably at times of scarcity.

Pileated, Mueller's gibbons, and siamang travel 0.49–0.56 mi (0.8–0.9 km) daily on average, while the others travel 0.74–0.93 mi (1.2–1.5 km). Siamang have been seen to travel as little as 490 ft (150 m) a day (when fruit were scarce) and as much as 9,380 ft (2,860 m) a day; hoolock gibbon day ranges vary 919–11,155 ft (280–3,400 m); other gibbons show comparable variation from about 1,312–8,202 ft (400–2,500 m). These changes reflect variation in food distribution, but in the monsoon forests, where leaves are not such a viable alternative for the smaller gibbons, increased day ranges may reflect a wider search for sufficient fruit.

Home range varies between 39.5 ac (l6 ha) for lar gibbons in Thailand and 42 ac (l7 ha) for moloch gibbons, to 111 or more mi (45 or more ha) for hoolock in Bangladesh, 138 ac (56 ha) for lar gibbons in Malaya, where siamang home ranges are also large at 74–99 ac (30–40 ha). Where there are two species of gibbon, which always involves the larger siamang, it is likely that the homes ranges of both are larger than when alone, because of competition for particular fruit trees.

Of the home range, 62% (siamang) to 94% (moloch gibbon) are defended as territories for the exclusive use of the resident group; most are clustered around 75%. Again, the gibbons of the more seasonal forests are not traveling further around a larger area, but they are defending 80–90% of the home range. Thus, home ranges average about 86.5 ac (35 ha), of which about 75% is defended. While siamang travel around their home range in single file, the smaller gibbons more often scatter to forage as they move between food sources in which they all feed.

A pileated gibbon (*Hylobates pileatus*) climbing. (Photo by Animals Animals ©Michael Dick. Reproduced by permission.)

Reproductive biology

There has been extensive discussion of the key features of gibbon sociology—monogamy and territoriality. They confer both benefits and costs. In being monogamous, the male is reducing his potential reproductive success, and it is thought to be the available niche and distribution of food that leads to this sacrifice, and to the energetic costs of patrolling and defending this territory with its rich and predictable food supply. Females exclude other females, and males exclude strange males to maintain the system. The elaborate duets performed by most gibbons serve, to different extents, both to form and develop the pair bond and to establish and maintain the territory. These songs are reinforced by boundary patrols while seeking food, and by chases back and forth across the boundary. The complex interaction of all these factors defies simple explanations of such behaviors.

It is not clear whether the greater frequency and duration of disputes in hoolock gibbons, compared with other species, is a function of greater tension in smaller forest patches, or some specific feature of hoolock socioecology. With the male tending to be promiscuous, even polygynous, it is important for the female to impose monogamy on the male to increase her reproductive success and to help in finding food, detecting predators, and excluding neighbors.

Given the stability of gibbon family groups for long periods, the details of dispersal of the maturing young and of the formation of new groups are of special interest because of their dynamism and relative rarity. The pattern that emerges is of young adults, recently excluded from the natal group, acquiring a territory with or without parental help, and thence a mate. Daughters tend to wander less far from the parental territory than sons and are more likely to receive parental help. A rare alternative is to take over the natal territory when one or both parents disappear; if one parent survives, the young may mate with him or her, but this incest is usually transient and/or reproductively ineffective. Parental-care strategy is to promote reproductive success in offspring, but the subadult emerges as a potential sexual competitor to the same-sexed parent; hence, it has to be excluded.

Female Mueller's gibbon (*Hylobates muelleri*) sunning. (Photo by Animals Animals ©J. & P. Wegner. Reproduced by permission.)

Gibbons are monogamous, because they are adapted to surviving on small fruit trees; it is almost impossible to get enough data to prove this. Reichard and Sommer (1997) echo the female resource/male mate defense argument, suggesting that extra-pair copulations (12% of those seen) help to confuse paternity and forestall infanticide; hence, kin relations extended into neighboring groups. They worked close to the *H. lar*/*H. pileatus* hybrid zone in Thailand, studying the isolated lar population, whose home ranges unusually overlapped by 64%. They found encounters between groups were common, occupying 9% of the active day.

Gibbons have been argued to be monogamous and territorial because of their adaptation to small, scattered sources of pulpy fruit. Since they have had to learn the availability of such resources, they cannot afford to share them with conspecifics. The adult male can only effectively defend an area adequate for one female and their offspring, thus they have overcome the basic polygynous drive that characterizes most mammals, including most primates. In exploiting a niche unoccupied by other primates, they have sacrificed the reproductive success that occurs in polygynous breeding systems. Infants are born singly every two to three years, depending on food availability for the parents; that is, mating occurs when there is a seasonal increase in food, usually fruit.

Conservation status

Conservation embraces both the total protection of key areas (e.g., watersheds, rare/unique ecosystems, refuge of key animal/plant species) and the management of forests for the benefit of animals and plants as well as people. Forest clearance is the greatest threat to the survival of primates and many other animals, and to human welfare. For local and global environmental and economic welfare, close to 50% of tropical countries need to be kept forested; once the area dips below that proportion, climatic changes and water and soil problems seem to escalate catastrophically. Since few countries seem able to afford to keep more than 10% of their forests totally protected, the remaining 40% needed has to be managed for sustained yields of a wide variety of products. Managed forests provide a buffer zone for protected forests, which supply replenishment of plants and animals. The third part of the strategy is to use to maximum efficiency the land already cleared of forest or land that is so degraded that its role as forest cannot be redeemed.

Selective logging represents the compromise between human and animal needs in the long term, but it will only work if timber extraction is very light and carefully controlled. Even if only 10 trees/2.5 ac (1 ha) are extracted, 4% of trees and 45% of the total stand (68% of plant biomass) are damaged during access, felling, and extraction. It is the larger and more frugivorous species that are the most vulnerable, but their populations should recover fully within 20–30 years, if there is no further interference. Such logging enhances the diversity of microhabitats characteristic of the mosaic of succeeding successional stages of climax forest; it is these colonizing plants of immature forest that provide more nutritious, less chemically defended foods. The persistence of primary forest in an area may be crucial to the survival of certain animal species. In contrast to the tolerance of gibbons and langurs, orangutans and proboscis monkeys are seriously affected by selective logging.

Shifting cultivation has been practiced for centuries, especially along rivers, with peoples living in harmony with the forest, since the forest has recovered by the time people return. Increased population and less forest mean that return time is so reduced that this practice is no longer sustainable.

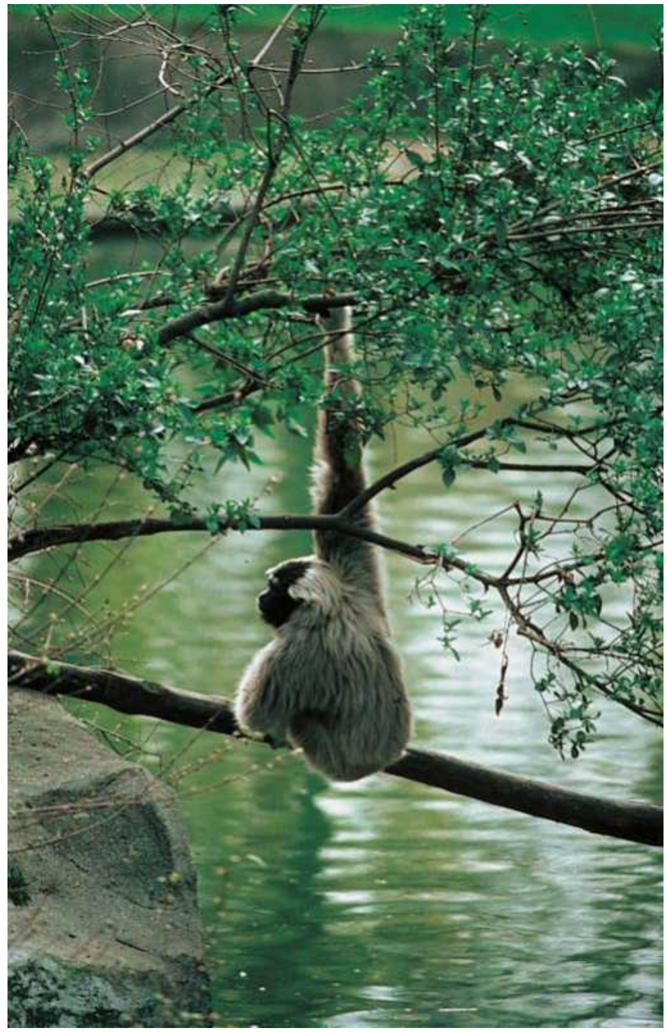
The loss of income from timber through reduced (sustainable) logging has to be balanced (easily exceeded in the long term) by income from other forest products. The exploitation of such forests can be maximized through knowledge of key animal-plant relations promoting the regeneration of such resources. The target has to be less damage to the forest and more produce on a sustainable basis. What is needed is the improved protection of watersheds and national parks representing all ecosystems, especially the richest, lowland ones, with the efficient, sustainable management of large buffer zones, and the more productive use of land already cleared of forest. Such a strategy should ensure that viable populations of all gibbon taxa survive in perpetuity, though it will not be easy.

The predictions of a drastic reduction in gibbon populations are being realized, but, as the clear-felling of forest declines, their prospects are boosted as long as adequate selectively logged forest persists, since gibbons have shown themselves to be very adaptable to such disturbance. The moloch, Kloss, pileated, and crested gibbons would seem to be the taxa most threatened with extinction, i.e., those with the most restricted and threatened ranges. No taxon is safe, however, from the extensive deforestation and other illegal activities that are currently rife throughout the Asian region. The larger mammals, with the greatest need for space, are the most vulnerable. Increased efforts by habitat countries, along with international support maintain extensive areas of forest for protection and sustainable management, may succeed. However, pressures from the human populations with their serious survival problems are understandably immense.

Captive breeding worldwide provides invaluable publicity of the plight of rainforest animals and education, including fundraising opportunities for conservation activities. It also helps to conserve the gene pool, by using meticulous studbooks. The prospects of reintroduction to the wild habitat are gloomy, given the costs involved and the lack of available habitat. However, a French nongovernmental organization (NGO), Eco-Passion, and facilities are being developed in Indonesia to accommodate confiscated gibbons, to form pairs, and, when ready, to reintroduce them to protected forest. If habitat is available, it is much more cost effective and successful to translocate social groups from doomed forest fragments to any under-stocked protected forest.

Little progress has been made in developing techniques of translocation, presumably because of the physical difficulties involved and the lack of empty suitable habitat. It remains a possible solution where populations become critically endangered, but adequate preparation, care (with veterinary supervision), and monitoring are essential. The prime effort must be to protect natural habitat and to conserve wildlife within it. It has yet to be determined to what extent costly captive breeding (at home or abroad), with research on nutrition and breeding, is necessary to boost populations.

Education is essential at various levels, as successful programs in many countries demonstrate, including Rwanda, Brazil, Peru, Costa Rica, and Indonesia. Most critical, however, is the need to influence the governments of tropical countries and, more importantly, the governments of "user countries" as well as the heads of international and national commercial concerns. Policy and activities must change rapidly, to avert impending catastrophes.



A moloch gibbon (*Hylobates moloch*) climbs over stream. (Photo by Animals Animals ©Gerald Lacz. Reproduced by permission.)

Significance to humans

Their upright posture, lack of tail, and bipedalism when not brachiating remind people of themselves, especially in view of their large eyes and appealing faces, enhanced by some kind of face ring, and melodic and mournful songs. Gibbons are utterly enchanting for these reasons, made more so by their graceful and dramatic arm-swinging locomotion, as they literally fly through the trees. They are the focus of a variety of folklore. Generally, they are respected, and local people are afraid to harm them, though they are hunted by indigenous people in Malaysia. They may also give way to pressures from outside, or outsiders come in and hunt them for food or medicine or live trade.

1. Male white-cheeked gibbon (*Nomascus leucogenys*); 2. Female hoolock gibbon (*Hylobates hoolock*); 3. Female black crested gibbon (*Nomascus concolor*); 4. Male golden-cheeked gibbon (*Nomascus gabriellae*); 5. Siamang (*Symphalangus syndactylus*). (Illustration by Emily Damstra)

1. Agile gibbon (*Hylobates agilis*); 2. Male mueller's gibbon (*Hylobates muelleri*); 3. Lar gibbon (*Hylobates lar*); 4. Moloch gibbon (*Hylobates moloch*); 5. Kloss gibbon (*Hylobates klossi*); 6. Female pileated gibbon (*Hylobates pileatus*). (Illustration by Emily Damstra)

Species accounts

Hoolock gibbon
Hylobates hoolock

TAXONOMY
Hylobates hoolock, Harlan, 1834, Chindwin River, Burma. Two subspecies east (*H. h. leuconedys*) and west (*H. h. hoolock*).

OTHER COMMON NAMES
English: White-browed gibbon; French: Hoolock; German: Hulock; Spanish: Gibon hulock.

PHYSICAL CHARACTERISTICS
Female size 19 in (48.3 cm); male weight 15.2 lb (6.9 kg); female 15.4 lb (6.1 kg). Sexually dichromatic: male is black with white eyebrows (flicked up laterally); female is golden, darker on cheeks and chest, whitish eyebrows; neonate is white to gray; juveniles of both sexes are black.

DISTRIBUTION
India (northeast states) east and south of Brahmaputra River, Bangladesh, and Myanmar (Burma) east to Salween River.

HABITAT
Tropical semi-evergreen and evergreen rainforest.

BEHAVIOR
Population density 1.7 groups/2.5 mi^2 (km^2); home range 94 ac (38 ha), 86% defended as territory 77 ac (31 ha); day range 0.8 mi (1.3 km). Notes in songs are diphasic, variable accelerating in both sexes; female great call, 19 notes, about 15 seconds duration.

FEEDING ECOLOGY AND DIET
Their diet is mainly figs and other fruit, also flowers, leaves, and animal matter.

REPRODUCTIVE BIOLOGY
Monogamous. Mate early in the day, probably seasonal, produce single young every two to three years.

CONSERVATION STATUS
Endangered. Relatively tame because humans work in the forest fragments.

SIGNIFICANCE TO HUMANS
Usually respected. ◆

Kloss gibbon
Hylobates klossi

TAXONOMY
Hylobates klossi (Miller, 1903), south Pagai Island, west Sumatra, Indonesia. One localized species.

OTHER COMMON NAMES
English: Dwarf gibbon, Mentawai gibbon; French: Siamang de Kloss; German: Kloss-Gibbon; Spanish: Siamang enano.

PHYSICAL CHARACTERISTICS
Size 18.0 in (45.7 cm); weight 12.8 lb (5.8 kg). Monochromatic, both sexes black at all ages.

DISTRIBUTION
Mentawai Islands, Indonesia, west of Sumatra; Siberut, Sipora, and north and south Pagai.

HABITAT
Evergreen tropical rainforest.

BEHAVIOR
Population density 2.8 groups/2.5 mi^2 (km^2; home range 79 ac (32 ha), 66% defended as territory: 52 ac (21 ha); day range 0.9 mi (1.5 km). Males of neighboring groups chorus before dawn with quiver hoots and moans, female great call, every 50 notes lasts about 45 seconds, with slow rise, long bubble, and fall in notes.

FEEDING ECOLOGY AND DIET
Their diet is mainly fruit, including figs, also leaves and animal matter.

REPRODUCTIVE BIOLOGY
Monogamous. Single young produced every three years or so.

CONSERVATION STATUS
Vulnerable.

SIGNIFICANCE TO HUMANS
Elusive; revered by some people. ◆

Pileated gibbon
Hylobates pileatus

TAXONOMY
Hylobates pileatus (Gary, 1861), Cambodia. Monotypic species.

OTHER COMMON NAMES
English: Capped gibbon, crowned gibbon; German: Kappengibbon; Spanish: Gibon de cresta negra.

PHYSICAL CHARACTERISTICS
Male weight 17–23 lb (7.86–10.45 kg); female 14–19 lb (6.36–8.64 kg). Sexually dichromatic: male is black, with white head ring, hands, feet, and preputial tuft; female is silvery buff, with black cheeks, cap, and chest; young is creamy, turning to gray by subadult.

DISTRIBUTION
Southeast Thailand and Cambodia (west of Mekong River).

HABITAT
Evergreen (and semi-evergreen) tropical rainforest.

BEHAVIOR
Population density 5.0 groups/2.5 mi^2 (km^2); home range 89 ac (36 ha), 75% defended as territory: 67 ac (27 ha); day range 0.5 mi (0.8 km). Male, short notes, diphasic, trill; female, short, rich rising notes to rich bubble, about 75 notes, great call duration 18 seconds.

FEEDING ECOLOGY AND DIET
Diet is mainly fruit, including figs, also flowers, leaves, and animal matter.

REPRODUCTIVE BIOLOGY
Monogamous. Single young produced every three years or so.

CONSERVATION STATUS
Vulnerable.

SIGNIFICANCE TO HUMANS
Elusive, respected, and has human-like face as well as upright posture. ◆

Lar gibbon
Hylobates lar

TAXONOMY
Hylobates lar (Linnaeus, 1771), Malacca, Malaysia. Two subspecies in Thailand and southwest China (*H. l. entelloides H. carpenteri*, and possibly *H. yunnensis*); one in the Malay Peninsula (*H. l. lar*); one in north Sumatra (*H. l. vestitus*).

OTHER COMMON NAMES
English: Common gibbon, white-handed gibbon; French: Gibbon lar, gibbon a mains blanches; German: Weisshand-Gibbon; Spanish: Gibon de manos blancas.

PHYSICAL CHARACTERISTICS
Male size 17.1–23 in (44–59 cm), female 16.5–22.8 in (42–58 cm); male weight 11–16.8 lb (5–7.6 kg), female 9.7–15 lb (4.4–6.8 kg). White face ring, hands, and feet. Asexually dichromatic in Thailand (either very dark or very pale), otherwise polychromatic (dark brown to light buff); white face ring, often fainter in female.

DISTRIBUTION
East of Salween to Mekong Rivers in Thailand, and across into southwest China, south to Mudah River, West Malaysia; south of Perak and Kelantan Rivers in West Malaysia; north of Lake Toba in Sumatra, Indonesia.

HABITAT
Tropical evergreen rainforest.

BEHAVIOR
Population density 2.9 groups/2.5 mi^2 (km^2); home range 101 ac (41 ha), 55% defended as territory 49.4 ac (20 ha); day range 0.9 mi (1.5 km). Male, simple or quiver hoots; female, longer climax to great call, eight notes, 21 seconds (Malaya), 18 seconds (Thailand), 14–17 seconds (Sumatra).

FEEDING ECOLOGY AND DIET
Diet is mainly fruit, including figs, also flowers, leaves, and animal matter.

REPRODUCTIVE BIOLOGY
Monogamous. Single young produced every two to three years.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Elusive, respected, popular as pet in some areas. ◆

Agile gibbon
Hylobates agilis

TAXONOMY
Hylobates agilis Cuvier, 1821, west Sumatra, Indonesia. Three subspecies: in the Malay Peninsula (*H. a. unko*); in most of Sumatra (*H. a. agilis*); in southwest Borneo (Kalimantan) (*H. a. albibarbis*)

OTHER COMMON NAMES
English: Dark-handed gibbon; French: Gibbon agile; German: Schwarzhand-Gibbon.

PHYSICAL CHARACTERISTICS
Size 16.5–18.5 in (42–47 cm); female 12.2–14.1 lb (5.55–6.4 kg). Polychromatic, dark brown, almost black to light buff,

through to brown and golden. Male, white eyebrows and whitish cheeks; female, white eyebrows; young, complete white face ring. Grayer and darker on cap and chest in Borneo.

DISTRIBUTION
Malay Peninsula, north of Mudah and Kelantan Rivers into southern Thailand; Sumatra, south of Lake Toba; southwest Borneo (Kalimantan Barat ande Tengah), south of Kapuas River and west of Barito River.

HABITAT
Tropical evergreen rainforest.

BEHAVIOR
Population density 4.3 groups/2.5 mi^2 (km^2); home range 72 ac (29 ha), 76% defended as territory: 54 ac (22 ha); day range 0.8 mi (1.3 km). Male, diphasic hoots; female, great call, eight notes, shorter, higher pitched, rising notes, stable climax, 15 seconds.

FEEDING ECOLOGY AND DIET
Diet is mainly fruit, including figs, also flowers, leaves, and animal matter.

REPRODUCTIVE BIOLOGY
Monogamous. Produce single young every two to three years.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Elusive, respected, popular as pet in some areas. ◆

Moloch gibbon
Hylobates moloch

TAXONOMY
Hylobates moloch (Audebert, 1798), west Java, Indonesia. Possibly two subspecies in Java.

OTHER COMMON NAMES
English: Javan gibbon, silvery gibbon; French: Gibbon cendre; German: Silber-Gibbon, Java-Gibbon; Spanish: Gibon ceniciento.

PHYSICAL CHARACTERISTICS
Weight 12.6 lb (5.7 kg). Monochromatic; silvery blue-gray, cap and chest variably darker.

DISTRIBUTION
Restricted to forest fragments in western half of Java, Indonesia.

HABITAT
Tropical evergreen rainforest.

BEHAVIOR
Population density 2.7 groups/2.5 mi^2 (km^2); home range 42 ac (17 ha), 94% defended as territory: 39.5 ac (16 ha); day range 0.87 mi (1.4 km). Simple hoots, no duet, female solo about 17 notes, 13 seconds.

FEEDING ECOLOGY AND DIET
Diet is mainly fruit, also flowers, leaves, and animal matter.

REPRODUCTIVE BIOLOGY
Monogamous. Produce single young every two to three years.

CONSERVATION STATUS
Vulnerable.

SIGNIFICANCE TO HUMANS
Very rare, prized in some quarters, but mostly revered. ◆

Mueller's gibbon
Hylobates muelleri

TAXONOMY
Hylobates muelleri Martin, 1841, Kalimantan, Indonesia. Three subspecies around northern and eastern Borneo (*H. m. abbotti H. funereus*, and *H. muelleri*).

OTHER COMMON NAMES
English: Bornean gibbon, gray gibbon; French: Gibbon de Mueller; German: Grauer-Gibbon, Borneo-Gibbon; Spanish: Gibon de Mueller.

PHYSICAL CHARACTERISTICS
Size 16.5–18.5 in (42–47 cm); weight 12.6 lb (5.7 kg). Brown to gray with dark cap and chest, more so in female; face ring in male.

DISTRIBUTION
Borneo, north of Kapuas River in west Kalimantan, Sarawak, Sabah, and east and central Kalimantan, east of Barito River.

HABITAT
Tropical evergreen rainforest.

BEHAVIOR
Population density 3.2 groups/2.5 mi^2 (km^2); home range 109 ac (44 ha), 89% defended as territory 96 ac (39 ha); day range 0.5 mi (0.9 km). Male, single hoots; female, short, rising notes, short bubble, about 58 notes, 12 seconds.

FEEDING ECOLOGY AND DIET
Diet is mainly fruit, including figs, also flowers, leaves, and animal matter.

REPRODUCTIVE BIOLOGY
Monogamous. Produce single young every two to three years.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Mostly revered, especially by the indigenous people, but probably eaten; traded by some non-indigenous visitors. ◆

Black crested gibbon
Nomascus concolor

TAXONOMY
Nomascus concolor (Harlan, 1826), Tonkin, Vietnam. At least two subspecies (possibly species): *N. c. concolor*, *N. hainanus*, possibly *N. jingdongensis*, possibly *N. lu*, and sp. cf. *nasutus*.

OTHER COMMON NAMES
English: Black gibbon, concolor gibbon, crested gibbon, Indochinese gibbon; French: Gibbon noir, gibbon a favoris blancs; German: Schwarzer Schopgibbon.

PHYSICAL CHARACTERISTICS
Size 18–25 in (45.7–63.5 cm); weight 9.9–19.8 lb (4.5–9 kg). Sexually dichromatic: male black; female yellow, orange, or beige brown with black cap; young born yellowy with reddish face, turning black at six months until puberty (females).

DISTRIBUTION
Southern China, including Hainan Island, northern Vietnam, and northwest Laos.

HABITAT
Tropical semi-evergreen and evergreen rainforest.

BEHAVIOR
Population density 0.4 groups/2.5 mi^2 (km^2); home range 113 ac (46 ha); day range 0.5 mi (0.8 km). Male: simple, staccato, multi-modulated notes; female twitter and vibrato, eight notes, eight seconds, male coda at end.

FEEDING ECOLOGY AND DIET
Diet is mainly fruit, also flowers, leaves, and animal matter.

REPRODUCTIVE BIOLOGY
Monogamous. Produce single young every three years or so.

CONSERVATION STATUS
Endangered (IUCN); Critically endangered (FFI).

SIGNIFICANCE TO HUMANS
Very rare, so highly prized by traders, but local people are being empowered to protect, with financial and pride incentives. ◆

White-cheeked gibbon
Nomascus leucogenys

TAXONOMY
Nomascus leucogenys (Ogilby, 1840), Muang Khi, Laos. Northern (*N. l. leucogenys*) and southern (*N. l. siki*) subspecies.

OTHER COMMON NAMES
French: Gibbon a favoris blancs; German: Weisswangen-Schopfgibbon.

PHYSICAL CHARACTERISTICS
Size 18–25 in (48–64 cm); male weight 12.3 lb (5.6 kg), female 12.8 lb (5.8 kg). Male, black with white cheeks; female, pale yellow, yellow, or orange yellow, thin white face ring; infants, whitish buff, then black until puberty (for females). Born yellowy with reddish face, turning black at six months until puberty (females).

DISTRIBUTION
Southern China (Yunnan), northern and central Vietnam, and central Laos.

HABITAT
Tropical evergreen and semi-evergreen rainforest.

BEHAVIOR
Male emits booms and multi-modulated phrases; female gives rapid great calls, with rising notes, 21–27 notes, 13–15 seconds, male coda at end.

FEEDING ECOLOGY AND DIET
Diet is mainly fruit, leaves, and buds, and a small amount of animal matter.

REPRODUCTIVE BIOLOGY
Monogamous. Produce single young every three years or so.

CONSERVATION STATUS
Listed as Data Deficient by the IUCN; likely endangered.

SIGNIFICANCE TO HUMANS
Revered by locals, but still hunted for food and trade, with medicines in mind. ◆

Golden-cheeked gibbon
Nomascus gabriellae

TAXONOMY
Nomascus gabriellae (Thomas, 1909), Langbian, Vietnam. Probably monotypic species.

OTHER COMMON NAMES
English: Buff-cheeked gibbon, yellow-cheeked crested gibbon; German: Gelbwangen-Schopfgibbon.

PHYSICAL CHARACTERISTICS
Weight 12.7 lb (5.8 kg). Male, black with yellowy out-brushed cheeks, rusty brown on chest; female, pale yellow or orange-yellow, yellowish incomplete face ring, cheek hair brushed out; infants born whitish buff, changing to black until puberty (females).

DISTRIBUTION
Southern Vietnam and Cambodia east of the Mekong River.

HABITAT
Tropical evergreen and semi-evergreen rainforest.

BEHAVIOR
Male emits staccato and multi-modulated phrases, no booms, soft and irregular; female great call of rapid rising notes, 11 notes, 13 seconds, terminating with male coda.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Monogamous. Single young produced every three years or so.

CONSERVATION STATUS
Vulnerable.

SIGNIFICANCE TO HUMANS
Indigenous people revere and fear them. Elsewhere, there is trade in live animals, often for food or to make medicines, in particular from the bones. ◆

Siamang
Symphalangus syndactylus

TAXONOMY
Symphalangus syndactylus (Raffles, 1821), west Sumatra, Indonesia. Two subspecies, Sumatra and Malay Peninsula.

OTHER COMMON NAMES
German: Siamang; Spanish: Siamang.

PHYSICAL CHARACTERISTICS
Size 29–35 in (74–89 cm); male weight 22–33 lb (12.3–14.8 kg), female 22–25 lb (10–11.1 kg). Monochromatic, black, at all ages, male or female, inflatable laryngeal sac (white/pink).

DISTRIBUTION
Most of Sumatra and Malay Peninsula, from between Perak and Muar Rivers.

HABITAT
Tropical evergreen rainforest.

BEHAVIOR
Population density 1.7 groups/2.5 mi^2 (km^2); home range 77 ac (31 ha), 76% defended as territory: 47 ac (19 ha); day range 0.5 mi (0.8 km). Elaborate duet, male screams at sub-climax and climax, female great call, bark series, 18, then eight notes (very variable according to individual), about 18 seconds, alternating booms across inflated sac in both sexes, largest and loudest in male.

FEEDING ECOLOGY AND DIET
Diet is mainly fruit, including figs, also flowers, leaves, and animal matter.

REPRODUCTIVE BIOLOGY
Monogamous. Single young produced every three years; mating most when fruit abundant, births mostly November–February.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Large, with a distinctive song, hence revered by local people, though others eat or trade, in particular for medicines. ◆

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Organizations

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Hominidae I

(Great apes)

Class Mammalia

Order Primates

Family Hominidae

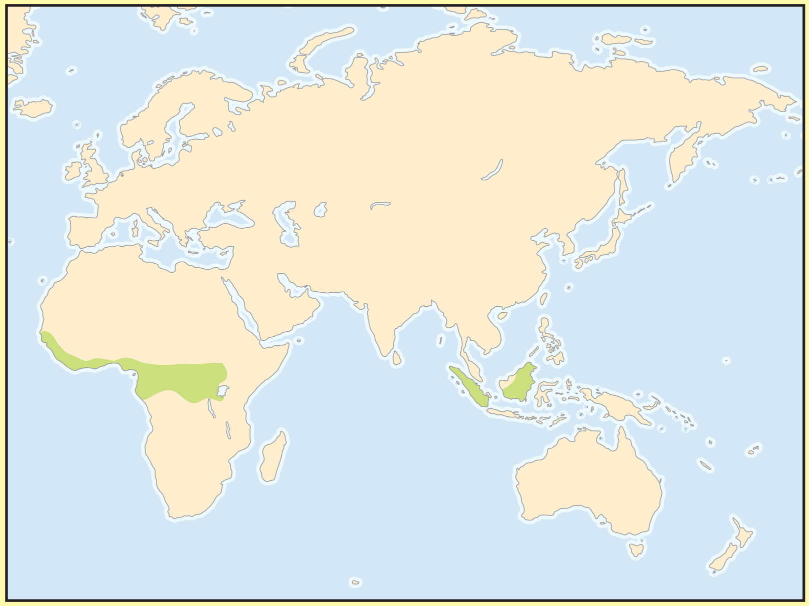
Thumbnail description
The largest members of the order; sharing the physical features that characterize all primates, great apes are distinguished by their impressive array of mental abilities

Size
Combined head and body length ranges from 28–67 in (70–170 cm); 68–388 lb (31–175.2 kg)

Number of genera, species
3 genera; 6 species

Habitat
Forest, savanna, swamp

Conservation status
Critically Endangered: 1 species; Endangered: 5 species



Distribution
Equatorial Africa, Borneo, and Sumatra

Evolution and systematics

The great apes have traditionally been grouped in the family Pongidae, clearly distinguishing them from the prosimians, monkeys, lesser apes, and humans. Three genera and four species were usually recognized within this family, which included the orangutans (*Pongo pygmaeus*), gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), and bonobos (*Pan paniscus*). In the past, bonobos have been referred to as pygmy chimpanzees, a misnomer attributed to their gracile appearance. They were not recognized as a distinct species until 1929.

Like any branch of science, taxonomic classification involves the search for greater comprehension. Incremental progress relies on debate among colleagues, constructive criticism, and innovative methods for measuring the relationship between species, such as DNA and chromosomal analyses. Based on these factors, Pongidae has been replaced by the family Hominidae, which more accurately describes the evolutionary relationship between all of the great apes and humans.

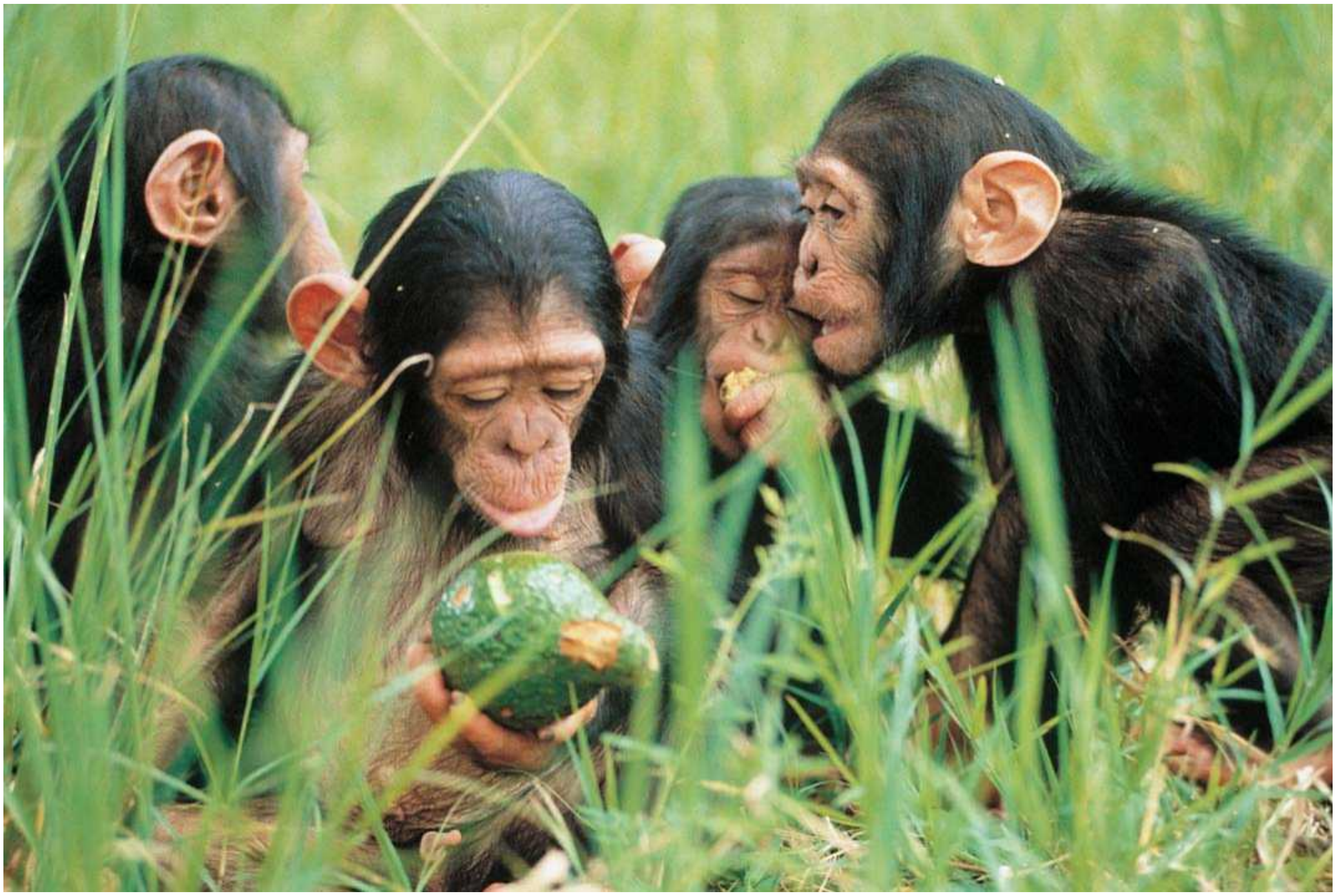
The family Hominidae consists of four genera and seven species. Orangutans, the only Asian great apes, are divided into two species based on their geographically distinct ranges. Those from the island of Borneo are *Pongo pygmaeus*, while those from the island of Sumatra are *Pongo abelii*. The remaining members of the family Hominidae are all African in origin. Chimpanzees, *Pan troglodytes*, are divided into four subspecies, *P. t. troglodytes*, *P. t. verus*, *P. t. vellerosus*, and *P. t. schweinfurthii*. Bonobos, *Pan paniscus*, are the remaining species in the genus. There are two species of gorilla, western gorillas (*Gorilla gorilla*), and eastern gorillas (*Gorilla beringei*). Two subspecies of eastern gorillas exist, mountain gorillas (*G. b. beringei*) and eastern lowland gorillas (*G. b. graueri*). The final species in the family Hominidae is *Homo sapiens sapiens*, otherwise known as modern humans. This species is discussed in a separate chapter.

Within the family Hominidae, two subfamilies further clarify the evolutionary and associated geographical origins of the species. The Asian orangutans are members of the subfamily Ponginae, while all of the African species are members of the subfamily Homininae. Based on comparisons of DNA from each species in both subfamilies, it is clear that orangutans diverged from the members of Homininae approximately 14 million years ago (mya). Within Homininae, gorillas split from *Pan* and *Homo* approximately 7 mya. Humans were the next to diverge approximately 6 mya. The final group to emerge was *Pan*, with bonobos and chimpanzees diverging approximately 3 mya.

Although commonly misunderstood, humans are not the "end-product" of great ape evolution. Humans did not evolve from chimpanzees (or any other living species of great ape), and the other species of great ape are not evolving into humans. Each species within Hominidae has evolved on its own distinct pathway, although all share a common ancestry.

Physical characteristics

Great apes are large when compared to other primates, although a range of sizes and body forms exist within the



Chimpanzee juveniles (*Pan troglodytes*) at play. (Photo by K & K Ammann. Bruce Coleman, Inc. Reproduced by permission.)

family. Without question, gorillas are the largest of the great apes. Adult males may exceed 350 lb (158 kg), while adult females are generally about half that size. Bonobos are the most slender great apes, having very long limbs and a gracile appearance. Adult males average less than 100 lb (45 kg) and adult females are usually about 20% smaller.

All of the great apes share an overall similarity in body type, having arms that are longer than their legs. When standing with both hands and both feet on the ground, their limb proportions slope their back downwards, and their head is positioned as the highest point of their body. While this is their most common posture, all are also able to stand bipedally and walk upright for short distances. Whether on the ground or in the trees, great apes are able to move their arms with maximum rotation at the shoulder joint, unlike most other species of primates that have a more limited degree of flexibility. This superior range of motion allows great apes to suspend themselves with their arms, and move using a style of locomotion referred to as semi-brachiation. The gibbons, genus *Hylobates*, are the only true brachiators.

The African species (gorillas, chimpanzees, and bonobos) are primarily terrestrial, although they do spend considerable amounts of time in the trees. When moving on the ground, they "knuckle-walk," meaning that they support their body weight on the knuckles of their hands, and the soles of their feet. Orangutans, the largest arboreal species on Earth, have a number of physical adaptations that make them uniquely suited for life in the trees. Spending most of their lives in the forest canopy, these apes have exceptionally long arms, and the majority of their strength is located in the upper body. Their fingers and toes are also elongated, allowing them to secure themselves with a vise-like grip. When moving high above the ground, orangutans use their hands and feet interchangeably in a style that is referred to as quadrumanous, literally translated as "four-hands." Unlike the African apes, orangutans descend from the trees infrequently. When moving on the ground, they do not knuckle-walk, but either hold their hands and feet open and flat as they move, or close them completely and support themselves on their fists.

The general appearance of the great apes varies by species. All of the African apes have dark hair, and orangutans are aptly called the "red ape" due to their rusty orange appearance. Gorillas and orangutans show extreme sexual dimorphism, with males reaching an adult size that is usually twice that of most females. In addition to their size, adult male gorillas are most easily recognized by their prominent sagittal crest, which becomes dome-shaped as they mature. Male orangutans develop very long hair, a beard, cheek pads, and an obvious throat sac, as they reach adulthood. These physical indications of sexual maturity all serve to intimidate rival males, as well as to attract potential mates. Male and female chimpanzees and bonobos lack these extreme differences in size and appearance, with males being approximately 20% larger than females. However, bonobos and chimpanzees are distinct in their appearance. The skin coloration on the faces of adult chimpanzees may be lighter than the very dark complexion of bonobos, who also have pinkish lips. Bonobos have longer hair on their head, with an obvious part in the middle. In terms of general appearance, chimpanzees are robust and muscular, while bonobos appear much slighter by comparison.

Distribution

The current distribution for gorillas, chimpanzees, and bonobos is limited primarily to the tropical forests of Africa. Bonobos have a very restricted range, occurring only in the Democratic Republic of the Congo (formerly known as Zaire), south of the Congo River. Chimpanzees range across the middle band of the continent, from Senegal in the west, to the Democratic Republic of the Congo near the center of Africa, to southern Sudan, Uganda, Burundi, and Tanzania in East Africa. Gorillas may be found as far west as Nigeria, Cameroon, and Gabon. Their range extends to the Central African Republic, and east into the Democratic Republic of the Congo, Rwanda, and Uganda.

Orangutans are the only species of great ape that exist outside of Africa. Wild populations exist only on the islands of Borneo and Sumatra. Due to massive loss of habitat, most orangutans exist in areas of forest that are threatened by human development.

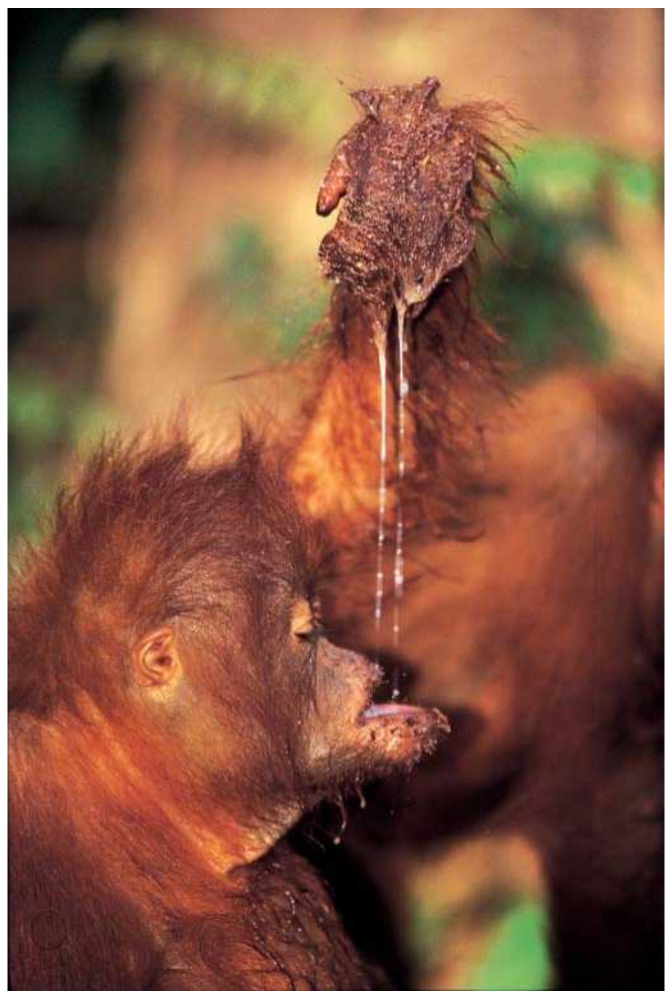
Habitat

Great apes are generally found in forested areas that are located on, or near, the equator. However, behavioral flexibility allows for some variation in habitat utilization that may be seen among populations of the same species. Availability of appropriate foods is the primary factor that limits the number of individuals that may occupy any given area. The range of great ape habitat includes primary forest, bamboo forest, lowland swamp, grasslands, and woodland savanna.

Gorillas, chimpanzees, and bonobos utilize all levels of their habitat, but are primarily terrestrial. Each species is well adapted for moving and foraging in the trees, although the amount of time that each spends off the ground varies. Chimpanzees and bonobos, smaller and lighter than gorillas, utilize the trees throughout their lives. As male gorillas mature, their increased bulk prevents them from using the trees as easily, and they may spend the majority of their time on the ground. This difference is well illustrated by the fact that all great apes construct their night nests in the trees, except for adult male gorillas, which commonly build their sleeping nests on the ground.

Chimpanzees occur in very diverse habitats throughout their range. They may be found in primary or secondary forest, tropical rainforest, grasslands, or woodland savanna. Bonobos are not found outside of primary or secondary forest. Lowland gorillas occur in primary and secondary forest as well, but also utilize marshy habitats, such as areas known as bais (pronounced "buys"). Bais are large, natural clearings within the forest that are brightly lit and populated by plant species that grow in very wet areas. Gorillas, as well as other forest species, consume these preferred foods, sometimes wading waist high in water to collect handfuls of the succulent plants. Mountain gorillas live at higher altitudes than chimpanzees, bonobos, or lowland gorillas, existing in montane and bamboo forest. Unlike these other species, they have much longer and thicker hair to protect them from the colder temperatures.

Orangutans possess a number of physical and behavioral traits that make them particularly well adapted for life in the trees. They live in the canopies of rainforests, montane forests, and lowland swamps, and are the only great apes that are primarily arboreal. Their distinctive anatomy allows them to perform all of their most essential behaviors, such as traveling, foraging, and mating, while suspended in the treetops. Orangutans are fully capable of movement on the ground,



An orangutan (*Pongo pygmaeus*) drinks by scooping water with its hand and pouring it out, catching the stream in its mouth. (Photo by Tim Davis/Photo Researchers, Inc. Reproduced by permission.)

Dominant mature male mountain gorillas (*Gorilla beringei*) are referred to as silverbacks. (Photo by © Karl Ammann/Corbis. Reproduced by permission.)

although it is awkward by comparison. This clear disadvantage restricts the range of habitats that they can successfully occupy when compared to the African apes.

Behavior

The social organization for each type of great ape is distinct, and has evolved in response to a variety of factors such as territory defense, competition for mates, and food availability. The social system that emerges to balance the costs and benefits of these factors maximizes the potential for the reproductive success of each individual and the survival of the group. Clear distinctions between social systems are evident when comparing gorillas, orangutans, chimpanzees, and bonobos. While generalizations about each of these systems can be used accurately, it is also important to remember that a normal range of behavior exists, and variation may occur in response to different environmental conditions or pressures.

The members of the genus *Gorilla* demonstrate flexibility in their social organization. Most commonly, gorillas are found in groups that consist of one dominant adult male, several adult females, and their offspring. Gorillas travel within a specific home range, but do not defend an exclusive territory. Group size varies, and can range from a total of three or four individuals to more than 30, although the number of individuals in most groups usually falls between these extremes. In these polygamous social situations, the dominant male is referred to as the "silverback," a title that refers to the normal change in hair color that occurs as males mature. These males occupy the highest ranked position in their group, which generally allows them exclusive breeding access to the females. Silverbacks lead the group as they travel and forage, but their most important function is to protect the group against attacks by rival males, which commonly involve attempts at infanticide. This classic model of gorilla social life may lead to the inaccurate assumption that the largest, strongest male simply controls the females in the group through brute strength. While male size and associated strength may contribute to social rank in general, the relationship between an alpha male and a group of females is mutually beneficial. At a minimum, in a polygamous social system, females provide the male with an opportunity to reproduce, and the male provides safety and security for the females and their offspring. Males demonstrate their capability to function as the leader of a group through a combination of social finesse, paternal attention to offspring, physical vigor, and effectiveness in repelling rival males. Based largely on the behavior of the silverback, females choose to remain in his group, or to emigrate into the group of another adult male. Instances of females living alone, or social groups composed only of females, are unknown for gorillas.

Male gorillas, by contrast, demonstrate a number of different social strategies. As they reach adolescence, males may abandon their birth group, and begin to travel alone. During this phase of their life, these individuals avoid direct encounters with silverbacks, but attempt to attract females in order to create their own group. In some instances, lone males congregate with each other, and form bachelor groups that travel and forage together. These associations are probably the least stable of all gorilla social groupings, and have a higher rate of change over time. Much more commonly, males pursue a distinct strategy, and simply remain in their birth group into adulthood. Silverbacks may be remarkably tolerant of these younger males, termed "blackbacks," who are usually their sons or brothers. These young adult males are subordinate in rank to the silverback, and may be dominated by adult females as well. Their primary social role is to provide additional protection and vigilance for the females and infants, who are also likely to be related to them. Gorilla groups with more than one adult male can be remarkably stable, and persist for many years. As time passes, the group may even have two silverbacks holding the highest ranked positions and sharing leadership roles. As these groups become very large over time, primarily as a result of births and female immigrants, it becomes increasingly likely that a fission will occur. When this rare event happens, females follow their preferred male, establishing the core membership for a traditional, polygamous grouping. The male-female bond provides the foundation for all of gorilla society.

Unlike gorillas, the social behavior of orangutans is centered almost entirely on individuals acting independently, and there are no long-term bonds between adults. Historically, orangutans have been described as "the solitary ape." While it is true that they are the least social of all the great apes, it is an exaggeration to suggest that they are truly solitary. Adults interact infrequently, compared to the rates of association observed for the other great apes, and it is more accurate to describe orangutans as living in an extended social system with individuals dispersed over large home ranges. Interactions between adult males are usually volatile, and contact between them involves threats or aggression. Adult females can be more tolerant of each other, and may even forage for fruits in the same tree. But, this level of association is the exception rather than the norm, and can vary depending on individual personality. Overall, there is no evidence that females form close bonds or provide each other with any form of social support. However, these behavioral traits are clearly obvious in the relationships that mothers form with their offspring, to whom they show great devotion and affection. Mothers and offspring may travel together for 7–8 years, at which time these young adolescents begin to move away and establish their own home range.

The unique social structure exhibited by orangutans is directly linked to the quantity and quality of food that they need to sustain their big bodies. As the largest arboreal species on Earth, these great apes require a sizable amount of food each day. Fruit is their most preferred choice, although its availability can be inconsistent. As a result, orangutans distribute themselves in such a way as to maximize their ability to find sufficient amounts. Given the impressive amount of fruit that one orangutan can consume in a day, two or more adults regularly traveling together could easily exhaust the quantity that is found within their home range. The availability of fruit is the major factor that limits the number of orangutans that can simultaneously occupy any portion of the forest. Orangutan social behavior does have some flexibility when this ecological factor fluctuates. If fruit becomes super abundant in a specific area of the forest, social tensions may ease. Adult females become more tolerant of each other, and may form a small aggregation as they forage independently. This same scenario does not apply to adult males.

In order to meet their nutritional needs and reduce social tension, female orangutans normally occupy large home ranges. Individuals do not defend entire territories, but they may certainly compete for specific forage sites, and attempt to repel rivals. In general, female home ranges regularly overlap although interactions between these females are infrequent. The situation for males is similar, although magnified due to their higher levels of intolerance for each other. Adult males may occupy home ranges that are three or four times bigger than those used by females, and they appear to be less stable. Males may suddenly move from their usual range, and travel far into the forest with no apparent explanation. An area in the forest may have a male that can be considered a resident, although transient males may also occur. The resident male may or may not be dominant to the transient males. Adult males regularly produce a "long call" vocalization that is estimated to travel as far as 0.6 mi (1 km) through the forest. This booming call advertises the presence and location of a specific male, and it is presumed to have a variety of functions. The long call allows males to space themselves throughout the forest. Males can choose to avoid or initiate an aggressive interaction when they locate another male. The call also serves as an advertisement to adult females, who also choose to approach or move away from a male who could be a potential mate. Females do have a number of vocalizations, but nothing that resembles the imposing long call produced by the males.

Relationships between adult males also play a pivotal role within chimpanzee society, but one in which the primary emphasis is on coalitions and mutual support within a community rather than competition and avoidance. Chimpanzees live in a highly complex social system described as a "fusion-fission" society. In this dynamic social setting, individuals within a community freely intermingle with all others. Communities may have dozens of members depending on local ecological conditions, and the smaller groupings that regularly form within a community are called parties.


Chimpanzees (*Pan troglodytes*) wade through a stream. (Photo by K & K Ammann. Bruce Coleman, Inc. Reproduced by permission.)

Chimpanzee parties form and re-form on a continual basis, reflecting the needs and preferences of the individuals within a community, and the size and composition of parties are almost never the same two days in a row. Depending on the situation, party size can range from five or less, to more than half of the total community. A number of factors are involved, although the most influential of these is the local food supply, specifically correlated with the amount of fruit that is available in an area. An increase in food promotes larger parties, while a decrease encourages fewer individuals to congregate. Hunting and meat-eating are associated with relatively large parties that stay together for longer than average periods of time. In addition to food, opportunities for sexual interaction also play a very important role in the formation of parties. Ovulating females attract significant amounts of attention from males, creating a very charged social situation. Other important factors that have an effect are the demographics within the community, such as the total number of males, ovulating females, and mothers with infants. Dangers from predation also may be involved, since chimpanzees are certainly at risk from leopards, and lions in some cases. However, this link has yet to be thoroughly investigated and firmly established. In general, the size, composition, longevity, and duration of each party are influenced by a number of factors that must be balanced against the desires and social goals of each individual chimpanzee.

Parties can be grouped into several specific types, with each promoting a different social function. Male chimpanzees generally prefer each other's company, and regularly form all male parties. Coalitions between males are very common, although they vary over time and change when it is politically advantageous. Male parties are one way that males can advertise and strengthen their coalitions. Males that share a strong bond may

An eastern lowland gorilla (*Gorilla beringei graueri*) family. (Photo by Eric & David Hosking/Photo Researchers, Inc. Reproduced by permission.)

also groom each other, share food, and provide support during threatening or aggressive encounters with other individuals. Male parties also patrol the peripheral areas of their home range, keeping track of neighboring communities. Although chimpanzees do not maintain well-defined territories, they will engage in attacks on parties from outside of their community. When males are on patrol, they appear very cautious, and move silently as they travel. They are highly vigilant, and clearly uneasy while outside of their normal home range. In a number of cases, male patrols appear to have targeted and planned attacks on individuals from other communities. Many of these attacks have been fatal.

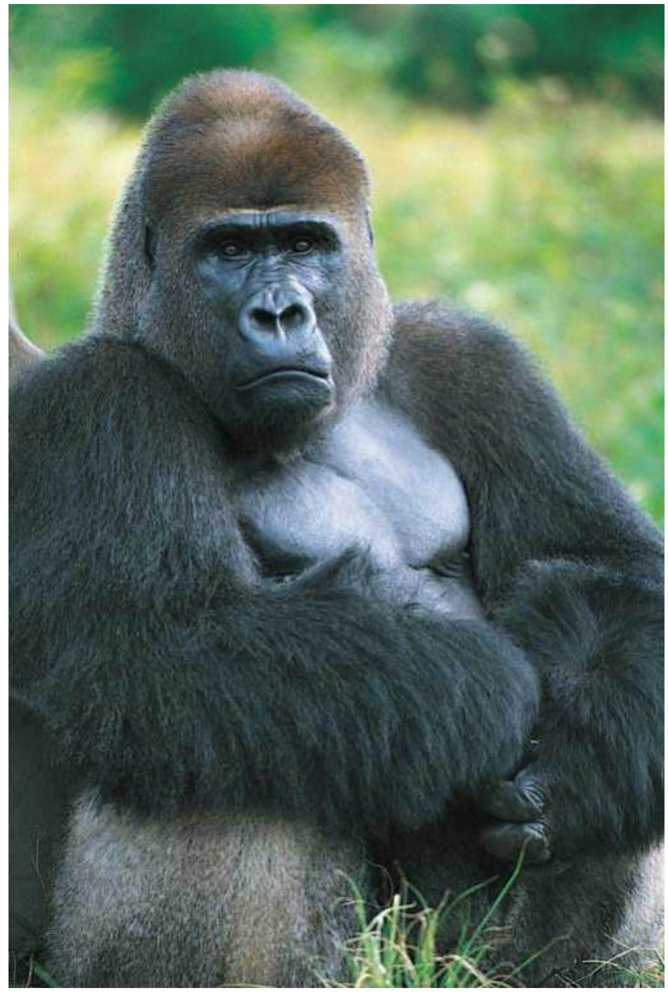
Females form the core for other types of parties, which also usually involve their offspring. A mother and her dependent young may travel as a family, with no other individuals in attendance. "Nursery parties" also may form, in which multiple adult females with infants and juveniles join together. On occasion, adolescent or adult females with no offspring may join this congregation as well. Ovulating females draw the immediate attention of adult males, and easily disrupt all male groupings. Parties may form in these situations, consisting of one or more sexually receptive females as well as multiple adult males. A single male and female may form a consortship while she is fertile, distancing themselves from all other members of the community. Mixed sex parties are also apparent in non-sexual situations, such as when many individuals forage on an abundant source of food. The size of these groupings varies, but may include a large percentage of the total community. Lastly, individual chimpanzees may simply prefer to spend time traveling alone, forming a party of one.

These complex and highly flexible social behaviors demonstrate that chimpanzees frequently make decisions that are calculated to increase personal gain. In addition to adjusting party size and composition based on food availability, chimpanzees pursue their personal social agendas as well. These may be associated with sexual behavior, gaining status within the hierarchy of the community, or simply finding ways to reduce stressful interactions with other individuals. Chimpanzees live in an intense social environment, where dominant and subordinate rankings are regularly reinforced. Adult males are generally dominant within the community, and maintain their status using a variety of techniques, including strategy, alliances, and aggression. Changes in party composition that reflect preferences in social partners demonstrate one important way that males, in particular, may relieve tension and stress. These behaviors also provide evidence of the sophisticated cognitive skills that chimpanzees must possess to manage the intricacies that form the basis of their society.

Bonobos also live in a complex and dynamic social environment, with some behaviors that are similar to those exhibited by chimpanzees, and others that are completely distinct among the great apes. Like chimpanzees, bonobos are gregarious and live in fusion-fission communities. However, the bonds between males are weaker by comparison, and relationships between females are much more influential in their society. Adult male bonobos have a social role that is largely defined through their mother, and the closest male-male relationships are usually between maternal brothers. Males generally stay in their birth group throughout their adulthood, and their social rank is largely determined by the status of their mother. Unlike chimpanzee males, who may form coalitions with any other male in their community, kinship is a very influential factor in the formation of male-male relationships for bonobos.

As female bonobos mature, the bond with their mother weakens, and they normally emigrate from their birth group. During this time, young females who have yet to reproduce may move between communities and begin the process of forming alliances with other, unrelated females. As these strong bonds develop over time, they form the core of the bonobo community. While a female hierarchy exists, it is less obvious than the dominance structure found among chimpanzees, and their age and residency status appear to be the most important factors that determine their rank. Females are clearly capable of monopolizing food resources, and may singly or cooperatively dominate males. While both males and females exhibit aggressive behavior, male dominance over females is uncommon. The unified force that females represent in bonobo society is explained, at least in part, by the development of strong and persistent social bonds between unrelated individuals, a behavioral strategy not seen among males.

Bonobo behavior at the party and community level has some similarities and differences when compared to chimpanzees. The community members of both species regularly divide themselves into parties, and the total number of individuals in each party can be correlated with the amount of food that is available. As is the case for chimpanzees, abundance promotes larger congregations of bonobos. In places where there is a risk of predation, especially from humans, bonobo party size is reported to increase. Overall, party size ranges from a minimum of 2–6 individuals to a maximum of 11 or more. Communication between party members also appears to vary by species. Chimpanzees effectively use loud vocalizations, as well as drumming on tree buttresses, to exchange information between parties. Using these methods, field researchers report that the community may stay in contact even while divided into multiple parties. It is also speculated that drumming may exchange specific information about the direction in which individuals travel, as well as when they stop to rest. While bonobos may communicate between parties, their vocalizations are less effective for long distance exchange. It appears that most of their efforts are focused on communicating with other members of the same party. Bonobo parties also are more stable than those of chimpanzees, with membership changing less frequently. Most are usually a mixture of males and females rather than a nursery, family, or other configuration. Female bonobos are not reported to travel alone, although males occasionally exhibit this behavior. Unlike chimpanzees, bonobo parties are much more likely to fuse back together as a community each night. An additional distinction is that bonobo communities are more flexible in their behavior towards each other. While aggressive interactions have been documented, peaceful interactions between communities have also been seen.



The western gorilla (*Gorilla gorilla*) is an herbivore. (Photo by Mark Newman/Photo Researchers, Inc. Reproduced by permission.)

The most notable behavioral difference between bonobos and all of the other great apes is their reliance on sexual behavior as a means for promoting social affiliation. In addition to sexual behavior between adults that occurs for reproduction, all members of a community regularly engage in pleasurable, non-reproductive sexual interactions that function as a way of offering appeasement, reinforcing bonds between individuals, and easing social tensions. Erotic behaviors may occur between a male and a female, as well as male-male and female-female pairings. These species-typical interactions begin well before bonobos are capable of reproduction, and continue throughout adulthood. However, specific associations may be avoided, such as sexual behavior between mothers and their sons.

More than any of the other great apes, bonobos appear to live in a society with a greater emphasis on reciprocity. Sex is used as a form of social currency that can be offered to defuse tension between individuals, promote reconciliation, encourage alliances, and ease competition. This unique social strategy clearly assists migrating females as they move between communities and form bonds with resident females. It also may account for the high frequency with which males and females associate and form mixed sex parties. Aggression is clearly not absent from bonobo society, erotic behavior simply allows it to be reduced in frequency and severity. In some instances, expressions of reciprocity may be very literal. While bonobos are known to have high rates of food-sharing behavior in general, they may specifically offer preferred foods to another individual in a direct exchange for sex.

An adult male orangutan (*Pongo pygmaeus*) at Bukit Lawong, north Sumatra. (Photo by B. G. Thomson/Photo Researchers, Inc. Reproduced by permission.)

While it is clearly true that bonobos engage in social behaviors that are not seen among the other great apes, all of the great apes are faced with the same survival challenges. Reproduction, foraging, protection from predators, and territory defense are the basic concerns that shape all social systems. For example, the comparatively low rates of association between orangutans are associated with a limited availability of preferred foods. In contrast, gorillas may forage in large groups, with little competition, due to the abundance of the vegetation that they consume. The behaviors that characterize each great ape society have evolved as a balance between the costs and benefits of living socially. This dynamic process may have been a primary factor that influenced the emergence of complex cognitive skills. Individuals with greater mental flexibility are able to out-compete rivals, giving them an overall advantage in surviving and reproducing. This benefit favored the development of mental abilities that allowed individuals to think strategically, expressed by such behaviors as coalitions, alliances, cooperation, and even deception. The sophisticated minds that are commonly and accurately associated with great apes are assumed to have their basis in the complicated social behaviors that are used to promote survival and reproduction.

Feeding ecology and diet

The foods that are eaten by the great apes generally include a wide variety of items such as fruits, assorted types of vegetation, bark, seeds, insects, and meat. However, great apes in certain habitats may have access to a more limited array of foods due to local ecological conditions, which affect the composition of their diet. For example, mountain gorillas (*G. beringei*) live at higher elevations than other great apes, where vegetation, rather than fruits, are the predominant foods. Their environment can be described as a giant salad bowl, filled with abundant amounts of leaves, shoots, pith, and vines, which are easily collected. Western gorillas (*Gorilla gorilla*), eastern gorillas (*Gorilla beringei*), and eastern lowland gorillas (*G. b. graueri*) all live at lower elevations that have a greater array of food types, including fruits, leading to more diverse diets. While many different types of food may be consumed, gorillas have not been seen to eat meat. In general, the food items in gorilla habitats are plentiful, and relatively easy to acquire, process, and consume. As a result, feeding competition between individuals is fairly low, and gorillas have no need for complex foraging techniques in order to meet their nutritional needs.

Bonobos also depend on vegetation as a staple in their diet, although they spend large amounts of their time foraging for fruit, which is more highly preferred. In general, competition for food is fairly low and large numbers of individuals may be seen feeding together. This is also illustrated by the fact that bonobos have high rates of food sharing with each other, a feature associated with their unique social system. Bonobos also eat a wide variety of non-plant foods, such as caterpillars, earthworms, and perhaps even shrimp found in shallow streams. Meat from prey such as squirrels and small antelopes is highly prized. These animals appear to be taken opportunistically rather than through active hunting. This limited food resource is not freely shared, and is likely to be dominated by adult females, who may totally exclude males when meat is being eaten. Although coveted, meat is estimated to make up a very small percentage of the normal diet for bonobos. Like gorillas, bonobos are able to successfully meet all of their dietary needs through foraging techniques that do not require any forms of tool-using behavior. The absence of tool-use by gorillas and bonobos in the wild can confidently be attributed to a lack of necessity, rather than lack of mental ability, since both easily demonstrate mastery of tools in captivity.

Compared with gorillas and bonobos, diet and food availability for orangutans exerts a much more restrictive influence. These large, arboreal great apes rely predominantly on fruit, such as figs (*Ficus* spp.) and durian (*Durio* spp.), which are patchily distributed both in space and time. Orangutans expend most of their foraging effort in finding, processing, and consuming fruit when it is available. As a result, access to this limited resource can be highly competitive, and limits the number of orangutans that can successfully forage in any area of the forest. When fruit is absent, a wide variety of other foods, such as leaves, seeds, bark, and insects, are consumed. All of these are less preferred and incite less competition. On rare occasions orangutans have been seen to eat animal prey such as a loris (*Loris* spp.), although these events are described as opportunistic rather than active hunting.

One of the ways in which orangutans meet their nutritional needs is through the use of tools to extract otherwise unavailable foods. Two specific forms of tool-manufacture and tool-use have been well studied in the wild. In the first, orangutans have been seen to construct and use probing tools that are inserted into tree trunks in order to remove insects, larvae, and honey. These tools were used to break open and probe the nest inside a tree hole, as well as for extracting the honey and insect prey. These nest holes were located far above the ground, and in most cases the orangutans climbed into position and utilized the tool while it was held with their teeth. In the second case, these apes made and used a short, blunt tool to remove the calorie-rich seeds encased inside of the spiny (*Neesia* sp.) fruit. These fruits are very hard, with imposing spikes on their skin. As they ripen, slits open in the sides that allow the seeds to fall onto the ground. Since the orangutans are unable to simply open the fruit and remove the seeds, they use a tool to scrape the seeds from inside the fruit, avoiding the spines on the outside as well as irritating fibers that are present on the interior. Using this strategy, they are able to exploit a calorie rich food that would be otherwise unavailable. Although these fruits are available to a number of populations, this behavior is only present at specific sites. This strongly suggests that the presence of this particular form of tool use is the result of innovation and inter-generational learning, the basic elements of culture.

Among the great apes, chimpanzees utilize the widest variety of potential foods, made possible by the most diverse collection of behaviors related to food gathering, extraction, processing, and consumption for any species except humans.

The orangutan (*Pongo pygmaeus*) has a short thumb and long fingers, enabling it to hook easily over branches. (Photo by © George D. Lepp/ Corbis. Reproduced by permission.)

Numerous types of food are eaten, including leaves, bark, sap, flowers, nuts, insects, meat, and fruit, which is highly preferred. In the wild, chimpanzees demonstrate superior overall ability in the manufacture and use of tools, especially tools used in food acquisition. The modification and use of slender grasses and stems by chimpanzees to "fish" termites out of their mounds is the classic example that shattered the long held assumption that humans were the only tool-maker and tool-user. While the catalog of tool-using behaviors demonstrated by chimpanzees is simply too large to list here, nut cracking exemplifies the importance of food-related tool-use.

Nut cracking involves the skilled use of a hammer and anvil to carefully open hard shelled nuts without damaging the food inside. This ability is learned over time through a combination of observing other chimpanzees, practice, and in some instances, direct assistance from another individual. This behavior does not occur in all populations of chimpanzees, even in areas where nuts and potential tools exist. Therefore, it is assumed that innovation and social learning are necessary for this behavior to become fixed within a population. The chimpanzee communities that do know how to crack nuts gain an important source of fat, sugar, protein, and amino acids. When nuts are in season, an individual chimpanzee may crack nearly 300 each day, which supplies most of the calories and protein that the individual needs.

Hammers and anvils may be stones, pieces of wood, or a combination of a stone hammer and wood anvil. Hardened, exposed tree roots are also used as anvils, creating a fixed tool-using site. Chimpanzees may transport their tools to where nuts are found, or they may carry nuts to where tools can be found. In a small number of instances, chimpanzees in Bossou, Guinea have attempted to use a stone anvil that was not flat, and the nuts rolled off before they could be cracked. These individuals inserted a third stone as a wedge that both leveled and stabilized the anvil, which was then used successfully. This complex behavior is termed “meta-tool” use. Nut cracking illustrates the interaction between chimpanzee mental skill, tool-use, and the ability to exploit otherwise unavailable foods. This phenomenon is not limited only to tool-use, but includes social behaviors as well.

Chimpanzees actively engage in hunting, and eat a variety of animals such as bushpigs, small antelopes, and monkeys. Unlike the opportunistic meat-eating seen with other great apes, chimpanzees are known to coordinate their efforts and then share meat with other party members. The most commonly sought after prey are the arboreal colobus monkeys, (*Colobus* spp.). As with most chimpanzee behaviors, there can be considerable variation both within and between populations. Individuals may successfully hunt alone, a collection of individuals may hunt in an uncoordinated fashion, or several chimpanzees may form a hunting party and cooperate with each other to drive colobus monkeys towards a group member who may be waiting in a nearby tree to make the capture and kill. After the hunt, the meat is divided among the members of the party, but is not shared equally, and some individuals may be completely excluded. Hunting and meat-eating may provide an important source of calories for some individuals, but unlike nut cracking, is not an essential part of the overall chimpanzee diet. Rather, meat appears to be a highly preferred food that is shared strategically. This behavior may strengthen alliances, maintain social status, or increase an individual’s opportunities for reproduction.

Across their ranges, all of the great apes exhibit some level of variation in relation to their diet. In some instances this may be related to local food availability, but in others, cultural norms between populations explain behavioral differences related to feeding and foraging. Preferences, skills, or specific techniques for food acquisition are transmitted between generations, establishing patterns of behavior that may be extremely resilient over time. Research devoted to the ways in which these behaviors emerge and are learned by other individuals provide one of the best opportunities for understanding the mental skills and abilities of great apes in the wild.

Reproductive biology

Each of the great apes has a distinct mating system that is directly associated with their social organization and behavior. Sexual activity is not seasonal, all female great apes have a predictable reproductive cycle that is usually about a month in duration. Offspring are most often singletons, although twins have been reported on rare occasions. A female makes an enormous investment in each of her young, who will remain dependent on her for years. Males do not take a direct role in the care of their offspring, although they do provide indirect care in the form of group protection and usually demonstrate amazing levels of tolerance and good will towards infants and juveniles. Neither of these generalizations specifically apply to wild orangutans, since males rarely encounter, or interact with, youngsters.

In any mating system, both males and females need to protect and promote the genetic investment that they make in their offspring. Males accomplish this primarily by competing for sexual access to females, hoping to assure their paternity. Females are choosy about their mates, and base their preferences on physical as well as behavioral traits. Most importantly, infants and juveniles need to be protected from rival males, who may attempt to enter the group and commit infanticide. Although this behavior is repugnant, it does serve an evolutionary purpose since males that commit infanticide decrease their rival’s reproductive success. Females that lose their infants begin cycling again, which may provide mating opportunities as well, a desirable possibility for the rival male. The combination of these factors has a profound influence on the structure of great ape mating and social systems.

Gorillas are the only polygamous great apes. Breeding groups are usually composed of one adult male, who is dominant, several adult females, and their offspring. The alpha male attempts to repel all rival males, guarding his opportunities for reproduction. In this system, mature males may normally be twice the size of adult females. This extreme sexual dimorphism is the result of female preference for larger males, as well as male-male competition. Larger males are able to provide better protection for the females and offspring in their group, minimizing the risk of infanticide. Female gorillas advertise their sexual receptivity through their behavior, rather than with any obvious physical changes. Females invite copulations by closely following a male, staring at him intently, and sometimes stimulating his genitals with their hand or mouth. Gorillas usually limit their sexual activity to the few days in each cycle when a female can become pregnant. Offspring are primarily dependent on the care provided by their mothers, although they may regularly interact with any of the other members of their group, including the dominant male.

Like gorillas, infant chimpanzees are at risk of infanticide from rival males in other communities. However, chimpanzees live in a promiscuous, rather than polygamous, mating system. Communities may have multiple adult males, females, and offspring, with males providing cooperative defense against rivals. Sexual dimorphism is greatly reduced, and males are only slightly larger. Female chimpanzees do not have concealed ovulation, and conspicuously advertise their fertile time (and associated sexual readiness) with a large, pinkish swelling of their genital area. This serves as a visual invitation to adult males, who compete for sexual access. During an ovulation, a female may copulate with a number of males, sometimes in succession. Therefore, paternity is never clear, and males protect all offspring equally. Usually, chimpanzees do not copulate outside of a female's fertile period. Offspring receive the majority of their care from their mothers, who spend much of their time traveling in family or nursery parties.

The situation for bonobos is very different, since adult females are constantly in a state of sexual receptiveness. Copulations are not in limited supply for bonobos, although mate choice is clear and males may compete for specific females. In these situations, higher ranked males copulate more often than lower ranked ones. Sexual dimorphism is greatly reduced, and infanticide has never been recorded in bonobo society. As with chimpanzees, paternity is never clear, and adult males show equal tolerance towards all youngsters. An additional distinction is that bonobo communities may also intermingle, with no apparent risk to infants. While young bonobos are predominantly dependent on their mothers, they also may interact with individuals both within and outside of their natal community.

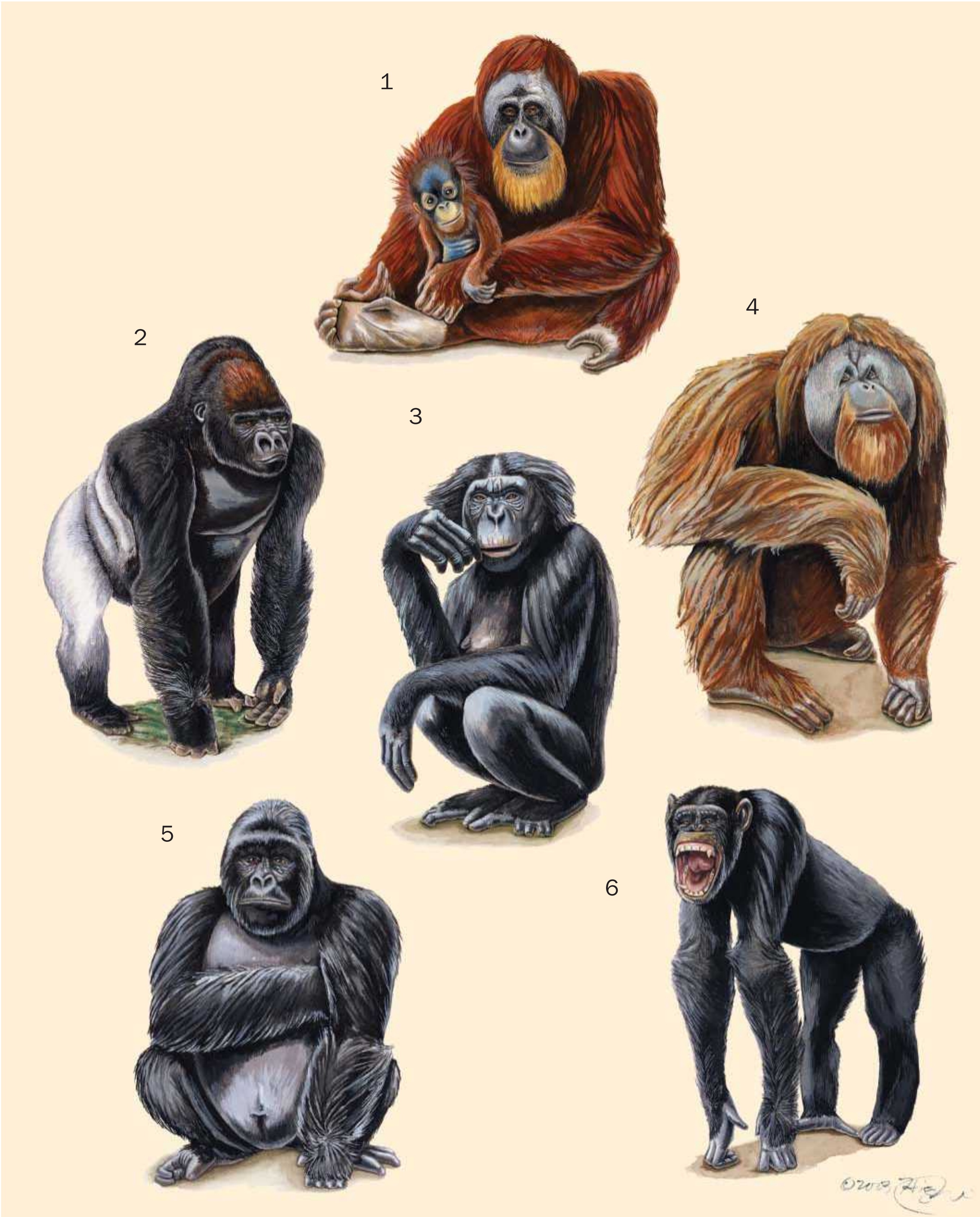
Orangutans have a unique set of circumstances related to mating and reproduction. Males and females travel separately, moving within overlapping home ranges. Males usually occupy larger areas, thereby increasing their access to both females and food patches. Orangutans have a very dispersed social organization with a promiscuous mating system. They have extreme sexual dimorphism with males reaching twice the size of females. Competition between these males is intense. However, two forms of sexually mature male orangutans exist. In addition to those that show the full expression of sexual dimorphism, others fail to develop these characteristics even though they are capable of reproduction. These males may be suppressed by the presence of more dominant males, but can develop fully dimorphic traits if the dominant individuals leave the area. Females show a strong mate choice preference for the fully dimorphic males, and may willingly engage in copulations with them. Non-resident males, suppressed males, and juvenile males are generally less preferred, and may pursue females to copulate with them forcefully. Infanticide has never been recorded among orangutans, even though females regularly encounter different adult males. Females show no physical signs related to ovulation, and sexual behavior may occur at any point during the female's cycle. In the wild, female orangutans give birth only once every 6–8 years, the longest inter-birth interval of any land mammal. Offspring are completely dependent on their mothers for survival, but may occasionally interact with other juveniles within their home range.

Conservation status

The IUCN considers the Sumatran orangutan (*Pongo abelii*) to be Critically Endangered. The remaining five species of great apes are considered Endangered. The conservation status of great apes can be easily summarized. Throughout their entire range, all species of great ape are likely to become extinct within a generation. The major threat to their survival is unrelenting competition with humans. Great ape habitat is being transformed for human agricultural and commercial uses, rapidly bringing all wild great ape populations into direct conflict with people. Hunting of great apes to fill cooking pots is completely unsustainable, and particularly acute throughout Africa. This trade in bushmeat has accelerated the already critical decline in all great ape populations. Scientists working in the field estimate that there are no more than approximately 200,000 chimpanzees left in Africa, perhaps 100,000 gorillas, 25,000 bonobos, and a combined total of 20,000 orangutans left in Sumatra and Borneo. Conservation of these species is primarily dependent on the governments of the countries in which they exist. The best hope for their survival is habitat protection and preservation which is supported by major conservation organizations throughout the world.

Significance to humans

The great apes are our closest living evolutionary relatives. The degree of genetic relatedness between humans, chimpanzees, and bonobos is greater than the relationship between gorillas, chimpanzees, and bonobos. Great apes make and use tools, form life-long social bonds, demonstrate grief, spontaneously adopt and care for infants, and show evidence of compassion for each other. They also wage war, rape, practice infanticide, and hunt baboons for food. In captivity, they have learned to use language and numbers, generously accepted humans as social equals, and taught us that the mental differences between humans and the other great apes are only in degree, not in kind. They provide us with the best measure of what is uniquely human, and what we must admit we share with them.



1. Female and infant Bornean orangutans (*Pongo pygmaeus*); 2. Male western gorilla (*Gorilla gorilla*); 3. Female bonobo (*Pan paniscus*); 4. Male Sumatran orangutan (*Pongo abelii*); 5. Male eastern gorilla (*Gorilla beringei*); 6. Male chimpanzee (*Pan troglodytes*). (Illustration by Jonathan Higgins)

Species accounts

Bornean orangutan
Pongo pygmaeus

SUBFAMILY
Ponginae

TAXONOMY
Pongo pygmaeus (Linnaeus, 1760), Borneo. Three subspecies.

OTHER COMMON NAMES
French: Orang-outan; Spanish: Orang-után.

PHYSICAL CHARACTERISTICS
Largest of the arboreal primates, demonstrating extreme sexual dimorphism. Females weigh 70–100 lb (31.8–45.4 kg), males may reach 200 lb (90.7 kg). Hair color ranges from reddish to brown. Adult females lack the prominent cheek pads and throat pouch that are obvious on mature males.

DISTRIBUTION
Borneo. *Pongo pygmaeus pygmaeus*, northwest Kalimantan; *Pongo pygmaeus wurmbii*, southwest Kalimantan; *Pongo pygmaeus morio*, Sabah, south to Sungai Mahakam.

HABITAT
Lowland primary forest canopy and swampy areas. Mature fruit trees must be present.

BEHAVIOR
Dispersed social system. Males spend most of their time traveling alone, and are highly intolerant of each other. Long calls are used as a spacing mechanism. Females are found with their juvenile offspring.

FEEDING ECOLOGY AND DIET
Rely primarily on fruits, but also consume many types of vegetation. Meat-eating has been documented, but is exceedingly rare. Tools are used to extract imbedded foods.

REPRODUCTIVE BIOLOGY
Females have concealed ovulation, and demonstrate mate choice. Mating is promiscuous and may occur throughout the female's reproductive cycle. Copulations may be forced, most often by juvenile or non-resident males.

CONSERVATION STATUS
Endangered.

SIGNIFICANCE TO HUMANS
Currently hunted for meat, and for infants that are sold in the illegal pet trade. ◆

Sumatran orangutan
Pongo abelii

SUBFAMILY
Ponginae

TAXONOMY
Pongo abelii (Lesson, 1827). Monotypic.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Largest of the arboreal primates, demonstrating extreme sexual dimorphism. Reported to be slightly smaller than Bornean orangutans. Adult females lack the prominent cheek pads and throat pouch that are obvious on mature males.

DISTRIBUTION
Sumatra.

HABITAT
Lowland primary forest canopy and swampy areas. Mature fruit trees must be present.

BEHAVIOR
Dispersed social system. Males spend most of their time traveling alone, and are highly intolerant of each other. Long calls are used as a spacing mechanism. Females are found with their juvenile offspring.

FEEDING ECOLOGY AND DIET
Rely primarily on fruits, but also consume many types of vegetation. Meat-eating has been documented, but is exceedingly rare. Tools are used to extract imbedded foods.

REPRODUCTIVE BIOLOGY
Females have concealed ovulation, and demonstrate mate choice. Mating is promiscuous and may occur throughout the female's reproductive cycle. Copulations may be forced, most often by juvenile or non-resident males.

CONSERVATION STATUS
Critically Endangered.

SIGNIFICANCE TO HUMANS
Currently hunted for meat, and for infants that are sold in the illegal pet trade. ◆

Western gorilla
Gorilla gorilla

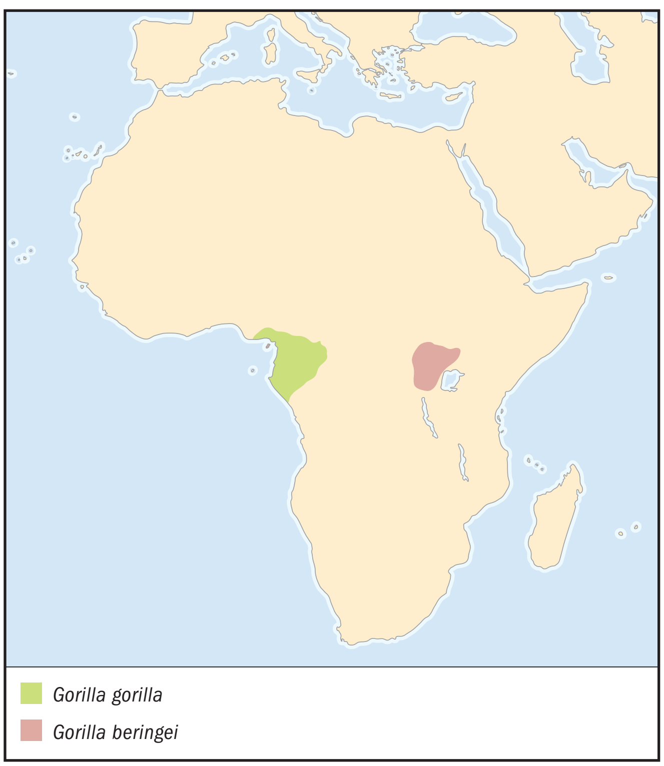
SUBFAMILY
Homininae

TAXONOMY
Gorilla gorilla (Savage and Wyman, 1847), Gabon Estuary, Gabon. Two subspecies.

OTHER COMMON NAMES
French: Gorille; Spanish: Gorila.

PHYSICAL CHARACTERISTICS
Largest of the terrestrial primates, demonstrating extreme sexual dimorphism. Females generally weigh about 150 lb (68 kg), males may approach 400 lb (181.4 kg). Hair is generally black over most of the body, red to brown on the crest of the head. Mature males sport silver hair on their back.

DISTRIBUTION
West Africa, including Nigeria, Cameroon, Gabon, extending into Congo, and Central Africa Republic. *Gorilla gorilla gorilla*, Cameroon; *Gorilla gorilla diehli*, border area between Nigeria and Cameroon, extending into the forest of the upper Cross River.



HABITAT
Found in primary and secondary forest, may venture into swampy clearings as well.

BEHAVIOR
Polygamous social system. Mixed sex groups generally include one dominant male, multiple adult females, and offspring. Variations may be seen in which more than one adult male is present. Males may also travel alone, or congregate in bachelor groups.

FEEDING ECOLOGY AND DIET
Consume a variety of types of vegetation and fruits. Meat-eating has not been documented, and tool use appears to be absent.

REPRODUCTIVE BIOLOGY
Females show no physical signs associated with ovulation, but give behavioral signals that invite copulation. Mating system is polygamous, and adult males repel rivals who may attempt to lure females away. Infanticide by rival males is well known.

CONSERVATION STATUS
Endangered.

SIGNIFICANCE TO HUMANS
Populations are being severely affected by unsustainable hunting for meat. ◆

Eastern gorilla
Gorilla beringei

SUBFAMILY
Homininae

TAXONOMY
Gorilla beringei (Matschie, 1903). Two subspecies.

OTHER COMMON NAMES
English: Mountain gorilla, eastern lowland gorilla.

PHYSICAL CHARACTERISTICS
Largest of the terrestrial primates, demonstrating extreme sexual dimorphism. The hair is primarily black, and may be quite long with a shaggy appearance. Mature males sport silver hair on their back.

DISTRIBUTION
East Africa, Democratic Republic of Congo into Rwanda and Uganda. *Gorilla beringei beringei* (mountain gorilla), Uganda, Rwanda, and Democratic Republic of Congo; *Gorilla beringei graueri* (eastern lowland gorilla), eastern Democratic Republic of Congo.

HABITAT
Found in primary, secondary, and bamboo forest, but at higher altitudes than the western gorilla.

BEHAVIOR
Polygamous social system. Mixed sex groups generally include one dominant male, multiple adult females, and offspring. Variations may be seen in which more than one adult male is present. Males may also travel alone, or congregate in bachelor groups.

FEEDING ECOLOGY AND DIET
Primarily dependent on vegetation and some fruits. *G. b. beringei* relies entirely on vegetation. Meat-eating has not been documented, and tool use appears to be absent.

REPRODUCTIVE BIOLOGY
Females show no physical signs associated with ovulation, but give behavioral signals that invite copulation. Mating system is polygamous, and adult males repel rivals who may attempt to lure females away. Infanticide by rival males is well known.

CONSERVATION STATUS
Endangered.

SIGNIFICANCE TO HUMANS
Some portions of the population are being severely affected by unsustainable hunting for meat. ◆

Chimpanzee
Pan troglodytes

SUBFAMILY
Homininae

TAXONOMY
Pan troglodytes (Blumenbach, 1775), Mayoumba, Gabon. Four subspecies.

OTHER COMMON NAMES
English: Common chimpanzee, robust chimpanzee; French: Chimpanzé; Spanish: Chimpancé.

PHYSICAL CHARACTERISTICS
Compact and muscular build. Hair is generally black, but may turn gray with age. Slight sexual dimorphism. Females weigh 70–100 lb (31.8–45.4 kg) and males may be 80–130 lb (36.3–59 kg).

DISTRIBUTION
Large portion of Africa, beginning in Senegal and reaching the Democratic Republic of Congo, Sudan, Uganda, Rwanda, Burundi, and Tanzania. *Pan troglodytes troglodytes*, Cameroon, Nigeria, Central African Republic; *Pan troglodytes verus*, Senegal; *Pan troglodytes schweinfurthii*, Democratic Republic of Congo, Sudan, Uganda, Rwanda, Burundi, and Tanzania. Actual borders between subspecies are difficult to assess and overlap may occur in some areas.

HABITAT
Found in a range of habitats including primary forest, secondary forest, grassland, and woodland savanna.

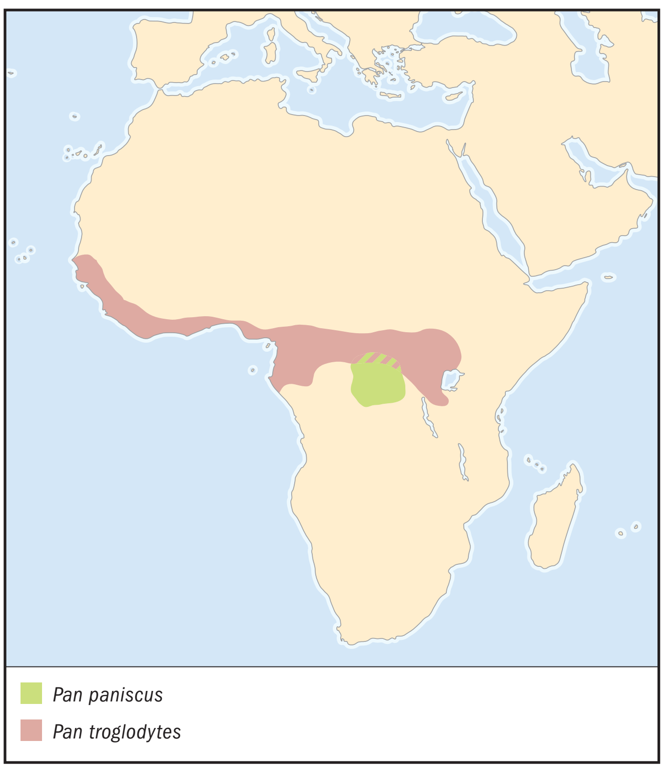
BEHAVIOR
"Fusion-fission" social system. Communities regularly break into smaller parties of varied composition. Males are generally dominant and form coalitions. Females are generally subordinate to adult males. Social interactions can be highly complex.

FEEDING ECOLOGY AND DIET
Exploit the widest variety of foods of any species of primate. Fruits, vegetation, insects, nuts, and animal prey are all included. Hunting and meat-eating are common. A diverse collection of tools are used to acquire and process regularly eaten foods.

REPRODUCTIVE BIOLOGY
Promiscuous mating system. Females advertise their ovulation with prominent genital swellings. Males compete for sexual access to females, although females may mate with many males when they ovulate. Paternity is difficult to assess. Offspring are at risk of infanticide from rival males.

CONSERVATION STATUS
Endangered.

SIGNIFICANCE TO HUMANS
Populations are being severely affected by unsustainable hunting for meat. ◆



Bonobo
Pan paniscus

SUBFAMILY
Homininae

TAXONOMY
Pan paniscus Schwarz, 1929, south of the upper Maringa River, Democratic Republic of the Congo. Monotypic.

OTHER COMMON NAMES
English: Pygmy chimpanzee, gracile chimpanzee, dwarf chimpanzee; French: Chimpanzé nain, chimpanzé pygmée; Spanish: Chimpancé pigmeo.

PHYSICAL CHARACTERISTICS
Much more slender than the chimpanzee. Hair is black, and is distinctly parted down the center of the head. Slight sexual dimorphism. Females may weigh around 70 lb (31.8 kg), and males less than 100 lb (45.4 kg). The skin on the face is always very dark.

DISTRIBUTION
Democratic Republic of Congo.

HABITAT
Primary and secondary forest.

BEHAVIOR
"Fusion-fission" social system. Communities divide into smaller parties that change less frequently than those of the chimpanzee. These parties usually have a mixed sex composition. While tension and aggression exist between individuals, it is reduced through frequent erotic interactions. These may be male-female, male-male, or female-female. Females are dominant, and males are subordinate. Communities may peacefully intermingle.

FEEDING ECOLOGY AND DIET
Primarily reliant on fruits and vegetation. Some meat is eaten, but comprises a very small part of the overall diet. Tools are not used to acquire foods.

REPRODUCTIVE BIOLOGY
Promiscuous mating system. Sexual activity is extremely common, but is not indiscriminate. Incest taboos are in place, and males compete for access to specific females. Higher ranking males have increased sexual access for reproduction. Infanticide is unknown in bonobos.

CONSERVATION STATUS
Endangered.

SIGNIFICANCE TO HUMANS
Populations are being severely affected by unsustainable hunting for meat. ◆

Resources

Books

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Robert W. Shumaker, PhD

Hominidae II

(Humans)

Class Mammalia
Order Primates
Family Hominidae
Subfamily Homininae

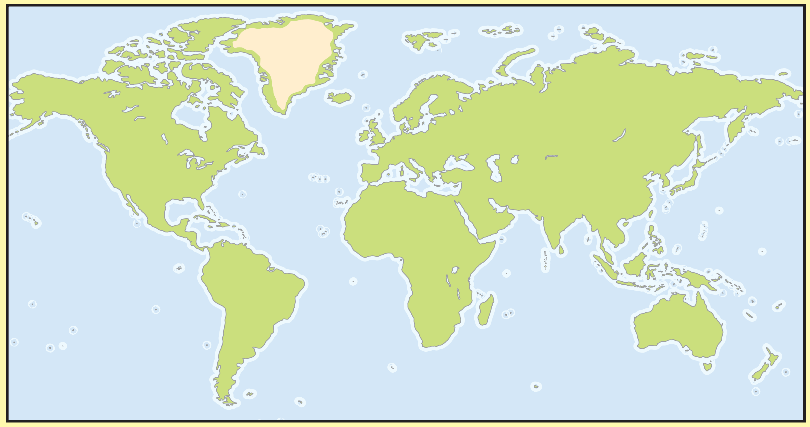
Thumbnail description
Large mammals; obligate bipeds; largest brain to body size ratio among terrestrial mammals; moderate degree of sexual dimorphism; species-specific vocal communication (language); obligate reliance on tool behavior and technology; complex sociality

Size
Variable, depending upon population. Normal adult stature: 53.5–72.8 in (136–185 cm); normal adult weight: 83.8–198.4 lb (38–90 kg)

Number of genera, species
1 genus, 1 species, 1 subspecies

Habitat
All terrestrial habitats, aided by domestication of animals and plants, technology, and extensive environmental modification

Conservation status
Not threatened



Distribution
Cosmopolitan; exploration of outer space and the solar system is now proceeding apace; colonization of other worlds within the solar system will probably take place within the foreseeable future

Evolution and systematics

Humans are members of the primate infraorder Catarrhini. This infraorder encompasses the Old World monkeys (family Cercopithecidae), lesser apes (family Hylobatidae), and great apes and humans (family Hominidae). It has been clear since the 1930s that all of the living catarrhines comprise a closely related group of organisms that is both morphologically and physiologically very similar.

The taxonomy for humans is *Homo sapiens* Linnaeus, 1758, Uppsala, Sweden. All living humans belong to the subspecies *Homo sapiens sapiens*.

Humans have 46 chromosomes, in contrast to the 48 chromosomes of pongids. DNA-DNA hybridization studies initially highlighted the close genetic relationship between humans and common chimpanzees. However, in general, there is a high degree of genetic similarity between humans and other mammals. The genetic similarity between human and mouse is approximately 90%. Sequencing of the human genome was completed in 2001. A 2002 comparison of human and mouse genomes showed the existence of about 30,000 genes in both organisms. The same genetic elements can be rearranged, and appear on different chromosomes. The mouse genome has evolved 2–5 times more rapidly than the human genome, probably because the shorter generation length of mice allows for greater rates of change. Mouse genes appear to be more subject to physical reordering, and mouse genes in different locations on the same chromosome can evolve at different rates. About one-third of the genes shared between human and mouse do not encode proteins. Some of these may encode RNA, while others may serve regulatory functions. Studies of evolutionary development in humans and other vertebrates demonstrate the existence of conservative *Hox* genes that are responsible for establishing the embryonic blueprint.

Hominins (members of the subfamily Homininae) are descendants of an unknown pongid from the late Miocene of Africa. The first hominin may be the late Miocene *Sahelanthropus chadensis*, dating to 6–7 million years ago (mya), from Chad, in Central Africa. However, this species is known only from cranial and dental remains. *Orrorin tugenensis* is a slightly more recent (6 mya) fossil species from western Kenya with postcranial remains. Femurs of *Orrorin* indicate that it had bipedal locomotion, which is the hallmark of the hominid family. A climatic trigger for hominin origins is often invoked. A period of late Miocene aridity in Africa is thought to have eliminated forests and caused the spread of extensive open-country grasslands, and thus created selection pressures for the origins of terrestrial bipedal hominins. However, *Sahelanthropus*, *Orrorin*, and later hominins that are well known postcranially are found in environmental mosaics that include

Fossil hominid skeleton (*Australopithecus afarensis*) known as "Lucy." Lucy was part of a rich find of fossils made in the Afar region of Ethiopia between 1973 and 1977. She dates from 3.3 million years ago and is widely accepted as the earliest link in the human record. The remains comprise 40% of an entire skeleton. (Photo by John Reader/Science Photo Library/Photo Researchers, Inc. Reproduced by permission.)

forested areas. The origins of terrestrial bipedal locomotion, therefore, cannot be simply linked to the disappearance of forest and the spread of grasslands.

The poorly known species *Ardipithecus ramidus* occurs between 5.8 mya and 4.4 mya, but the density of hominin fossils increases later, after 4.4 mya. A suite of hominin species appears in East Africa during this time range. Hominin species also occur at South African sites, although these sites lack volcanic materials, and are therefore more difficult to date. However, the South African species *Australopithecus africanus* and *Australopithecus robustus* appear to be later in time than East African material. These South African species were the first fossil hominins recognized from Africa, and are now among the most well known fossil hominins from the Plio-Pleistocene.

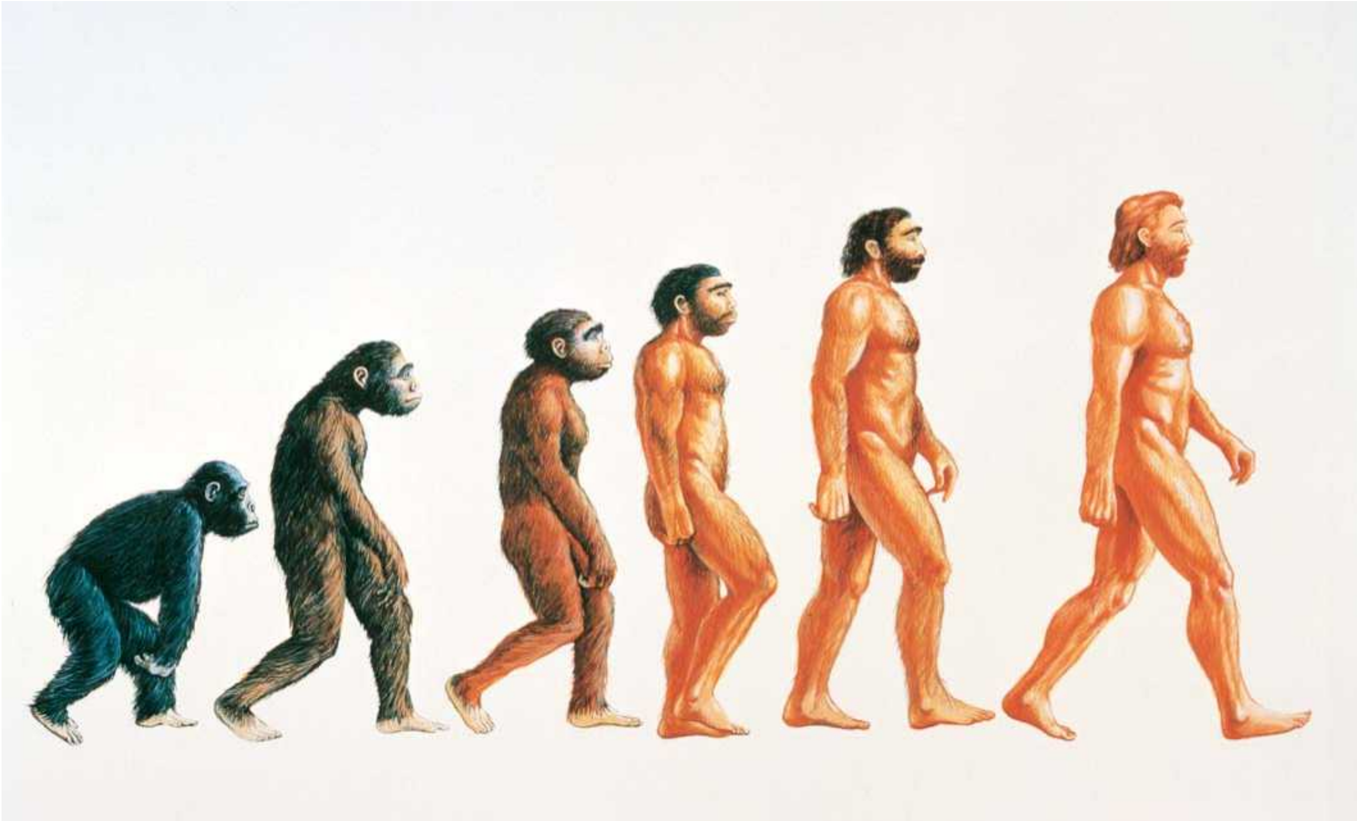
The genus *Australopithecus* alone contains eight species of hominin. Members of the genus occur principally in East and South Africa, and date from 4.4–1.2 mya. The longest-lived species (*Australopithecus boisei*) has a million year span, dating from 2.2–1.2 mya. It is clear that an evolutionary radiation of hominins occurred during the late Miocene through the early Pleistocene. Furthermore, there is definite evidence of sympatric species, indicating that niche differences allowed species to divide the shared resource space.

Besides the possible hominin *Sahelanthropus*, there is an additional hominin species recognized from Chad. This is *Australopithecus bahrelghazali*, dating to about 3 or 3.4 mya. Its principal importance lies in the fact that the site lies 1,550 mi (2,500 km) west of the East African rift. These fossils demonstrate that hominins had a wide geographic distribution, and excellent dispersal abilities even at this early date. This fact might not be obvious from the plethora of human fossils that come from the rift. The richness of the fossil finds from the East African rift is a taphonomic accident, and is caused by the fact that the rift is a sediment trap with the potential for excellent fossil preservation, as well as chronometrically datable volcanic materials. A wide geographical range of hominins at this date indicates that intrinsic biological properties are contributing to dispersion, and not necessarily complex sociality or cultural behavior.

The site of Laetoli, in Tanzania, has hominin footprints laid down in trackways dating to 3.6 mya. These footprints were preserved in a gentle fall of volcanic ash that was deposited by rain. The importance of this site lies not only in its unequivocal record of bipedal locomotion, but also in its documentation that three hominins made the trackways—this is the earliest record of hominin sociality. Because fossils of *Australopithecus afarensis* occur at Laetoli, hominins belonging to this species were apparently responsible for the trackways. This agrees with traits that are unequivocal adaptations for bipedality in the vertebral column, pelvis, and lower limb of this species. Slightly later in time, *Australopithecus afarensis* is also found at localities in Hadar, Ethiopia. As of 2002, the remains of 17 contemporary individuals of this species have been found at the Hadar locality AL 333. A sudden, unknown event—not a flood—was responsible for the mass mortality. This material is also important in documenting sociality, because these individuals were apparently members of the same social group.

Although a large brain relative to body size was long considered the hallmark of the Homininae, by 2003 it became clear that the earliest hominins had a brain to body size ratio comparable to those of living pongids. Brain size increases only with the appearance of genus *Homo*. However, because there is a concomitant increase in body size, the relative increase in brain size does not become obvious until the late Pleistocene.

What of archaeology, which is the evidence of hominin behavior? The earliest stone tools, belonging to the Oldowan Industry, appear in Africa at 2.5–2.6 mya. Stone tools thus occur long after hominin origins. Besides the stone tools themselves, animal bones that show hominin modifications, such as cut-marks or percussion marks, yield a record of hominin behavior. Some early archeological sites contain no stone tools at all, but only modified bone. The earliest archaeological evidence occurs without substantial brain size increase. For example, the Ethiopian site of Bouri, dating to 2.5 mya, contains the hominin species *Australopithecus gahri*, along with modified bone. This species has a brain size of 450 cc, which is equivalent to that of a pongid, and smaller than that of most australopithecines. Hominin tool behavior is thus not dependent on brain size.



An illustration showing stages in the evolution of humans. At left, proconsul (23–15 million years ago) is depicted hypothetically as an African ape with both primitive and advanced features. From it, *Australopithecus afarensis* (>4–2.5 million years ago) evolved and displayed a bipedal, upright gait walking on two legs. *Homo habilis* (2.5 million years ago) was truly human. About 1.5 million years ago *Homo erectus* (at center) appeared in Africa and migrated into Eurasia. *Homo neanderthalensis* (200,000 years ago) lived in Europe and the Middle East and was closely related to modern humans (right). (Photo by David Gifford/Science Photo Library/Photo Researchers, Inc. Reproduced by permission.)

In 1999, a major taxonomic revision of Plio-Pleistocene hominins collapsed two early species of genus *Homo* (*H. habilis* and *H. rudolfensis*) into the genus *Australopithecus*, reserving genus *Homo* for material that unequivocally showed an increase in body size, had modern human proportions, and had no traits indicating a retention of climbing or arboreal adaptations. Some researchers argue that six or more species of genus *Homo* coexisted in the early Pleistocene, only to be winnowed out with the advent of *Homo sapiens*. However, it is unlikely that early genus *Homo* was speciose. One can assess the species richness of early *Homo* in contrast to other mammalian genera by examining the species richness of extant mammalian genera with a similar body size. Using this method, one or two hominin species is the number expected for a mammal genus of 66–143 lb (30–65 kg), which is the size range usually estimated for early *Homo* fossils.

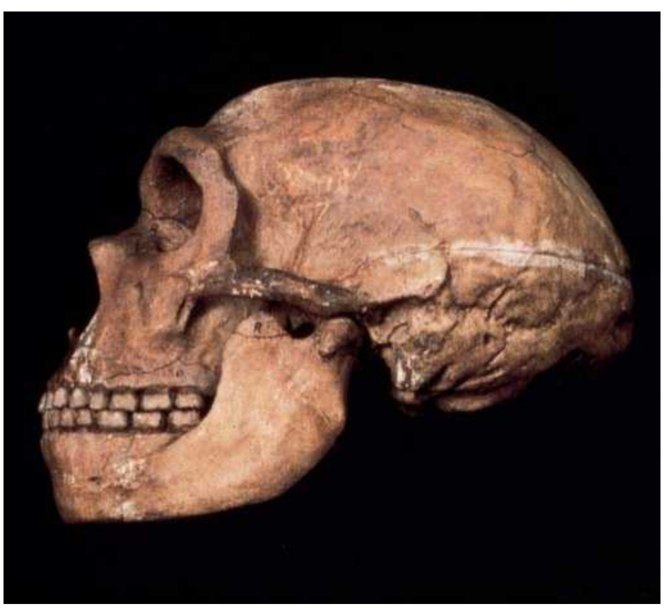
African *Homo erectus*, appearing at 1.8 mya, is the first unequivocal member of genus *Homo*. Postcranial fossils indicate that body size has increased in this species. A higher quality or more predictable diet must underlie this increase in body size. Details of tooth enamel formation demonstrate that *Homo erectus* matured quickly, in an ape-like fashion. Sexual maturity may have been reached by females at 8–9 years, and by males at 10–12 years. This faster maturation may be a major factor in the dispersal abilities of this species, which was the first hominin to emerge from Africa to penetrate other regions of the Old World.

Slow maturation, equivalent to that of modern humans, appears only with the Neanderthals. Neanderthal fossils date from 300,000–28,000 years ago, and occur in Europe, Central Asia, and the Middle East. They are the most well known of fossil humans, because of the completeness of their skeletal remains. Nearly all researchers agree that this completeness results from deliberate burial of remains, rather than accidental preservation. Neanderthals possess a distinctive suite of skeletal traits. These traits (especially traits in the nasal region) appear to be adaptations to extremely cold, dry conditions. Neanderthals had highly carnivorous diets, as established by the bone chemistry of these fossil humans and contemporary animals. The taxonomic status of Neanderthals has been problematic since the discovery of the first Neanderthal fossils in the middle of the nineteenth century. As of 2003, most researchers assign them to a different species (*Homo neanderthalensis*), but many argue that they are distinct only at a subspecies level (*Homo sapiens neanderthalensis*). The argument is not trivial, because it affects discussions of whether modern human populations incorporate genetic material from earlier, non-modern humans, or represent de-

A Cro-Magnon skull. (Photo by E. R. Degginger/Photo Researchers, Inc. Reproduced by permission.)

scendants of a completely novel small founding population that completely replaces earlier humans.

Mitochondrial DNA (mtDNA) evidence initially seemed to support the origin of anatomically modern humans from a very small late Pleistocene founding population in sub-Saharan Africa. This idea became a prominent feature in many textbooks, where it was categorized as the "Out of Africa" or "Complete Replacement" model, because it seemed to imply that modern humans completely replaced their predecessors in the Old World, who went extinct without issue. However, Templeton in 2002, using mtDNA and nuclear DNA from both autosomes and sex chromosomes, demonstrated that the evolutionary picture is substantially more complex, with a series of migrations out of Africa and another migratory vector out of Asia. There was no single small founding population for modern humans, during either the middle or late Pleistocene. Mitochondrial DNA has also failed to elucidate lower level questions about human evolution and dispersal. For example, it is clear in 2003 that mtDNA from Native Americans cannot illuminate crucial questions about the peopling of the Americas, such as the number or timing of migration events, or the source of the founding populations.



Neanderthal man's skull. (Photo by E. R. Degginger/Photo Researchers, Inc. Reproduced by permission.)

Global dispersal

With the advent of the fossil species *Homo erectus*, humans emerged from sub-Saharan Africa and rapidly colonized broad areas of the Old World. By 1.7 mya, several specimens of this taxon are found at the site of Dmanisi, in the Republic of Georgia. Abundant fossil remains of *Homo erectus* have been recovered from the island of Java. Two of the sites from Java have very early dates (1.8 mya and 1.6 mya), and much of the Javanese fossil material dates from about 1 mya. Pleistocene human fossils occur at a later period in Iberia, England, northern, southern, and eastern Europe, Central Asia, and China.

When anatomically modern humans appear, additional continental expanses were penetrated. The continent of Australia was reached between 46,000 and 50,000 years ago, and quickly settled. A global fall in sea level during the Pleistocene allowed humans to travel on dry land between areas that are now separated by water. They crossed from Asia to North America via a now submerged land bridge in the Bering Straits. Humans were in the Americas by 14,000 years ago, as shown by the important archaeological site of Monte Verde in Chile. These migrants may have used a narrow coastal passage along the western continental margins to penetrate quickly to the south. Boating technology, navigational techniques, and logistical preparedness for deliberate colonization allowed humans to settle the South Pacific islands. Settlers from Indonesia crossed the entire expanse of the Indian Ocean to reach Madagascar around 1,200 years ago. The North and South Islands of New Zealand were settled 1,000 years ago. This represents the last major human migration event using traditional modes of transportation.

Physical characteristics

Bipedal locomotion is the hallmark of the hominin family. Both the morphology and the orientation of bones and joints must be extensively altered from the ancestral pongid condition in order to accommodate bipedality. These alterations affect the foot, leg, pelvis, and vertebral column. Extensive biomechanical analysis of bipedalism has been conducted in living humans. This analysis demonstrates that there is very little electrical activity in muscles when subjects walk at a normal pace and are unencumbered by burdens. Hence, although it is slow, bipedalism is a very energy efficient mode of locomotion. A human walking at a normal speed uses only about

A woman wears the traditional clothing of Korean dancers. (Photo by © Dallas and John Heaton/Corbis. Reproduced by permission.)

87% of the energy used by a similarly sized, generalized quadrupedal mammal moving at the same speed.

Normal humans carry large amounts of subcutaneous fat. This is peculiar for terrestrial mammals, which typically accumulate fat only before breeding, migrating, or hibernating. Unlike marine mammals, humans do not need this fat for maintaining the core temperature of the body. Furthermore, given constant supplies of abundant food and little physical activity, humans can quickly increase their store of subcutaneous fat. The most likely explanation for this human peculiarity is that it evolved to allow humans to survive periods of starvation or near-starvation. Indeed, seasonal calorie restriction is documented today for hunter-gatherers, as well as for agriculturalists. Many contemporary humans experience famine, if rainfall is low, or inadequate emergency stores of food have been set aside. There may be no extra food to cache for emergencies. Seasonal want appears to be the norm for humans, and thus natural selection has provided a built-in reserve of fat to tide humans over the inevitable lean period.

The surface of the human body is virtually hairless. With high ambient temperatures, sweat evaporates from this hairless skin. The temperature of the human body surface is thus lowered through evaporative cooling. This physiological adaptation is seen in all humans. It is a species-specific trait, because it is based on the presence of eccrine sweat glands on the surface of the skin. Hairlessness promotes evaporation. The abundance and density of eccrine sweat glands are unique to humans among other mammals. These glands are mainly restricted to the bottoms of the paws and adjacent regions in other mammals. Eccrine sweat glands do not produce the fatty secretions that are associated with scent and scent-marking in mammals. Instead, eccrine glands produce abundant watery secretions that contain salt, potassium, and calcium. The human sweating response is entirely dependent upon access to abundant fresh water, because any water lost through sweating must be quickly replaced. If this water is not replaced, death, caused by shock through loss of blood volume and heat stroke, can occur within a single day. A normal human sweating rate is 0.5–1 liter/hour, but this can be increased to 2 or sometimes 3 liters/hour in working humans accustomed to high temperatures. This rate, however, cannot be sustained.

Human body build shows climatic adaptation to extremes of temperature. This has been noted since the nineteenth century, and confirmed in many studies during the twentieth century. In 1847, Bergmann observed that endothermic animals had heavier bodies in cold climates, and lighter body builds in hot climates. In 1877, Allen observed that endothermic animals had shorter extremities in cold climates, and longer extremities in hot climates. Humans conform to Bergmann's and Allen's rules. In 1994, Ruff established that human pelvic breadth, which is a good proxy for body width, is correlated with temperature. Pelvic breadth is wide in cold climates, and narrow in hot climates.

High altitude also affects humans, principally through low oxygen pressure. However, cold temperature, high winds, rough terrain, poor soils, and impoverished ecosystems also exercise a profound affect on humans living at high altitudes.

Humans, like other mammals, initially receive nourishment from the mother. (Photo by George Bernard/Earth Scenes. Reproduced by permission.)

Cultures have different ideas of beauty. A long neck is desirable in Paduang, Thailand. (Photo by © David Cumming; Eye Ubiquitous/Corbis. Reproduced by permission.)

Humans entering high altitude areas from the lowlands gradually increase the number of red blood cells in their body. These cells carry hemoglobin, which binds to oxygen, and transports it through the system. This response is caused by reduced oxygen at higher elevations. Humans born at high altitudes have a larger heart and lungs, and grow more slowly. Human populations that adapt to high altitude through evolutionary time have larger placentas, and consequently develop better contact between the blood supply of fetus and mother. Newborns of these populations have a higher birth weight, and greater survivorship than infants from other groups that are new migrants to the region. Native people in Tibet, who may have evolved high altitude adaptations through the longest time, have a genetically based variant hemoglobin that has enhanced oxygen binding properties.

Human populations differ in skin pigmentation. Since the 1930s, a relationship has been documented between skin pigmentation and latitude. Darker skin occurs at low latitudes, and lighter skin at high latitudes. The pigment melanin, produced by melanocytes in deep layers of the skin, is responsible for variation in human skin color. The skin also synthesizes vitamin D when it is exposed to sunlight. Vitamin D has an important role in calcium metabolism, which affects not only skeletal density, but also proper functioning of the nervous system. The adaptive significance of melanin in the skin appears to involve maintaining critical amounts of vitamins—vitamin D synthesis and the preservation of adequate amounts of folate, necessary for normal development of the fetal nervous system. Light skin allows more vitamin D to be synthesized in high latitudes where sunlight is weak. Dark skin decreases vitamin D synthesis and preserves folate in low latitudes where sunlight is intense.

Human adaptation to extreme climates is dependent upon culture and technology. Culture and technology allow humans to create pleasant or balmy microhabitats in which to live. Fire, clothing, shelter, transportation, food acquisition, processing, and caching, water storage, and complex behavioral adaptations underlie and complement human morphology and physiological response.

Since the early 1950s, physical anthropologists have studied human populations, not races. This reflects an understanding of the importance of variation within populations, and an overriding interest in natural selection, adaptation, and other evolutionary processes. The earlier approach, defining races and human types, was typological in nature. It categorized humans, devised schemes for human classification, and was relatively indifferent to evolution. In 2003, race is prin-

Although humans have the ability to swim, the only way they are able to physically observe undersea life is with the help of scuba equipment. (Photo by © Amos Nachoum/Corbis. Reproduced by permission.)

cipally used by forensic anthropologists in the analysis of human DNA and skeletal and soft-tissue traits, where the ancestry of forensic material needs to be ascertained.

Distribution

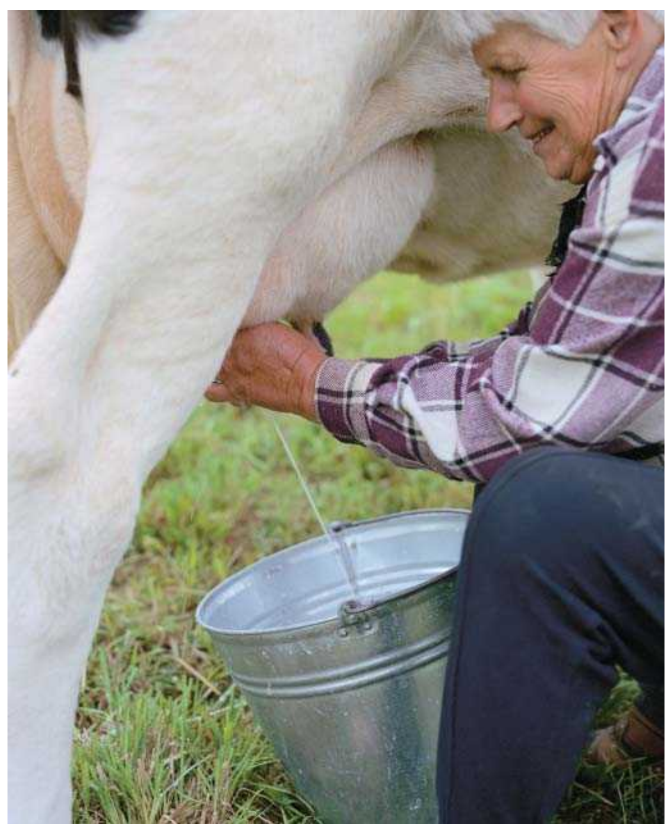
Humans are global in distribution. They are not restricted by major geographic barriers, because of the use of technology to travel over water and land, and through the air. This dispersal ability is not new. By 1.7 mya, humans occupied an Old World geographic range that extended from the East African rift to the island of Java. This early broad distribution was accomplished without the benefit of transportation technology. It is based on intrinsic biological properties for ranging and foraging that allowed humans to expand their geographic distribution. Anatomically modern humans occupied and rapidly penetrated the continent of Australia between 46,000 and 50,000 years ago. The Australian evidence demonstrates that humans were able to cross a substantial water gap by this time, and could rapidly disperse through the entire continent.

Habitat

Humans occupy all terrestrial habitats. Only human ectoparasites and endoparasites or vermin that attend humans occupy a comparably broad range of habitats. Yet, humans have experienced no speciation in spite of a vast array of occupied habitats. Therefore, the wide distribution of humans is associated with biological factors underlying good dispersability and a very broad niche. These factors include a wide tolerance for habitat diversity and pronounced seasonal variation. Humans therefore fall into the category of *r*-selected organisms, in spite of their large body size, longevity, and low intrinsic rate of increase.

Nutritional ecology

Humans are omnivorous. Humans were eating wild plant foods from the origins of the subfamily Homininae about 6 mya until the inception of agriculture 11,000 years ago. Comparisons with omnivorous, widespread non-human primates such as baboons make it likely that the earliest hominins consumed a variety of plants and plant parts, and also consumed insects, eggs, and small animals like birds and hares. Bone chemistry analyzing stable carbon isotopes shows that South African australopithecines were omnivores. This is true even for the species *Australopithecus robustus*, which had been considered highly vegetarian since the mid-1950s. Neanderthal bone chemistry shows that these fossil humans were highly carnivorous, as one might expect, given that they lived in



Humans have domesticated other mammals, such as the cow (*Bos taurus*). (Photo by Paul Gun/Corbis. Reproduced by permission.)

A seven-week-old human embryo. (Photo by © Garvis Kerimian/Peter Arnold, Inc. Reproduced by permission.)

highly seasonal environments where carbohydrates were impoverished during certain periods. Humans lack the high complex molar teeth or ruminant stomachs that allow ungulates to process grass, and they lack the ability to detoxify secondary compounds in mature leaves or other plant parts. Only the advent of food processing or cooking technology allows humans to compensate for these biological restrictions, and to incorporate certain plants into their diets.

Cut-marks and percussion marks made by stone tools on animal bones show that vertebrate meat, fat, and marrow were incorporated into the hominin diet beginning at 2.5–2.6 mya. Tools are necessary to cut through the tough skin of a carcass, sever tendons and dismember a carcass, remove meat from bones, and break open bones to extract marrow. It is likely that hominins first acquired meat, fat, and marrow by scavenging carcasses brought down by large mammalian carnivores. By 1.8–1.6 mya, however, some archaeologists argue for the definite presence of either confrontational scavenging (where hominins displace large carnivores at a fresh and relatively intact carcass) or the hunting of vertebrate prey.

In 1968, the social anthropologist Marshall Sahlins famously described living hunter-gatherers as having the "Original Affluent Society." The depiction of hunter-gatherers as experiencing a leisurely and affluent lifestyle is no longer considered accurate. Detailed information on living hunter-gatherer groups shows that nutritional intake can be extremely variable between groups. Seasonal variation in total caloric intake or nutrient quality can be quite marked.

The domestication of animals and plants is a milestone in human history, and represents a fundamental difference in the human ability to alter ecosystems on a global scale. Animal and plant domestication occurs when humans intervene in the reproduction of other species. This intervention gradually becomes deliberate, and humans consciously select for certain phenotypic traits in the domesticated species. Dogs are the first domesticated species. Unequivocally domesticated dogs appear in the Natufian of the Middle East at 14,000 years ago. Goats, sheep, pigs, cattle, and donkeys follow. Evidence of farming first appears in the Middle East, about 11,000 years ago. Food crops have multiple centers of origin in both the New and Old Worlds.

The body mass index is widely used to study human body build and the relationship between nutrient intake and activity levels. This index is weight divided by height (BMI = kg/m^2). A BMI of less than 18.5 indicates a chronic energy deficiency. Harsh environments increase the probability of insufficient calories, at least seasonally. The body mass index is rising in nearly all populations that are experiencing industrialization. This is caused by an ever more sedentary lifestyle, in which decreased physical activity is accompanied by an abundance of readily available, high calorie foods. As of 2003, this trend is becoming so pronounced, and has such deleterious health consequences, that many medical and governmental agencies are investigating ways to halt the increase in human obesity.

Reproductive biology

Humans have diverse mating systems. There is no consensus about which, if any, mating system is the oldest, and the triggers initiating human pair-bonding remain obscure. Many ideas are not testable. Species-specific mating systems occur in many mammals, and are often affected by the degree of sexual dimorphism. However, unlike other mammals, there appears to be no relationship between the degree of sexual dimorphism and a particular mating system in humans. Formal social rules often govern the choice of mate, and elaborate marriage customs can exist. Incest taboos forbidding the mating of relatives are widespread. These taboos are most effective in maintaining genetic diversity when group size is small. Human partners may travel significant distances after marriage to live with the spouse's family. This activity promotes gene flow, while increasing inter-group contacts and the dispersal of ideas. Both sexes can leave their natal group. Some genetic analysis tracking male (Y chromosome) versus female (mitochondrial DNA) dispersion indicates that females may disperse more.

Humans have no breeding season, and human females experience no estrous cycling. Singleton births are the norm, but some families and populations have an elevated frequency of dizygotic twinning, because more than one egg can be released and fertilized. The human sex ratio is usually skewed at conception and birth to favor males. The neonatal sex ratio is highly responsive to a variety of local influences. Male mortality exceeds that of females, and so the sex ratio gradually declines with age. The sex ratio is approximately equal at reproductive maturity; after this, females tend to outnumber males. Male mortality caused by violence and accident exceeds that of females. Male mortality caused by infectious diseases is also higher than that of females, and parasite load is higher in males. Higher male mortality caused by violence and the increased male parasite susceptibility appear to be the evolutionary consequences of sexual selection.

In comparison to other catarrhine primates, where males may be more than twice the size of females, humans have only a small degree of sexual dimorphism. Depending upon the population, humans have 4–7% statural dimorphism. Statural dimorphism differences are higher in populations with tall stature, and lower in populations with small stature. Human body weight dimorphism averages about 11%. Much human sexual dimorphism involves soft-tissue characters. Subcutaneous fat patterning, seen especially in breast, thigh, and buttock fat depots, is markedly different in human males and females. Females also carry a larger percentage of subcutaneous fat than males do. Even in hunter-gather groups, where humans are very active and lean, subcutaneous body fat as measured by skinfold thickness is 5–15% in males and 20–25% in females.

Humans mature slowly, so that the onset of puberty is delayed relative to pongids and other catarrhines. In females, the onset of puberty is signaled by menarche, or first menstruation. This is triggered by a critical amount of body fat. The hormone leptin, released by fat, appears to trigger menarche. Reduction of body fat in a cycling female suppresses menstruation.

Relative brain size and intelligence

Humans have the largest brain to body size ratio among terrestrial mammals, rivaled only by the smaller odontocete whales. The modern human brain has nearly tripled in size since the origins of the subfamily Homininae. The brain reaches its modern size relative to body size at approximately 300,000 years ago, which is late in human evolutionary history. Brain size reaches its apogee among the Neanderthals, where the average cranial capacity was about 300 cc more than that of the average for living humans (1,200 cc).

Using other primates for comparison, many researchers argue that human brain size increase is associated with social intelligence, driven by complex social interactions and the ability to predict and manipulate the behavior of other members of the social group (Machiavellian intelligence). However, tool behavior also must be a factor that contributes to human technical intelligence and innovation. Furthermore, humans have an ability to understand and manipulate the behavioral ecology of other species, and understand the physical properties of inanimate objects. This ability distinguishes humans from other primates, whose intelligence is oriented towards conspecifics.

Homo erectus skull. (Photo by E. R. Degginger/Photo Researchers, Inc. Reproduced by permission.)

Humans have the ability to use symbols and engage in symbolic behavior. In living humans, this powerfully affects all social and economic interactions. Artifacts can have symbolic properties. Archaeologists have tried to study the beginnings of symbolic behavior by investigating symmetry and other properties of stone tools. Art and bodily ornamentation are widely considered to signal the unequivocal beginning of human symbolic behavior. Pigments like red ochre and signs of pigment processing are found in archaeological sites dating to 250,000 years ago. Representational art and ornaments occur much later, and do not become abundant until about 40,000 years ago.

Species-specific behaviors: Language, tool behavior, and technology

Humans are characterized by language, which is a species-specific type of vocal communication. Special neuroanatomical centers, usually located in the left cerebral hemisphere, underlie human language abilities. Human sign languages, which are non-vocal, also utilize these centers. Although other mammals and birds possess complex vocal communication with referential signaling, human language has the unique property of recursion. This is the ability to create an infinite number of expressions by permutations of discrete components such as words or numbers. Consequently, there is no limit to the possible communications based on language or numbers. A critical period for the acquisition of human language occurs during infancy, and infants who are not exposed to language during this time fail to develop normal language abilities later in life, despite intensive training. The human infant's ability to reproduce the sounds of its native language depends on imitation. Imitation is also responsible for the faithful reproduction and cultural transmission of other human behaviors. Imitation is found in some other animals, but appears to be lacking in non-human primates, where the

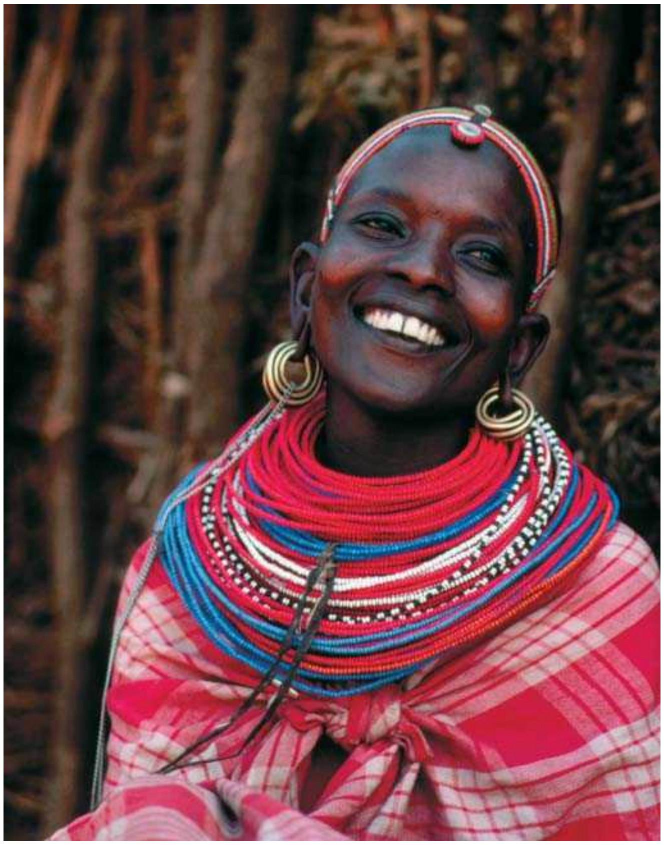
The hang glider gives humans the ability to "fly." (Photo by © Bill Ross/Corbis. Reproduced by permission.)

transmission of behavior occurs through emulation or goal-directed behavior, and faithful reproduction is absent. Humans can acquire multiple languages, although the ease of acquisition is affected by age.

Using all available genetic information, Cavalli-Sforza et al. discovered that genetic differences between human groups are frequently, but not always, associated with language differences. This implies that language often functions as a reproductive barrier between humans, and can lead to a reduction in gene flow and subsequent population demarcation. However, a 2000 study of Y chromosome haplotypes in Europe showed that geography influences genetic diversity more than language does, at least in males.

Reliance on tools and technology is another species-specific human behavior. With the exception of the New World monkey genus *Cebus*, tool behavior is rare in wild non-human primates, in comparison to other animals, such as birds, where tool behavior may be much more frequent. Human tool behavior is not based solely on the ability to manipulate objects. All catarrhine primates have truly opposable thumbs, but the mere existence of truly opposable thumbs does not generate tool behavior. Nevertheless, fossil human hand anatomy has been scrutinized. Fossil hand bones presumably belonging to the taxon *Australopithecus robustus* have been recovered from the site of Swartkrans in South Africa. These bones date to 1.5 mya and indicate frequent manipulation. Bone digging tools also have been recovered from the site. The recovery of tools from a time before relative brain size increase indicates that hominin tool behavior is also not predicated on brain size.

The ability to control fire—i.e., to maintain and transport it away from a naturally occurring source, such as a brush fire caused by a lightning strike or volcanic event—was a milestone in human evolutionary history. Some researchers argue that control of fire may have begun as early as 1.6 mya in East Africa, although this date is controversial. The control of fire meant that, unlike other higher primates, humans did not need to seek shelter at night in trees or cliffs, where they would be safe from nocturnal predators. Fire further permitted humans to remain active after nightfall, and provided warmth at higher altitudes or in colder habitats. Fire permitted humans to cook foods and drive hunted animals, and thus expanded human dietary range. Fire also allowed humans to modify ecosystems in a profound fashion, as they burned grasslands, cut down trees, and burned forests. The control of fire marks the beginning of human modification of the earth's surface, the signs of which are now universal. In fact, charcoal lenses appearing in pollen spectra or sediment horizons are sometimes used by archaeologists as a signature of



Facial expressions transcend language barriers. This Masai woman shows that she is happy by smiling. (Photo by © Yann Arthus-Bertrand/Corbis. Reproduced by permission.)

human presence, even if human skeletal material or cultural remains are absent.

Human behavioral ecology

Humans mature slowly, although this trait appears late in human evolutionary time, appearing first among the Neanderthals. This slow maturation necessitates that adult caretakers must rear the young, even after the young are independently mobile and completely weaned. Human social complexity also mandates long periods to acquire recondite social knowledge. Consequently, much human social behavior is geared towards care, protection, and teaching of the young. Biological kin, as well as non-related individuals, engage in these care-taking behaviors.

Food acquisition and processing can be a major influence on human social organization. Relatively subtle dietary shifts may underlie significant transitions in human history. The abundance and predictability of critical food resources influences the complexity of traditional societies. Humans have the ability formally to exchange resources. Barter, trade, and economic transactions are universal. Formal marriage systems and other alliance systems promote harmony between groups. However, humans also exhibit aggression and violence. Interpersonal aggression, raiding, and warfare occur in all human groups, and they are found deep in human prehistory. They are not the fruits of an all-corrupting civilization.

Human population increase and population aggregation lead to social complexity. Five general levels of human social complexity are usually recognized. These levels are the band, the tribe, the chiefdom, the state, and the nation-state.

At the band level, humans are hunter-fisher-gatherers, living in groups of 30–100 people. There are no permanent settlements, but temporary aggregations can occur for specific reasons (e.g., seasonal hunting). The society is egalitarian, and only shamans (individuals with an ability to contact and control supernatural forces) exhibit any degree of specialization. Inter-group aggression over scarce, defensible resources can occur. Tribes exist either when hunting-fishing-gathering occurs in a rich environment, or when agriculture or pastoralism exists. Multiple kin-groups are found in a tribal society, and some division of labor takes place. Raiding is possible.

Chiefdoms exist when populations are large, and when hunting-fishing-gathering occurs in a rich environment, or when agriculture or pastoralism exists. A more sedentary lifestyle and permanent aggregations can lead to village life. Villages appear before agriculture in both the Old and New Worlds. For example, an intensive use of wild grass seeds, a sedentary lifestyle, and villages appear among the Natufian people of the Middle East, who lived between 14,000 and 11,000 years ago. Chiefdoms have food storage, hoarding, and formalized distribution of food and other resources. There is

Humans use tools to eat, such as chopsticks or forks, in the same way that a chimpanzee (*Pan troglodytes*) uses a stick to gather ants. (Photo by Corbis. Reproduced by permission.)

Humans use different types of musical instruments to relay thoughts, emotions, and even events. (Photo by © Macduff Everton/Corbis. Reproduced by permission.)

centralized leadership vested in a chief, ranking or hierarchical division, and an artisan class. Elaborate trade networks can exist, and formalized warfare is possible.

States occur with the advent of large populations, agriculture, and the rise of urban life in cities. Cities are large, permanent aggregations of people that have multiple activity areas. Cities serve as organizational centers for a broad region. States possess a complex bureaucracy with centralized power vested in a ruling class, often a royal or noble class. The state has many nonagricultural specialists, including religious specialists for formal religion. There are central services, with a complex organization of labor, goods, and services. Complex record-keeping, culminating in the invention of writing systems, assists in facilitating these intricate activities and exchanges. Complex trade networks can occur over long distances, and monumental architecture appears.

Finally, nation-states occur with large populations, agriculture, and cities. The nation-state first emerged more than 5,000 years ago in pre-dynastic Egypt, when the unification of Upper and Lower Egypt took place. The nation-state has a broad geographic spread, and incorporates many different habitats. Multiple ethnic groups, languages, and religions exist within a nation-state. Elaborate organized warfare and conquest are possible.

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Susan Cachel, PhD

Carnivora

(Land and marine carnivores)

Class Mammalia
Order Carnivora
Number of families 12
Number of genera, species 114 genera; 264 species

Photo: Gray wolf (*Canis lupus*) mated pair courtship. (Photo by Tom Brakefield. Bruce Coleman, Inc. Reproduced by permission.)

Introduction

The order Carnivora is one of the 20 orders of mammals. The Carnivora are a diverse group of animals, living in almost any habitat, including the oceans, with over 260 species. Most carnivores are land animals, some like the otters spend much of their lives in water and about 30 species, the seals and their relatives, are marine, only leaving the sea once a year to breed.

Despite the name, not all Carnivora live exclusively on meat. Bears, jackals, and foxes are omnivorous, surviving on a diet of meat and fruits, the aardwolf eats almost nothing else but termites, and the giant panda lives almost entirely on bamboo shoots. The unifying feature of the Carnivora is a set of scissor-like teeth set back in the mouth and used for shearing through meat, called the carnassials. However, it is not quite as simple as that, as some of the modern day Carnivora like the giant panda and the aardwolf do not possess carnassials. It is sufficient qualification for a species to be included in the Carnivora if its evolutionary ancestors did.

Eating meat has many advantages over a diet of vegetable matter, particularly grass. Meat is easy to digest and rich in protein. On the other hand, meat is more difficult to procure than vegetable matter. Swift-footed and wary prey have to be caught and killed before they can be eaten and "static meat" in the form of carrion is usually widespread and scarce. It is not surprising, therefore, to find that carnivores are often highly intelligent animals with sophisticated social systems.

Evolution and systematics

The evolutionary history and systematics of the Carnivora are clouded in controversy, as the fossil record is patchy and incomplete. In spite of this limitation it is remarkable what paleontologists, evolutionary biologists and geneticists have managed to uncover in the way of the early history of mammals. A major breakthrough has been the development of accurate methods to date fossils.

About 65 million years ago (mya) the dinosaurs, which were the dominant animals on Earth, underwent a rapid and mass extinction. At this time the mammals were small shrew-like creatures. With the extinction of the dinosaurs many ecological vacancies, known as niches, opened up, including that of predator, and the mammals quickly filled many of them. The early mammalian predators were marsupials, mammals whose young develop in a pouch, the ancestor of which was a small, opossum-like creature with a pointed snout and large ears. These early marsupial carnivorous creatures soon evolved into all shapes and sizes and dominated the southern continents for 30 million years.

Meanwhile, placental mammals were evolving in the northern continents. Instead of their young developing in a pouch after being born, placental mammals grow their young inside them, in a womb. One of these placental mammals was a squirrel-sized creature called *Cimolestes* that lived on insects. A very important feature possessed by *Cimolestes* was a flattening of the cheek teeth providing the beginning's of a

Silverback jackals (*Canis mesomelas*) feeding. (Photo by K & K Ammann. Bruce Coleman, Inc. Reproduced by permission.)

scissor action. Over several millions of years these teeth became refined to slice meat in what became the carnassial shear. This feature was inherited by two separate groups of animals. One gave rise to the modern Carnivora, the other to a group known as the Creodonts. At first the Creodonts dominated as the earth's meat eaters. In the fossil record from 55 to 35 mya a number of cat-, dog-, bear- and hyena-like animals are found, some even with saber teeth, but none of these were true Carnivora. Then the fossil record shows a change; more Carnivora species are found and fewer and fewer Creodonts.

It is not known for sure why this replacement of Creodonts by Carnivora took place. The carnassial shear in the Carnivora was situated more to the front of the mouth than in the Creodonts. This meant that the teeth further back in the mouth could still be used for feeding on other foods, for example on vegetable matter. Perhaps the Carnivora could be more flexible in diet and therefore exploit more ecological niches, both meat eating and vegetable, than the Creodonts, who had no teeth behind their carnassial shear and so could only eat meat. Support for this idea comes from evidence of climatic change during the demise of the Creodonts. The earth became cooler and more seasonal. This may have led to a situation where prey became less available, but fruit crops and insects more abundant due to the seasonal bloom.

The early Carnivora, known as miacids, were small and rather unspectacular, many resembling the genets of today. The major division into dog- and cat-like Carnivora took place some 55 mya and all the modern carnivore families had evolved by 7 mya. Among the cat-like Carnivora were the saber-toothed cats that dominated the carnivore scene from 26 to 2 mya. As the Carnivora moved south, they out-competed the marsupial predators mentioned earlier. Today, only a handful of their descendants such as the Tasmanian devil and quoll survive in Australia. Perhaps the best known was the thylacine or Tasmanian wolf that was exterminated about 70 years ago by bounty hunters.

Traditionally Carnivora are divided on the basis of their anatomy and behavior into two suborders, terrestrial carnivores (Fissipedia) and marine carnivores (Pinnipedia). This subdivision is incorrect, for blood serum analyses have shown that the pinnipeds are closely related to bears and evolved from a single bear-like ancestor. Today most scientists involved in the field of carnivore classification recognize 10 families in the two major divisions; the cat-like and the dog-like Carnivora. The former are the Viverridae (civets and genets), Herpestidae (mongooses), Felidae (cats) and Hyaenidae (hyenas). The latter are the Ursidae (bears), Otariidae (eared seals—fur seals and sea lions—although the most recent classification puts the walrus in a separate family, the Odobenidae), Canidae (dogs), Procyonidae (a collection of mainly South American carnivores including the raccoons and coatis and a taxonomic group that is still surrounded by much controversy), Mustelidae (otters, badgers, skunks, weasels and polecats), and Phocidae (true seals—elephant seals, monk seals, leopard seals, etc.).

Physical characteristics

Carnivores come in all shapes and sizes, ranging in size from the 1.76 oz (50 g) least weasel (*Mustela nivalis*) to the 48,000 times heavier, 5,300 lb (2,400 kg) southern elephant seal (*Mirounga leonina*). Most are so distinctive that even laypeople can easily distinguish the various families, even though the order has considerable diversity. Bears, dogs, hyenas, mongooses, martens and weasels, cats, and even viverrids are readily recognizable, although the marine families and procyonids are more difficult to tell apart.

The pinnipeds have streamlined, oval-shaped bodies with limbs modified as flippers. Terrestrial carnivores either walk on the soles of their feet (plantigrade) or on their toes (digitigrade). The limbs of evolutionarily ancient carnivores underwent a fusion of bones in the feet that probably originally provided a firm basis for flexion at the midcarpal joint. This gave them the flexibility to climb, grapple with prey, or absorb the shock of running and leaping. Another skeletal characteristic is an undeveloped collar-bone or clavicle. The main function of the well-developed clavicle in primates is to allow attachment of muscles to give the necessary flexibility of lateral movement to the limbs. This is not necessary for the back and forth movement of the limbs needed for a long stride for running as is the case for most carnivores. With the exception of the hyenas, carnivores possess an elongated penis bone known as the baculum to prolong copulation. This is probably especially important in species where ovulation is induced by copulation. Modified skin glands often located in the anal region secrete substances as a means of communication and information exchange between members of the same species.

The typical dental formula for carnivores is (I3/3 C1/1 P4/4 M3/3) $\times$ 2 = 44, with variation in the number of molars and premolars. The canines are usually large and the car-

Silverback jackals (*Canis mesomelas*) eating a springbok kill. (Photo by Nigel J. Dennis/Photo Researchers, Inc. Reproduced by permission.)

nassial shear, the modified fourth upper premolar and the lower first molar, with high cusps and sharp tips, is adapted to cutting and slicing meat. The typical carnivore skull shows a powerful jaw for the capture of prey and tearing up of meat, and the skull often has a sagittal and/or occipital crest to enlarge the area for muscle attachment.

Distribution

Carnivores are found throughout the world, although many islands do not have indigenous populations. Antarctica and Australasia have no naturally occurring terrestrial carnivores, although the dingo (*Canis familiaris dingo*) has lived in Australasia for at least 3,500 years, having been brought there by Asian seafarers. Introduced carnivores, feral cats in particular, occur on many islands and are often a conservation management problem as they prey on indigenous fauna naive to predation.

Habitat

Carnivores have a very wide habitat tolerance and are found in all habitats both on land and sea. Only the tops of the highest mountains, the most extreme deserts and ocean depths are devoid of carnivores. Although terrestrial carnivores spend most of their time on the ground, leopards, (*Panthera pardus*) and martens (*Martes* spp.) are adept at climbing trees, otters are at home in rivers and lakes, polar bears (*Ursus maritimus*) live much of their lives on sea ice, and the least weasel is able to hunt underground or under snow. The marine carnivores breed on land and forage in the sea. The elephant seal can stay under water for up to two hours and dive to a depth of 5,000 ft (1,500 m).

Behavior

The large number of species, wide habitat tolerance, diverse diets and well developed brains of carnivores have combined to lead to the evolution of a wide range of behaviors and social systems. Only the higher primates have more complex behavior patterns and social systems than the social carnivores. This flexibility in behavior within the order can be seen between species and, perhaps most interestingly, within a species as it adapts to different environmental demands.

Many carnivores are solitary in that when they move about looking for food they do so on their own, or at most as a mother with her dependent offspring. However, detailed studies of theses so-called solitary species have revealed that although they may appear to be solitary, they share a terri-

A fennec fox (*Fennecus zerda*) by its den in the desert. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

tory with others of their kind and cooperate and communicate with their fellow group members.

The civets and genets (Viverridae) are a good example of the solitary template for carnivores from which the array of social systems seen in the order probably evolved. Solitary males live in comparatively large territories that encompass the smaller territories of several females. However, with palm civets, subordinate, usually younger males, occupy small areas within the dominant male's territory, avoiding contact with the dominant male as he moves through the area.

Bears are also mainly solitary, however, flexibility in behavior allows concentrations of brown and polar bears to collect at food sources. For example, brown bears (*Ursus arctus*) gather during the salmon migration on the northwestern seaboard of North America and polar bears may gather at a whale carcass in the Arctic Circle. Somewhat surprisingly, polar bears also concentrate during times of food shortage. During summer and fall when the ice has broken up, a number of males may fast together in peace at certain preferred sites along the coast. Testosterone levels are low and there is no food to compete for.

Many of the 37 species of cat are truly solitary and only one, the lion (*Panthera leo*), is highly social. Lions live in prides of 2–12 related females and their young. The members of a pride do not stay together all the time but they defend a common territory and are friendly towards each other when they meet. Males form coalitions, usually of 2–4, but up to 7. Males join prides, but their tenure is variable and they may be displaced by a stronger coalition, or themselves move on to another pride. Pride and territory size is variable with respect to resources, as is the association between the females and the males. In open areas males spend much time with the pride, probably because the females and their cubs are more detectable by strange males that may kill the cubs. In wooded savannas the males can leave the pride and look for other females to mate with when the cubs are quite small. It is easier to hide them from infanticidal males in the thicker bush. The cheetah (*Acinonyx jubatus*) is the only other cat whose adult individuals form long-lasting relationships, in that cheetah males also form coalitions of 2–3 individuals that cooperatively defend a territory.

The basic social system of dogs is different from the cats and is based on monogamy. However, canids show far more flexibility in their social systems both within and between species than the cats. African wild dogs (*Lycaon pictus*) and dholes (*Cuon alpinus*) live in very tight and close knit packs that always hunt together, but where the alpha pair are the breeders. Gray wolves (*Canis lupus*) may do the same, or go off in pairs. Red foxes (*Vulpes vulpes*) often forage alone, but may not always maintain a monogamous mating system and sometimes a territory may comprise one adult male and several vixens.

The mustelids, with over 50 species, are the largest carnivore family. They appear to be predominantly solitary, although sea otters may occur in "rafts" of several hundreds. The European badger (*Meles meles*) is one of the best studied carnivores and illustrates the fact that so many carnivores are

A coyote (*Canis latrans*) chases after a mouse. (Photo by Nicholas DeVore. Bruce Coleman. Inc. Reproduced by permission.)

"blatantly solitary, but secretly social rafts" and has evolved a tendency to live in groups. Several badgers, mainly close relatives, may share a territory and live together in a large set, but forage on their own. The honey badger (*Mellivora capensis*) is another species that has been found to have a rather different social system than was thought before a detailed study was conducted. This time what was considered to be social, is in fact a solitary trait. Although sometimes seen traveling in pairs, a larger male and smaller female, these are not mated pairs, but mother and son. The single cub is dependant on its mother until it is larger than her. Males do however sometimes come together in groups of up to six and have very large overlapping home ranges when the solitary living females come on heat.

Mongooses show a very wide diversity of social systems. Most tend to be solitary, but three species, banded mongoose (*Mungos mungo*), dwarf mongoose (*Helogale parvula*), and meerkat (*Suricata suricatta*) have evolved complex and different social systems. In dwarf mongooses the dominant pair are most likely to breed, whereas in the banded and meerkat groups several females do so. One of the larger mongooses, the nocturnal white-tailed (*Ichneumia albicauda*) is another seemingly solitary species that exhibits a degree of sociality as several females have been found to have overlapping ranges.

The hyenas, with only four species, are the smallest carnivore family. Three species, the brown hyena (*Parahyaena brunnea*), spotted hyena (*Crocuta crocuta*), and aardwolf (*Proteles cristatus*) have been well studied and have shown a remarkable degree of diversity and flexibility in social systems. The spotted hyena is highly social living in female dominated clans of 5–80 individuals, living in fiercely defended clan territories that may be as large as 400 mi^2 (1,000 km^2), or as small as 16 mi^2 (40 km^2), depending on resources. In the Serengeti, with its migratory prey system, the clan system is flexible so that the hyenas can commute from their territories through other hyena territories to get to the feeding grounds. The brown hyena always forages on its own yet may share a territory with as many as 14 other hyenas. All clan members carry food to the den to feed cubs, not just the parents. The aardwolf is monogamous, yet during the mating season some males may be cuckolded by their mates, who may copulate with neighbors.


A wild dog (*Lycaon pictus*) pack attacks a hyena in Masai Mara, East Africa. (Photo by K & K Ammann. Bruce Coleman, Inc. Reproduced by permission.)


Young gray wolves (*Canis lupus*) showing two color phases in the same litter. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

The procyonids have not been well studied, and although some species like the ringtail appears to be solitary, most appear to move in large groups. It is thought likely that all species maintain complex social relationships within and among the sexes. This is an important family for understanding sociality in carnivores and more studies are needed.

Why these differences in social system, and particularly why do some species form groups? An obvious answer is that carnivores form groups in order to cooperate in hunting. While this may be partly true, it does not explain why, for example, invertebrate-eating meerkats are so social. Even in the case of large prey hunters like lions and spotted hyenas it has been found that hunting group size is not necessarily related to hunting success, nor that this strategy leads to the acquisition of more food than solitary hunting. For the smaller species it has been suggested that being in a group helps prevent predation by increased vigilance and cooperative defense. While this is also sometimes true—meerkat individuals take turns in guarding while the rest of the group is foraging—it does not explain why other species like European badgers, red foxes, and brown hyenas forage solitarily yet sometimes live in groups.

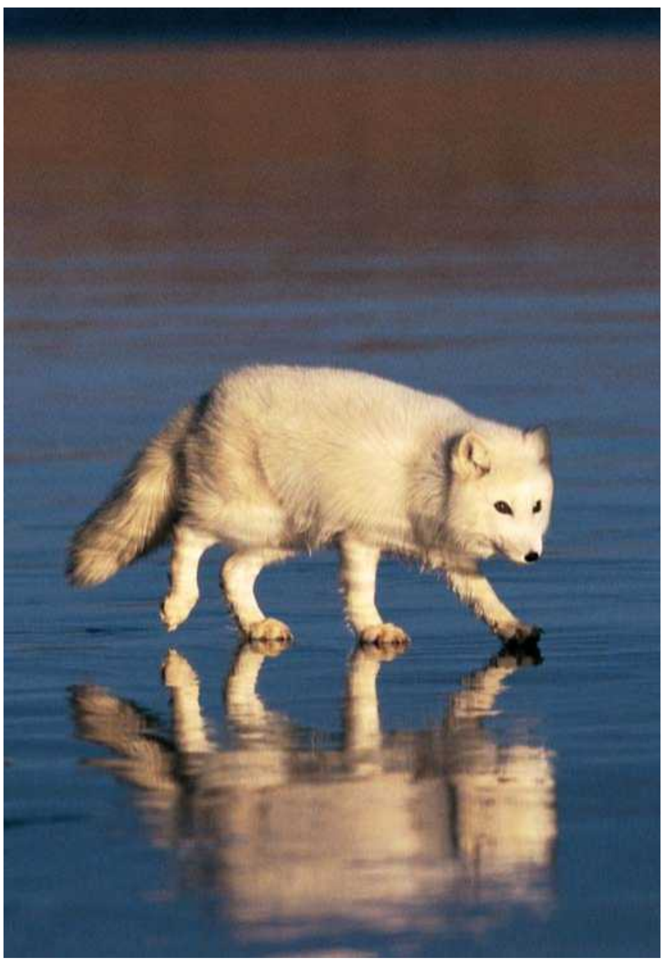
The evidence suggests that these and many other group-living carnivores are influenced by the dispersion pattern of their food. For many carnivores, food is often irregularly dispersed in patches and some patches moreover are richer than others. Territory size is influenced by the distance between the patches, and the number of animals living in the territory by the richness of the patches. This is known as the Resource

Dispersion Hypothesis (RDH) and has been found to explain group size and territory size in a number of carnivores. It also explains why group size and territory size are not related. A group of brown hyenas living in an area with a large number of rich food patches close together will have a small territory and contain more members than one living where food patches are poor and widely dispersed. Similarly, in conditions where food patches are poor but close together both group size and territory size will be small. Once there is enough food in a territory to support several individuals it makes sense to share these with close relatives rather than a bunch of strangers. Any coincidental benefits that accrue then will be shared by relatives and also they can assist each other, for example by helping to feed each others young. For lions, the major advantage accruing to females living in the pride is the cooperative defense of their cubs against infanticidal males.

Feeding ecology and diet

Carnivores do not eat only meat. In fact they have a varied diet and comparatively few are exclusively meat eaters. Some, such as the bamboo specialist giant panda (*Ailuropoda melanoleuca*), the frugiverous palm civets, kinkajou (*Potos flavus*), and raccoons, hardly ever eat meat. Mustelids are probably the most exclusively meat eating family, weasels and their allies being known as fierce and combative predators capable of killing prey up to 10 times their body weight and otters living mainly of fish, crayfish, crabs, and frogs. However, European badgers rely mainly on earthworms. Mongooses live mainly off insects, although some species are known as snake killers. Cats too are mainly carnivorous, the large cats are probably the most spectacular of all predators. Bears, viverrids, dogs, and hyenas are more omnivorous, although all, except viverrids, have meat-eating specialists amongst their ranks. Polar bears, African wild dogs, and spotted hyenas rarely divert from a meat diet, but brown bears, brown hyenas, and jackals are all truly omnivorous. The aardwolf is another strict specialist feeding almost exclusively on snouted harvester termites of the genus *Trinervitermes*. The marine carnivores feed on a variety of marine animals including fish, mollusks, crustaceans, penguins and, particularly in the case of the leopard seal, other seals. The world's most abundant mammal after humans, the crab-eater seal (*Lobodon carcinophagus*), feeds mainly on krill, and one of the giants, the walrus (*Odobenus rosmarus*), mainly eats mollusks.

Bat-eared foxes (*Otocyon megalotis*) play fighting in Kalahari Gemsbok National Park, South Africa. (Photo by Nigel J. Dennis/Photo Researchers, Inc. Reproduced by permission.)



An Arctic fox (*Alopex lagopus*) crosses the ice. (Photo by J-L Klein & M-L Hubert/Okapia/Photo Researchers, Inc. Reproduced by permission.)

A characteristic of most of the food eaten by carnivores is that it is of high quality, but difficult to obtain, therefore, they have to make full use of their opportunities. Many carnivores live under what has been called a feast or famine regimen. They are able to gorge themselves when the opportunity is presented, a spotted hyena can eat a third of its body weight in one sitting, and are also able to go for long periods without eating. Hibernating bears are the most extreme in this regard and are able to survive for half a year without eating,

A harbor seal (*Phoca vitulina*) rests at the water's edge. Seals are known to eat at least 67 species of fish, and more than 70 kinds of invertebrates, (Photo by E. & P. Bauer. Bruce Coleman, Inc. Reproduced by permission.)

drawing on fat reserves built up during the bountiful summer. If more food is found than an individual can consume, some species will cache the remains. Brown hyenas will scatter hoard ostrich eggs under bushes and in thick grass clumps should they find an unattended nest. Canids actually bury their excess food and show an uncanny ability for relocating it.

The impact that predators have on their prey is a complicated subject of great controversy and emotion as it often clashes with our own interests. Certain important principles need to be taken into account. Predators do not kill at will, or even the first prey they come across. They have to pit their skills and stamina against formidable opponents. The kill is the culmination of a range of behavioral strategies that may have taken hours or even days to succeed. The relationship between predator and prey is a delicate balance, an evolutionary arms race, where neither has managed to gain the upper hand. Ecologically speaking, predation is an important process that contributes to the dynamic nature of ecosystems. Predators help to keep prey numbers in check and often to dampen drastic fluctuations. They may weed out the less fit members of the prey population by selecting the old and infirm. They also often select males over females from the prey population, thereby lessening their impact as most prey species are polygamous; i.e. one male mates with several females. Furthermore, the impact they have on the prey populations is often mediated by environmental conditions such as droughts in Africa and severe winters in north America and Europe.

Reproductive biology

Mating systems are the most complex and variable aspects of social behavior. Carnivores give birth to altricial young that are dependent on adults for their survival for an extended period. Much of their behavior is therefore centered around not only producing young but also raising them. There are two basic types of mating system in carnivores; monogamy where a male mates with one female, and polygyny where males mate with several females and/or vice versa. Monogamy is the least common of the two systems and is practiced by all canids, and also in the aardwolf and some mongooses, although in most species the rules are broken. Either a male attracts more than one female to the territory, or cuckoldry occurs. Monogamous systems are characterized by both sexes and often older offspring helping to raise young by feeding and guarding, and by a lack of sexual dimorphism. An extreme case is found in pack living animals such as African wild dogs and dwarf mongooses where normally only one pair breeds while the other sexually mature adults abstain and help to raise the young. In polygynous species the males are usually larger than the females and often are equipped with spectacular adornments to attract females, like the lion and elephant seal. Cooperation in raising young is less common but does occur in some social polygynous species, for example female lions suckle each others' cubs.

The black-footed ferret (*Mustela nigripes*) depends on its prey prairie dogs (*Cynomys* sp.) for food and shelter. (Photo by © Jeff Vanuga/Corbis. Reproduced by permission.)

Many carnivores range widely and spend their time alone and so it is important for the females to advertise when they are ready to mate. Scent marking through urination and anal secretions is widespread in carnivores, and is the obvious mechanism to achieve this. Even then the best male may have difficulty in being at the right place at the right time. One way that a female can ensure that she mates with the best available male is to adopt a reproductive strategy known as induced ovulation. The females come into estrus, but do not shed eggs until stimulated to do so by copulation. The other strategy is called spontaneous ovulation, where the eggs are shed in a cycle that is unaffected by mating. Although there are exceptions, spontaneous ovulators are likely to be more social species than are induced ovulators.

Smaller animals have faster metabolic rates and breed faster than larger animals. The females of the smallest carnivore, the least weasel, are sexually mature at three months. Litter size is usually six, so if she lives long enough—the average life expectancy is less than one year—a female can potentially produce 30 descendants a year. This is achieved by producing six in her first litter, another six in her second, plus six offspring from each of the three daughters she would be expected to produce in her first litter. Males are not sexually mature in their first year. At the other end of the scale, lions may only produce a litter of three or four cubs in three and a half years as the cubs only become independent at about three years of age. If, however, the female loses all her cubs she will quickly come into estrus again. African wild dogs have higher metabolic rates than would be predicted from their size and their populations turn over rapidly. This is reflected in their high reproductive potential. They are seasonal breeders that produce large litters, the record is 21 for a single female.

Pinnipeds, so well adapted to a life in the sea, must come to breeding grounds on land in summer in order to reproduce. The males arrive slightly earlier than the females and set up territories. The females arrive shortly before giving birth to a single pup that was conceived the previous season. The lactation period is very short and intense, not more than six weeks, in the true seals. The pups are weaned and deserted abruptly and the females mate, before going back to sea for another year. In eared seals, the female comes into season and mates about one week after giving birth. Lactation lasts 4–6 months during which time the mother makes periodic feeding forays into the sea.

Conservation

Conservation is the wise use of resources on a sustainable basis. The Species Survival Commission of the World Conservation Union (IUCN) is divided into a number of taxonomic or functional specialist groups. In the case of carnivores these are mainly based on families such as the Canid, Cat, and Hyena Specialist Groups. These groups have produced a series of status surveys and action plans that assess the conservation status of the relevant species and make recommendations for their conservation. The conservation status of each species is assessed and placed into one of a number of categories depending on its status, the most important of which are Extinct, Extinct in the Wild, Critically Endangered, Endangered, and Vulnerable. The 2002 IUCN Red List of Threatened Species lists 120 carnivores of which three, the Falkland Island Wolf (*Dusicyon australis*), the sea mink (*Mustela macrodon*), and the Barbados raccoon (*Procyon gloveralleni*), are classified as Extinct; one, the black-footed ferret (*Mustela nigripes*), as Extinct in the Wild; and five, the red wolf (*Canis rufus*), the Ethiopian wolf (*Canis simensis*), the Iberian lynx (*Lynx pardinus*), the Mediterranean monk seal (*Monachus monachus*), and the Malabar civet (*Viverra civettina*), as Critically Endangered. Thirty-two species comprising three viverrids, five mongooses, four cats, one bear, two eared seals, one canid, eight procyonids, seven mustelids, and one true seal are classified as Endangered, and 40 including five viverrids, four mongooses, 12 cats, three bears, five eared seals, two canids, eight mustelids, and one true seal are Vulnerable. The only family with no members classified as Endangered or Vulnerable is the small hyena family. The remaining listed species are classified as either Data Deficient (19), meaning that there is not enough known about them to be sure of their status, or as Near Threatened (20), which is the lowest category of threat. Thus, besides the three recently extinct species, nearly half the living carnivores are under some sort of threat of extinction and 65% are Endangered or Vulnerable. Clearly, the situation is serious. Although protected areas are a vital component of the conservation action plans, many species and populations do not enjoy the security of protected area management and other ways need to be found for humans and wildlife to coexist. Innovative solutions such as protecting livestock from predation, the use of guard dogs to protect livestock, and education of local people have met with limited success.

Significance to humans

Human relationships with carnivores are extreme and of mixed emotions. On the one hand we respect and revere them. Indeed two species, the wolf and the wild cat, have been domesticated and become our closest animal companions. In the case of the domestic dog, we have also developed and trained many breeds to work for us as hunting dogs, herd dogs, and guide dogs. Carnivores are also important to us aesthetically and economically. We admire their hunting ability and their striking beauty. Many symbols of royalty and heraldry are carnivores. They are a prime attraction for ecotourists, especially where they can be viewed in their natural habitat. Through the ages man has also hunted carnivores for food, medicine, and their pelts, and today they are also hunted for recreational purposes as trophies, often at great expense.

On the other hand, humans and carnivores have long been in conflict because of similar ecological interests. Our ancestors on the African plains competed for food with the larger carnivores. With the development of agriculture and animal husbandry this conflict increased as carnivores of all sizes tended to prey on animals that we had domesticated and were important for us economically. In addition, large carnivores sometimes kill people. Animals that compete most with each other display most aggression towards each other. Moreover, the larger and more powerful ones have a negative impact on the smaller and less powerful competitors—lions influence cheetah and wild dog numbers and wolves impact on coyotes. Humans as the supreme carnivorous animal (not carnivore, which is a taxonomic term) have impacted all their competitors and carnivores have suffered from the brutal and efficient actions of humans as much as, if not more than, any other group of animals. With the human population explosion and the development of more efficient mechanisms for killing, this carnage has accelerated: shooting, trapping, poisoning, and over harvesting have taken a very heavy toll on many carnivore species. Even through the domestication of dogs and cats, their wild ancestors are threatened through crossbreeding with them and spreading disease.

In an attempt to redress the imbalance, a network of governmental and nongovernmental organizations have been established throughout the world and millions of dollars have been spent and are being spent on research, protection and management programs, compensation schemes, and education. Although there have been some successes the situation is serious and a major human effort is required if more of these magnificent and important animals are not to go the same way as the Falkland Island wolf, the sea mink, and the Barbados raccoon.

Resources

Books

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Gus Mills, PhD

▲

Dogs, wolves, coyotes, jackals, and foxes

(Canidae)

Class Mammalia

Order Carnivora

Family Canidae

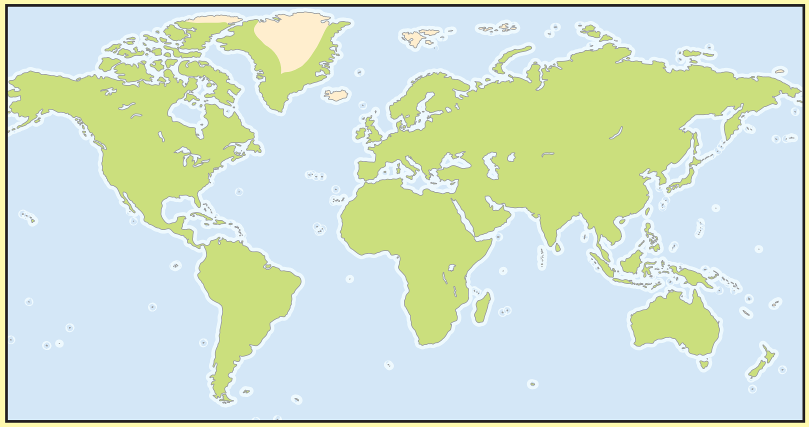
Thumbnail description
Coat colors may be black, brown, or red; cursorial predators, they have both cutting and grinding teeth.

Size
2.2–165 lb (1–75 kg)

Number of genera, species
14 genera; 35 species

Habitat
Open and lightly wooded country for most species

Conservation status
Extinct: 1 species; Critically Endangered: 2 species; Endangered: 1 species; Vulnerable: 2 species; Lower Risk: 3 species; Data Deficient: 9 species



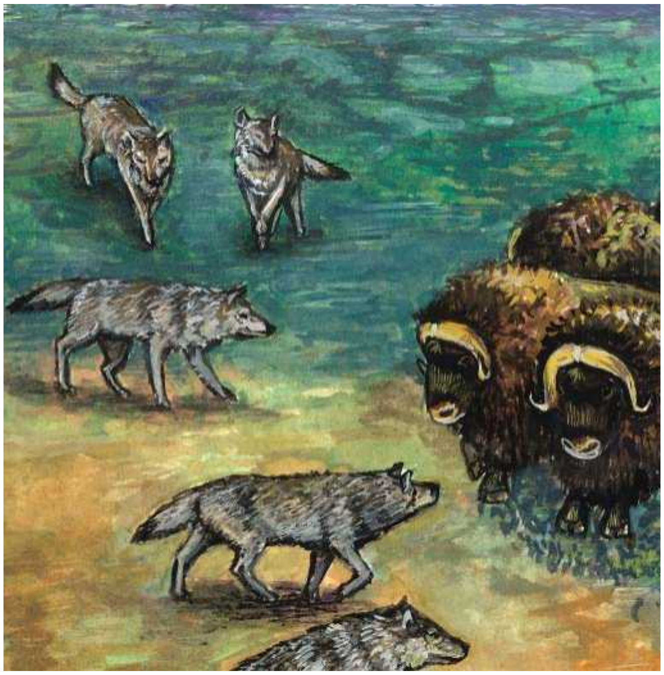
Distribution
All continents except Antarctica and Australia (wild canids); domestic dogs worldwide

Evolution and systematics

Fossils show that dog-like animals, i.e., animals with legs for running and teeth to tackle a range of food including other animals, have evolved on several occasions in the last 50 million years. The exact anatomical conformation that corresponds to the canids of today appears for the first time in 10 million-year-old fossils from North America. By seven million years ago the fossil skulls were similar enough to modern species to be put in the genus *Canis*. It is believed that it was at about the same time that canids colonized Eurasia and Africa. Wolf-like members of the dog family are common through the fossil record and vary in size from small jackals at 15 lb (6.8 kg) to the dire wolf (*Canis dirus*), which probably weighed over 200 lb (90.7 kg). The latter was very common in western North America as recently as 10,000 years ago. Its stocky build and large teeth suggest that it might have been more proficient as a scavenger than as a hunter. The modern members of the wolf-like group include the wolves (but not the maned wolf [*Chrysocyon brachyurus*] of South America), coyotes (*Canis latrans*), jackals, dholes (*Cuon alpinus*), and the African wild dog (*Lycaon pictus*).

An early offshoot from the *Canis* stock were the foxes (genus *Vulpes*). These smaller animals range in size from 4 to 24 lb (1.8–11 kg). There are 14 species of fox living in Eurasia, Africa, and North America, and they represent the typical canid. Many of the species have restricted ranges usually in arid areas. In almost any desert from the Namib to the Mojave, a small pale fox (*V. pallida*) can be found foraging at night for insects and small mammals. A few foxes, notably the large red fox (*V. vulpes*) and the gray fox (*Urocyon cinereoargenteus*) have been successful in more temperate areas and consequently have large ranges. Another unusual fox lives in the Arctic and its small ears and white coat are distinctive. However, genetic evidence suggests that it diverged quite recently from the swift fox (*V. velox*) that lives on the dry plains of Canada and the United States. The bat-eared fox (*Otocyon megalotis*) is specialized to eat insects with modified teeth and a special muscle to help it open its mouth rapidly and bite up its prey. Fossils with these special teeth show that the species diverged at least 3 million years ago (mya).

More specialized still is the raccoon dog (*Nyctereutes procyonoides*). With its stocky build and mask on the face, some experts have considered it a member of the raccoon family. The animal lives in dense, temperate forest often along watercourses in eastern Asia and Japan (and has been introduced to parts of eastern Europe as an escapee from fur farms). Genetic data show that it is clearly a dog but one that diverged early. Two continents require special consideration. The first is South America, which had almost no placental mammals until it became connected to North America 2–3 mya. It appears that either two or three kinds of canid moved south. One of these groups was successful, radiating into niches occupied by coyotes and foxes. The zorros of the Chilean and Argentinean deserts look very similar to their vulpine cousins in the rest of the world although they are independently evolved, and the culpeo (*Pseudalopex culpaeus*) of the pampas could pass for a coyote. There are two specialized South American canids that may represent independent lineages. The maned wolf stands taller than all but the largest gray wolves, but despite its size it is solitary and has a large



Gray wolves (*Canis lupus*), the largest canids, circling musk oxen. (Illustration by Wendy Baker)

proportion of vegetable material in its diet. Its legs appear to allow it to see over the tall grass. The other peculiar South American species has the opposite morphology, looking like a barrel with short legs—the bush dog (*Speothos venaticus*) lives in thick forest where it hunts in packs, often along rivers and streams. It is an accomplished swimmer.

For the last 100 million years, there has not been a land bridge between Australia and Asia. It is therefore fairly certain that the dingos (*Canis familiaris dingo*) were brought with humans in their canoes and have gone feral. By now the dingos are a self-sustaining species with only their curly tails hinting at their ancestry. They even show a behavior, regurgitating water, that has not been reported from other canids. The dingos are one end of a spectrum from completely feral to completely domesticated. Other forms, such as the New Guinea singing dog, live mostly independent of humans while the village dogs of much of the Third World and the urban dogs of Western cities rely more on their owners.

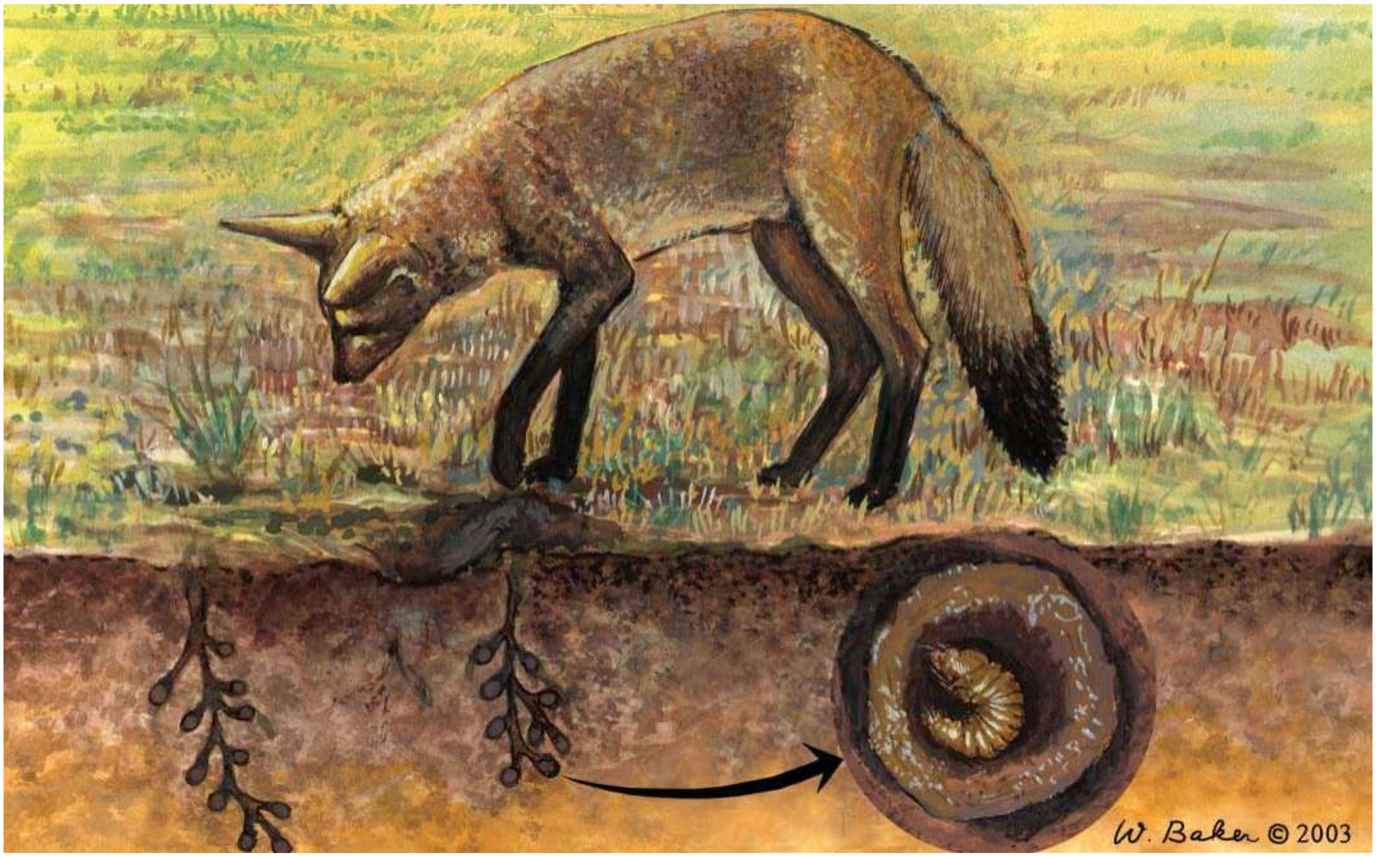
Physical characteristics

Members of the dog family range in weight from 3–165 (1.3–75 kg). Coat colors and patterns vary significantly: black, black and white, brown, and red are all very common coat color in many dog breeds. As a family they have longer legs in relation to their weight than the other carnivore families. Their economical trotting gait allows them to cover large areas in search of prey, and most species can accelerate to 25–35 mph (40–56 kph) to run down prey. Top speed can usually be maintained for at least a mile, although prey are seldom pursued for that distance. Three species with shorter legs, the small-eared dog and bush dog of South America and the raccoon dog of eastern Asia live in dense forest. Five claws on the front feet and four on the back is typical. The fifth claw on the foreleg, the dew-claw, is almost vestigial and does not reach the ground. This claw is absent in African wild dogs.

Jaws and teeth are adapted to grab and chew prey. The tooth formula is 3/3, 1/1, 4/4, 2/3 for all species except the bush dog which has lost two molars on the upper and lower jaw, the dhole which has lost one molar on the lower jaw, and the bat-eared fox which has added two molars to the upper jaw and one to the lower jaw. The canines are longest in rodent catching species and shorter and sturdier in species killing larger prey. The last premolar in the lower jaw and the first molar in the upper jaw are modified into blades, or carnassials, which can cut flesh. The molars have grinding surfaces for crushing either bone or vegetable food. All the cheek teeth of the bat-eared fox look similar with multiple sharp cusps for penetrating insect exoskeletons, their primary prey.

The gut is simple and usually about five times the length of the animal. It is a bit shorter in highly carnivorous species. Most canids “wolf” their food, rapidly swallowing it. When pups are present they can regurgitate food up to 12 hours after eating.

Coyote (*Canis latrans*) pups play and practice fighting. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)



A bat-eared fox (*Otocyon megalotis*) listens to the larva in a dung beetle ball underground. (Illustration by Wendy Baker)

It is not clear if this represents an adaptation to slow digestion or just a result of swallowing large bits in the first place.

Canids can certainly smell better than humans; their sight appears to be comparable to that of humans for most species but they have a higher ratio of rods to cones which should produce less color discrimination but an ability to operate at low light levels. Many species forage at night. Hearing is always acute, although the size of the external ears can be misleading as the ears are also used to radiate heat. The Arctic fox (*Alopex lagopus*) and the raccoon dog have small ears. Body lengths without tail range between 18.3 and 28.7 and (46.5–73 cm) and tail lengths are approximately 9.8–20.5 in (25–52 cm). Bat-eared foxes can hear the sound of termites foraging under ungulate dung and many species locate rodents by their rustle in the grass.

Distribution

Wild canids occupy every continent except Antarctica and Australia. They occupy almost every habitat except permanent ice and they are rare in tropical rainforests. Domestic dogs have traveled with humans to every corner of the planet, from the South Pole to Death Valley, California.

Habitat

The habitats used by the dog family are as diverse as their prey and it is easier to define areas that are excluded from use than to enumerate the ecosystems they occupy. Only two species live permanently in closed canopy forests, the bush dog in South America and the raccoon dog in east Asia. Both have short legs and a comparatively compact body to negotiate tangled pathways. The bush dog is found near water. Forests typically support a lower density of ground living rodents and lagomorphs than more open areas. "Edge" habitats with a mixture of woods and open country are favored by many canids. Several species notably the red fox and the coyote have benefited from the human conversion of forests into cropland. As noted above several canids, and especially the fox species, live in deserts. For kit foxes living in the arid areas of North America, it has been calculated that the moisture in their prey may be more important then the calories, i.e. they kill to drink. The large pack hunting species due to their mobility and catholic prey habits have the widest ranges of habitats used. The gray wolf's (*C. lupus*) enormous range includes tundra, ice flows, boreal forest, and the deserts of the Sinai and northern Mexico. However the African wild dog may be even more extreme. It has been reported from deep in the Sahara, from the montane forests of Ethiopia and from over 19,000 ft (5,790 m) above the snowline on Mt. Kilimanjaro.

Behavior

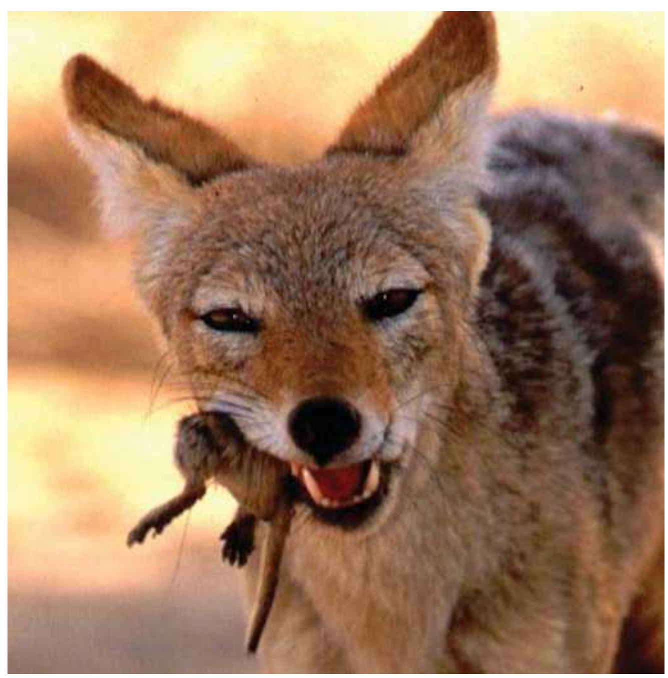
Watching wolves jostle for dominance or red foxes in courtship is to witness a complex, fast, and subtle dance, incorporating not just movement but sounds, smells, and touch.

A crab-eating fox (*Cerdocyon thous*) eating a crab, as its common name suggests. (Illustration by Wendy Baker)

The outcomes of such interactions will determine who mates with whom and which animals will disperse, i.e., whose genes will be represented in future generations. In many cases the information acquired during play and other non-hostile interactions will eliminate the need for more openly hostile confrontations later. An individual can assess where he or she stands without having to fight.

The complex interactions are built up from simpler units or elements (e.g., a growl, or a wagging tail). These elements combine to form gestures and gestures between individuals form interactions. Interactions between pairs (or larger groups) form relationships. The pattern of relationships in a pack or group, in turn, determines the social system. Social behavior is a complex hierarchy that is hard to study. Luckily at the lowest level, the elements of social behavior are quite uniform among all the canid species (and recognizable by the owners of domestic dogs). As an example, among facial expressions all canids can snarl aggressively (upper lips lifted vertically) and "grin" submissively (lips retracted backwards). All species may show a defensive gape with the mouth held wide open as a shield. However, it occurs much more commonly in fox-sized species. The position and movement of the tail is similar in most canids and there is a graded signal from the tail tucked between the legs in defensive submission to tail held high in assertive dominance. In a study on jackals a scientist noted the exact element of behavior from twelve parts of the body (e.g., ears, muzzle, head turning, tail, hackles) as they were combined to produce gestures. The exact gesture virtually never repeated itself, reflecting the complexity of the interactions.

Vocalizations are integral in many close interactions and loud vocalizations, e.g., howls, can also carry to communicate with animals far away. One problem with studying vocalizations in canids is that we know they can hear at higher frequencies that we can. Humans probably hear only a part of the signal with their ears. (Ultrasound analysis allows us to "see" these noises but few have been analyzed.) As with the other elements of behavior, many of the squeaks, grunts and growls of close interactions seem similar across the canids (modified by the size of the voice box so that small species produce a higher pitched version of a noise). The growl is one of the sounds made by all canids and indicates threat. In an intense form it grades into a bark but barks are not commonly heard. However, this warning vocalization must have been found useful by the early domesticators of the wolf and is now triggered by almost any arousing or threatening stimulus in domestic dogs. The most evocative and loudest of canid vocalizations are designed for long distance propagation. Wolves, coyotes, and jackals all have howls (and interesting variants occur in African wild dogs and dholes). A pure-tone howl produced by a lone individual wavering around a single frequency acts to bring the pack together. The much more complex group howl which includes several individuals, some howling, some barking, and some growling is a territorial signal asserting rights to the land. It has been suggested that the complexity of the group howl with certain wolves changing pitch may deceive listeners into believing that the pack has extra members. It was believed for years that African wild dogs did not howl and packs are so spread out that a vocal threat like a group howl would have nobody to hear it. Recently group howls have been heard on the rare occasions when two packs do bump into one another. They have the same rich texture as group howls by wolves and seem to act as a threat. The dhole uses a pulsed whistle to locate pack members and a group howl between packs.



A golden, or common, jackal (*Canis aureus*) with a mouse. (Photo by Rudi van Aarde. Reproduced by permission.)

Silverback jackals (*Canis mesomelas*) "body slam" play in Kenya. (Photo by K & K Ammann. Bruce Coleman, Inc. Reproduced by permission.)

Olfactory communication is almost completely outside human perception but probably plays a major role in the life of a canid. Glands on the feet, skin, lips and anus are modified for secretion and in some species many of the glands associated with the hairs on the dorsal surface of the tail produce odor. Anal gland secretions rub off on feces and a variable mixture of bacteria in the anal sacs ensures that individuals have a unique odor. Sex and reproductive status, at least, are detectable in the urine. Urine marking by cocking a leg is seen in all adult species. Unlike domestic dogs where only males cock a leg, in wild canids the dominant male and dominant female both usually display the behavior. Marks are usually distributed around the edge of the territory and typically both members of the pair mark consecutively. The bush dog female has a peculiar marking behavior in which it backs up against a tree or post and deposits urine about two feet above the ground, presumably to increase its dissemination in the forest habitat. Bush dog males exhibit a typical leg cock.

Many of the most complex interactions occur in the context of dominance and submission. Whether in pairs or larger groups, stronger individuals have the power to monopolize important resources. The degree to which they assert their status depends on the extent to which they depend on other members of the group. In packs of African wild dogs, the species with the greatest social interdependency, dominance hierarchies are established in both males and female but their expression is muted. Expressions of subordination, or the willingness to accept the position or status of the dominants, are usually demonstrated effusively in all species. Subordination comes in two forms passive and active. In passive submission the inferior dog rolls on it back in front of the dominant. The gestures of active submission (or greeting) are derived from the begging of pups and subordinates mob a dominant thrusting their muzzles into his or her face. In wolves a dominant animal may either regurgitate or drop a bone or other food item in response to these greetings. Dominant individuals breed and the dominant or alpha male will prevent other males from mating while the alpha female will keep other females away. Relationships within monogamous pairs are usually fairly egalitarian with time spent resting and traveling, grooming and greeting together. Males are typically 10–15% larger than their mates which may explain why the majority of active submission seems to be directed by the female to the male.

Feeding ecology and diet

Most members of the dog family receive the majority of their calories from mammalian prey. At particular times and for particular species, fruit, insects, and other invertebrate prey are important. Every canid species observed to date has been seen trying to catch mouse and rat sized prey. While mice may be a supplementary food source for wolves, they are central in the diet of many fox species. Even a species as large as the Ethiopian wolf (*C. simensis*) at 38–44 lb (17–20 kg) subsists almost exclusively on small rodents. Species specialized for catching rodents have long, pointed jaws with elongated canines to maximize snapping speed and holding power. There is also a specialized behavior, the pounce, for catching rodents. The prey animal is located by sound, a rustle in the grass, and the fox launches itself upwards at an angle close to 45°, dropping down to pin the prey with its forepaws. On open ground rodents may be stalked with a final rush of 33–66 ft (10–20 m). Digging can also be effective,

A red fox (*Vulpes vulpes*) carries two Arctic ground squirrels (*Spermophilus parryii*) to its den in Denali National Park, Alaska, USA. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

An Arctic fox (*Alopex lagopus*) chases a hare on the snow. (Photo by Tom Brakefield. Bruce Coleman, Inc. Reproduced by permission.)

particularly if a nest of newborn rats or mice is detected. Canids dig quickly and furiously using both front feet.

Rabbits and hares, the lagomorphs, feature in the diet of virtually every canid. Rabbits typically weigh from 1.1–4.4 lb (0.5–2 kg) while hares can weigh up to 10 lb (4.5 kg). In California, the 4.4 lb (2 kg) kit fox feeds primarily on the 4 lb (1.8 kg) black-tailed jackrabbit. Excluding the four or five species of specialized pack hunters, mammalian prey over 11 lb (5 kg) is usually taken only sporadically by members of the dog family. As a general rule, it is weak or young prey that are taken. Coyotes will kill young pronghorn and pairs of jackals cooperate to hunt young gazelles. Unfortunately, the young of domestic animals are sometimes vulnerable to this predation, although many studies show that lambs or calves being eaten by canids were probably stillbirths with embryonic membranes still covering the hooves.

A battle between a wolf pack and a moose weighing up to 1,650 lb (750 kg) and lasting up to several days in the snows of Nearctic winter is one of the grandest predator prey encounters left on the planet. The outcome is far from certain and the hoofs of the great deer can quickly kill an incautious wolf. Of course, it is usually the prey who are already weakened from starvation or disease that succumb. Comparable confrontations between African wild dogs and zebras (*genus Equus*) in Africa or Asiatic wild dogs or dholes with Sambhar deer (*Cervus unicolor*) in India, and perhaps the smaller bush dogs with capybara (*Hydrochaeris hydrochaeris*) in South America, reveal the rare cases in which members of the dog family form groups to hunt large ungulate prey. Popular opinion notwithstanding, there is little evidence that any of the pack hunters use complex hunting techniques such as setting ambushes or even relay running. By far the most common hunting behavior could be called "flush and rush." The pack moves through wooded or scrub habitat and will pursue any prey that breaks cover. These chases will seldom go for more than 1,640 ft (500 m). In open country the approach to prey can seldom be disguised and a pack's only chance is to stampede the prey and look for young or vulnerable animals that fall behind. Zebras in Africa and muskoxen (*Ovibos moschatus*) in the Artic that resist being stampeded and form a defensive circle will usually avoid predation. African wild dogs, wolves and dholes all have a top speed of about 35 mph (56.3 kph). The limit of the chase is set by the problem of overheating. After 3.5 mi (5.6 km), the effort of running in a wild dog has raised the body temperature to a dangerous 105.8°F (41°C) and only a special circuit of cool blood from the nose keeps the brain from over heating. Canids lack any specialized way to kill their prey (unlike the cats with their specialized throttle bite). Members of the pack will bite any exposed part, often grabbing a hind leg to topple the prey. Once on the ground the animal is usually quickly ripped open and dies quickly. All three of the main pack hunters have been seen to leap up and catch the upper lip of large prey. Once the lip is bitten the struggles of the prey are greatly reduced. (Humans

A dingo (*Canis familiaris dingo*) adult with pups in Queensland, Australia. (Photo by FRITHFOTO, Bruce Coleman, Inc. Reproduced by permission.)

have also discovered this and will twist a rope around the upper lip of a horse to quiet it.) Hunting is only rarely more efficient when the size of a pack goes above four individuals, but pack sizes in all the pack hunters often reach 20–30 animals. It is the very large prey items that can provide food for all the extra pack members.

Almost all members of the dog family will eat fruits and coyotes have been known to cause damage to commercial melon farms, while Aesop tells a story of the fox and the grapes. Young, dispersing canids often resort to fruit before their hunting skills in new territory are perfected. The maned wolf of South America feeds on fruit from the genus *Solanum*. Invertebrates are always a component of the diet of foxes. In the foxes of arid lands, where vertebrate prey may be scarce, most species will eat beetles, scorpions and spiders. The red fox of more temperate latitudes often includes substantial quantities of earthworms in its diet. In South America, the crab-eating fox (*Cerdocyon thous*) depends on its crustacean prey at certain times. Among non-mammalian vertebrates, any canid will pick up and eat the eggs and nestlings of ground nesting birds, and foxes may indeed kill many chickens if they get into the henhouse.

Another topic for this section is the killing of one canid species by another, "dog eat dog." In North America in particular, competition between members of the dog family may result in one species killing or driving off another. If wolves are common, coyotes are usually sparse and wolves have been seen to chase coyotes vigorously and kill them. In turn, coyotes are an important cause of mortality for the kit foxes in California, though the fox carcasses are not always eaten. To make matters worse, the small and endangered kit foxes are also persecuted by the larger, introduced red foxes.

Reproductive biology

Golden jackals (*C. aureus*) are common on the scrubby sand dunes just south of Tel Aviv in Israel. In December a young adult female approaches an adult male who, by his marking behavior, has established a territory for himself. The female is playful and submissive. The male is not very responsive at first and snaps at the female but she follows him and over the next two months they are seen resting and grooming together until they are seldom seen apart. Sometimes the female stands directly in front of the male to form a "T" and the male may put his forepaws on her back. In March the female is fully sexually receptive for about a week and some of the male's mountings end in a copulatory tie in which the head of his penis swells so it cannot be extracted for 4–5 minutes. Nine weeks later a litter of five pups is born in an underground den. For the first few days after giving birth, the female stays with and nurses the young while the male provides her with food. Soon after their eyes open at two weeks the pups start to crawl around and usually emerge above ground at about three weeks. The parents usually take turns staying by the den and foraging. Most food is carried back in the parents' belly and regurgitated, but larger items may be carried back whole. By three months the pups have achieved nearly adult size and over the next three months they become independent of their parents (although willing to beg if the opportunity presents itself).

A gray wolf (*Canis lupus*) pack at the edge of a snowy woods in California, USA. Gray wolves are not found in the wild in California, but may be found in fenced-in parks or other areas. (Photo by Tom Brakefield. Bruce Coleman, Inc. Reproduced by permission.)

The reproductive biology of the jackals in Israel is typical for the majority of the canids. The two salient features are monogamy and regurgitation, a combination that is common in birds but not seen in any other group of mammals. The two are linked. By having an efficient way to provision his young, a male canid can usually be more successful reproductively by helping his offspring than by attempting to mate with many females. Monogamous bonds, in all species studied to date, extend over several breeding seasons and are sometimes life-long. (In the pack-living species, most mating occurs between the alpha animals in the male and female hierarchies. Although a pair bond develops, it is determined by the outcome of competition within the sexes.)

Canids are almost always territorial. It pays a pair to keep other members of their species out of a defined area. This protects food supplies, keeps conspecifics away from the den where cannibalism could occur and perhaps most importantly keeps members of the opposite sex away from mates. It is striking that in territorial encounters aggression is usually between members of the same sex. Territoriality is not seen in African wild dogs that roam over such large ranges that they cannot defend its boundaries. However, one pack will chase another away if they meet. At the other end of the spectrum, the home ranges of bat-eared foxes overlap considerably. They live almost exclusively on insects. Food taken by other foxes does not reduce a resident's supplies and defense is not economic in this situation.

A territory that can supply the needs of a breeding pair can often provide food for other animals to survive. In many circumstances it is very beneficial for a young animal to remain on the territory where it was born. Most of the mortality in canids happens when young animals first move away from their natal range. Their hunting skills are not perfect, and they have to move though land occupied by hostile conspecifics (and not infrequently human persecutors). The retention of young in the parental territory is now known to be very common in the dog family. These animals may stay through one or more breeding seasons. These extended families usually gather for a morning and evening greeting although each individual will find food alone. Young from previous years are often present at the birth of the next litter, and regurgitate food and act as babysitters. In most cases this appears to help the parents reproductive efforts, but in one case the "helpers" in a pack of African wild dogs under food stress were seen to pull food from the mouth of the young pups. It is probable that pack hunting developed when pre-existing groups cooperated to tackle larger prey. Even the wolf, when it is living in forested or more arid regions, breeds in pairs and lives in the summer on comparatively small prey. Packs and group hunting occur in the winter.

The rule of monogamy has a few exceptions. In African wild dogs, the alpha female has been seen to mate with more than one male during her estrus, and the hierarchy among the males is unstable so that in different years the same reproductive female will mate with different males. The species is effectively polyandrous, a system in which one female has many male partners (despite the fact that at any one moment there is close relationship between the alpha pair). African wild dog females also produce very large litters averaging 10 pups. There is intense competition in this species between females to monopolize the help (in the form mainly of males) needed to raise their pups. At the other end of the spectrum there are cases in several fox species and most notably in the bat-eared fox of two females sharing a den with a single male. This is a form of polygyny in which a male has several female partners and it is also observed in red foxes. In contrast to the African wild dogs in which the regurgitation and hunting skills of the pack are crucial for survival of the pups, in the largely insectivorous bat-eared fox, the male can contribute little to his mate. An insect diet does not provide the nutritious surplus that can be regurgitated. In this species the male's main investment is to babysit while the females forage and produce milk. It is the same effort to babysit one versus two litters, and the females should choose to breed in the areas of most reliable insect abundance. Females usually produce one litter a year and in temperate regions birth usually comes in early spring. Pups require the most food several weeks after they are born, and an early spring birth peak means that growing young can be provisioned from the prey born in early summer. Litter size runs from two to 20 with an average of 5–6. Litter size is larger than that of the other carnivore families. The maned wolf, a large, solitary species with a largely vegetarian diet, gives birth usually to just two young while African wild dogs and Arctic foxes may give birth to 15–20 young. In the Arctic foxes the large litters occur in years of maximum lemming abundance.

A silverback jackal (*Canis mesomelas*) mother nursing her cubs. (Photo by K & K Ammann. Bruce Coleman, Inc. Reproduced by permission.)

Conservation status

As humans co-opt the resources of the planet, the capacity of any carnivore to survive depends on its ability either to coexist with humans or to live where humans cannot or have not introduced settled agriculture. Every species of canid has interactions with humans and often their domestic dogs. Several adaptable species, notably the red fox, the gray fox, the coyote, and the Asiatic golden jackals, have found the modification of the environment by humans to their liking and are flourishing. Most other species are less fortunate.

Only one species of canid has gone extinct in recent times. The last Falkland Island wolf (*Dusicyon australis*) was seen in 1875. These large, coyote-like animals were common on the Malvinas, which lie 250 mi (400 km) off the coast of Argentina. It is not clear whether they were domestic dogs that went wild or an indigenous species that crossed from the mainland when sea levels were very low. Their tameness and habit of greeting humans when they arrived suggests the former. However, their friendly traits made them very easy to kill when Scottish sheep farmers arrived in the mid-nineteenth century. Although only one full species of canid has disappeared, several races or distinguishable subspecies have been lost. Several types of wolves that occupied the American west and Europe have vanished, as have races of the African wild dog that used to live in south and west Africa. In general the large pack hunters have been excluded from areas of settled agriculture and now survive only in wilderness. The wolf in Europe has

A coyote (*Canis latrans*) with a ring-necked pheasant. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

been able to survive in quite small areas of uncultivated land and in frequent contact with humans. The problems of the African wild dog, the wolf of that continent, are more severe. The world population may be as low as 5,000. Perversely it does not necessarily flourish in the rich game reserves as it is competitively inferior to lions and spotted hyenas, and loses its kills to the larger predators. Its ability to travel very large distances and live on low densities of prey may allow it to survive in the large tracts of semi-arid land in the north and east of the continent. The fate of the dhole, the pack hunter of east Asia, is largely unknown but it has certainly suffered a huge contraction of its range.

Among the intermediate and smaller species, the forms that are most endangered have restricted ranges. The Ethiopian wolf, with about 500 survivors, is the most vulnerable species. This animal lives only on rodents above 9,840 ft (3,000 m) on Ethiopian mountains. Its range has been shrinking since the earth started to warm up at the end of the last Ice Age and it is now reduced to seven small populations largely isolated from one another on the tops of different massifs. Islands restrict the range and hence population size of two other endangered species. The island fox (*Urocyon littoralis*, related to the gray fox) exists only on an archipelago off the coast of southern California, and Darwin's fox (*Pseudalopex fulvipes*) lives almost exclusively on Chiloe Island off the coast of Peru.

The red wolf of the southeast United States is a small canid and the last known free-living sightings were made in restricted habitat of coastal marsh, although there are historic records from a range of wooded environments. Most of the surviving animals were brought into captivity, and genetic analysis has shown that all contain a mixture of gray wolf and coyote genes. This hybrid form represents a unique canid and has been treated as a self-standing endangered species. Even after some successful reintroductions, its numbers remain critically low. Programs for reintroducing and translocating gray wolves are currently ongoing in North America. In a recent review of canid conservation, 9 species or a quarter of the family had too little known about them to draw any conclusions about their rarity. Several of these species, such as the fennec (*V. zerda*) from the Sahara are living in areas where human impact is still minor.

Significance to humans

Some Native Americans near the Arctic Circle share their land with wolves. Both subsist mainly on the caribou herds. Although guns have upset the balance of the relationship in the twentieth century to the present, humans still talk primarily of their respect and admiration for their fellow carnivores. The two hunters do not interact frequently, although each will scavenge from the other or commandeer kills from smaller groups. A wolf-trimmed coat is a mark of a skilled hunter. For the past million years most humans, like the Native Americans, have probably lived within earshot of the howls of members of the dog family, but there is no archaeological evidence that they had strong ecological or economic interactions. However our hunter-gatherer ancestors certainly knew about the animals around them and the distinguishing characteristics of our canid neighbors are deep within the folklore of most cultures. From Romulus and Remus to Mowgli, the nurturing characteristics of the wolf family are renowned while the tricks of the coyote and the fox are legendary.

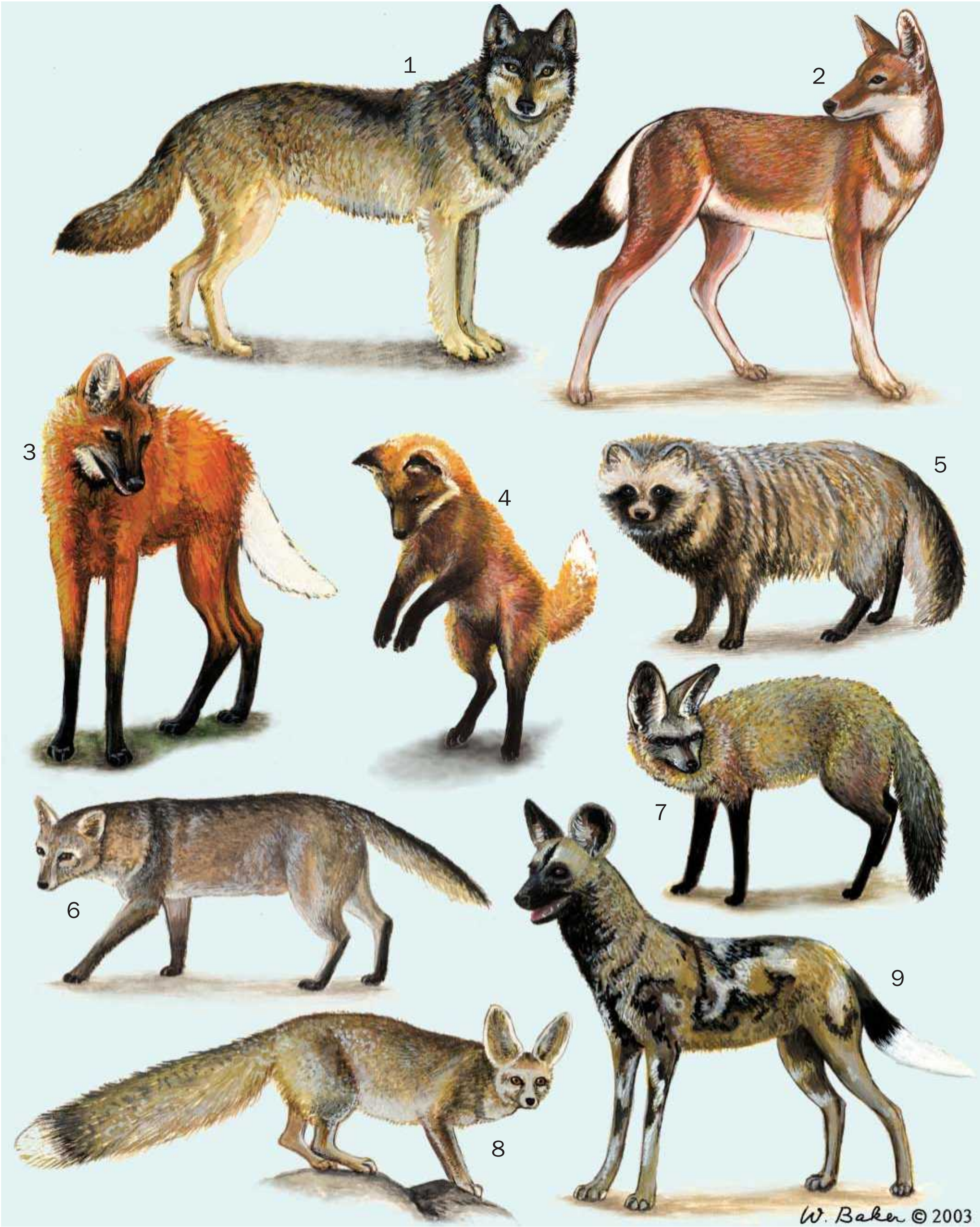
The spread of agriculture marked a downturn in canid-human relations. Domestic stock from chickens to cows are tempting targets and even cultivated fruit, like melons and grapes, are simple for a fox or a coyote to harvest. The wolf has suffered the most for its potential to kill domestic stock. From 1860 to 1920 a war waged on the species in western North America using guns, traps, and poison was overwhelmingly successful. By the 1930s only a few stragglers survived close to the Mexican border or in the forests of Minnesota where immigrants from Canada were available. Intensive settled agriculture had long since driven wolves into the corners of wilderness left in Europe. The wolf had become a creature of the wild and the forest and a bogeyman for the village dwellers. Fear replaced respect and Little Red Riding Hood's grandmother replaced the mother of Rome. However, at least in the Western world, attitudes to wolves are rapidly undergoing another 180° turn. They are now the icon of the wild places and wild nature that we are losing.

The wolf, a large animal often in packs, has been much easier to persecute than the intermediate sized canids—the dingo, coyote, jackals, and red fox. These species do not require a prey base of large mammals and can live surreptitiously at high population densities. Efforts to control these species have seldom been successful despite their depredations on the young of domestic stock especially sheep and goats. These intermediate sized canids live where they can find food. Dog food and earthworms provide nourishment for red foxes in the middle of English cities, while domestic cats are a staple in the diet of the coyotes living in Los Angeles, California.

Approximately 15,000 years ago a symbiosis developed between wolves and humans. Wolves, as village dogs in many parts of the world today, probably acquired some of the scraps from the increasingly efficient hunting of the humans. The

Bush dogs (*Speothos venaticus*) play fighting in Brazil. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

humans, in turn, chose wolves that were efficient in sounding an alarm (barking), and sometimes protecting stock. Initially in this relationship the benefits the wolves derived from food may have outweighed the advantages to their humans and it seems likely that wolves domesticated us. However, once wolves began reproducing under human control, selective breeding allowed humans to take canid characters that were useful to them and produce guard dogs, swimming dogs, retrieving dogs, and ironically foxhounds and wolfhounds; dogs to hunt other members of the family. In the western world traits of active submission and obedience have been selected to produce our loyal and friendly companion animals.



1. Gray wolf (*Canis lupus*); 2. Ethiopian wolf (*Canis simensis*); 3. Maned wolf (*Chrysocyon brachyurus*); 4. Red fox (*Vulpes vulpes*) pup; 5. Raccoon dog (*Nyctereutes procyonoides*); 6. Crab-eating fox (*Cerdocyon thous*); 7. Bat-eared fox (*Otocyon megalotis*); 8. Blanford's fox (*Vulpes cana*); 9. African wild dog (*Lycaon pictus*). (Illustration by Wendy Baker)

Species accounts

Gray wolf
Canis lupus

TAXONOMY
Canis lupus Linnaeus, 1758, Sweden. Twenty-six races are recognized. The largest races live exclusively on large ungulates while the smallest are from the desert regions. Two genetically distinct stocks appear to occur in North America, with wolves in the western part of the continent perhaps representing a separate colonization from Eurasia.

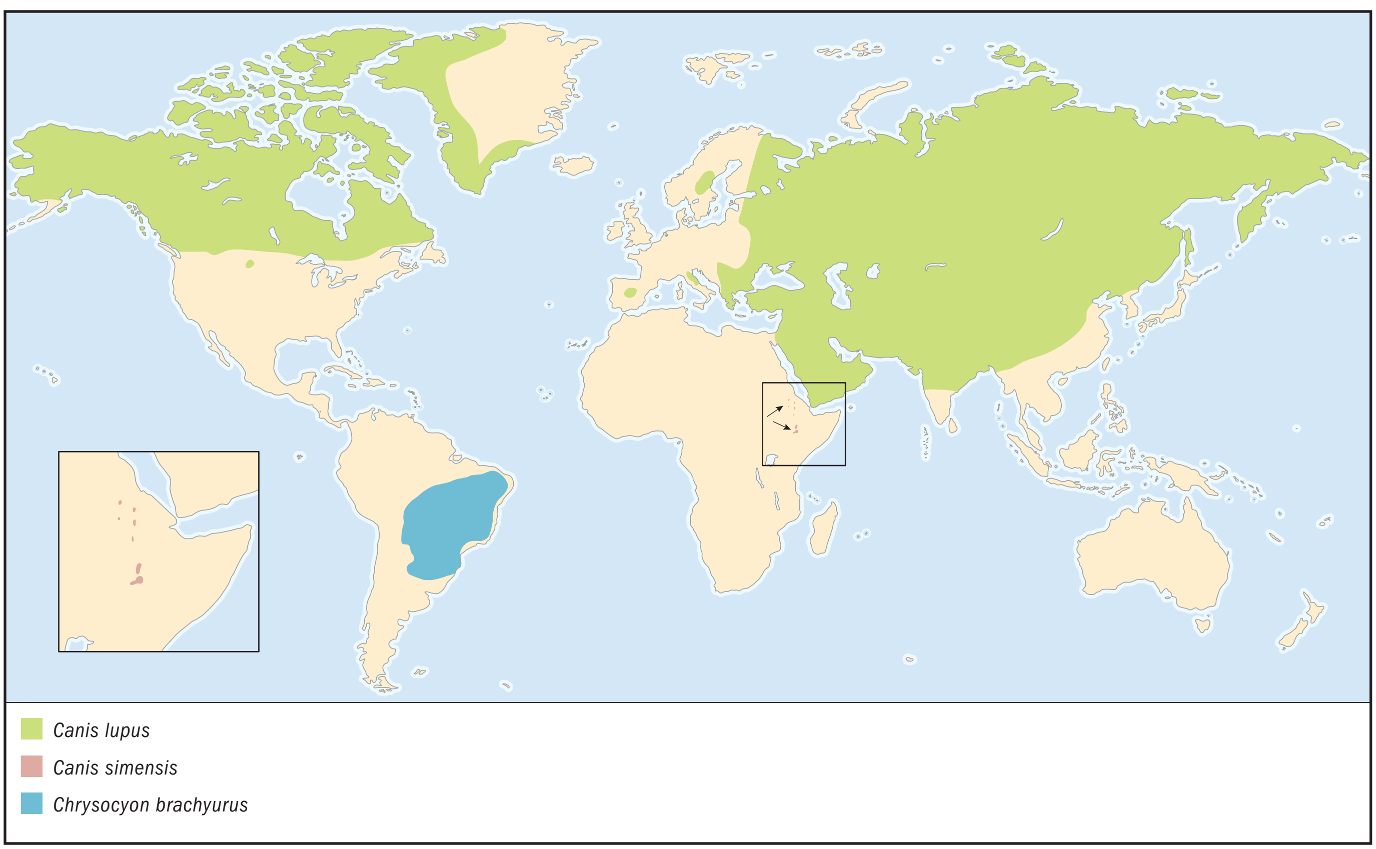
OTHER COMMON NAMES
English: Timber wolf; French: Loup; German: Wolf; Spanish: Lobo.

PHYSICAL CHARACTERISTICS
The gray wolf is the largest of the canids with males weighing up to 132.3 lb (60 kg) while females are typically 10–15% smaller than males. Shoulder height is from 26.0–31.9 in (66–81 cm). In the small desert wolves, e.g. the Mexican wolf, males weigh 66 lb (30 kg) or less. Coat color is typically an agouti brown but can vary from pure white (in the Arctic) to black, and shades of rusty color. The belly and chest is white; the fur is long with a bushy tail. The skull and teeth are large, but are less specialized for eating flesh than those of the dhole and the African wild dog.

DISTRIBUTION
Wolves occur where suitable densities of prey, usually ungulates, can provide food. This includes Arctic ice flows and the Sinai desert and all habitats in between.

HABITAT
The species used to inhabit the whole of North America, south to central Mexico. It also lived throughout Eurasia including the Sinai peninsula, but excluding the southern third of India and the southern portions of Southeast Asia. It has been exterminated from most of the U.S. except for a population in northern Minnesota, and a newly expanding population in the northern Rockies. A few Mexican wolves have been reintroduced to New Mexico in the United States. Wolves were wiped out in most of western Europe by 1750. Three small populations remain in the Iberian peninsula, the Apennines in Italy and south central Norway. Wolves have also been eliminated from the eastern two-thirds of China.

BEHAVIOR
Most wolves live in small social groups of two to six individuals, sometimes with pups. Packs are thought to consist of related individuals and females typically join males that have an established territory. However, many wolves such as those living in less productive areas are only seen solitarily or in pairs and packs themselves are fluid. Groups may split in the summer while individual pairs breed and then come back together



into larger groups in the winter. The size of the pack seems to be related to the size of the prey killed. A large group can obtain a meal from a large carcass. Little is known about the social behavior of wild wolves. However, information from many captive packs reveals a rather dictatorial society in which the alpha male exerts his authority by clasping the muzzle of the subordinates in his mouth. The other wolves show elaborate active submission rubbing their mouths against his head and licking his muzzle in a gesture derived from infantile begging. Alpha males have been seen to pick up a bone, with no food left on it, and drop it among the subordinates as a gesture of their dependence on his food provisioning.

FEEDING ECOLOGY AND DIET

Ungulates from 44.1–220.5 lb (20–100 kg) form the core of the wolf's diet. However prey up to the size of a moose (1543 lb; 700 kg) and as small as a mouse are included. Members of the deer family are the most common prey from the caribou of northern latitudes to the mule deer of the SW United States. Beavers are commonly killed in North America. Italian wolves raid human trash and some predation on livestock has been reported. There are no authenticated reports of wolves killing humans in North America, and no recent reports from Europe. Poor people in Europe and northern Asia may have been attacked by wolves in the past and there are a few reports of infants being taken by wolves in India.

REPRODUCTIVE BIOLOGY

Monogamous. Packs or pairs breed annually with young born from March-July depending on latitude. Gestation is 61–63 days and young are born blind in an underground den. The mother nurses her young and licks them to stimulate defecation and urination which she consumes so as to keep the den clean. Eyes open at about 14 days and young crawl to the surface a few days later. All members of the pack feed the pups with regurgitated food, and may carry some food items back to the den. The pups spend an increasing amount of time out of the den usually playing. As the pups become more mobile, adults may become less tolerant of their sharp teeth and frequently lunge at the pups to keep them at bay, but without inflicting any serious bites. By three months, the pups are starting to follow the pack, and will leave the area of the natal den. However, they usually cannot keep up with the hunts and are left alone or with a babysitter. The young are not fully mature until about two years old.

CONSERVATION STATUS

As indicated above, the wolf has been exterminated from a considerable portion of its range. It is a very rare animal in the United States (outside Alaska) and is listed as endangered in the U.S. Endangered Species Act. Recovery efforts have included protection and habitat acquisition in Minnesota, captive breeding and reintroduction of the Mexican wolf and reintroduction in the Yellowstone ecosystem. Wolves, without help from humans, have recolonized parts of the northern Rockies in Idaho and Montana. The remnant populations in Europe are being managed. The wolf does not survive in areas of settled agriculture but in the wilder parts of its immense range, it appears to exist in low numbers despite human persecution and some trapping for its fur. The gray wolf is not listed as a threatened species globally by the IUCN.

SIGNIFICANCE TO HUMANS

Wolves have been a potent force in human culture both economically and culturally. Wolves are still hunted through much of eastern Asia where people still herd their sheep and goats for a living. In Alaska they were killed using helicopters because they were blamed for depressing the caribou herds hunted by sportsmen. For people living a long way from wolves, the species and its howl represents the essence of wildness and it is a mark of machismo to own the dangerous and semi-wild wolves and wolf hybrids. ◆

Ethiopian wolf

Canis simensis

TAXONOMY

Canis simensis Rüppell, 1835, Ethiopia. There are some slight differences between wolves found on either side of the Great Rift Valley, suggesting isolation for part of the Pleistocene.

OTHER COMMON NAMES

French: Loup Abyssinie; German: Aethiopenfuchs; Ethiopian: Ky Kebero.

PHYSICAL CHARACTERISTICS

The Ethiopian wolf is a long-legged, long-snouted canid with males weighing 35 lb (16 kg) and females 28.7 lb (13 kg). It is 23.6 in (60 cm) at the shoulder. The coat is a bright red with black on the back of the ears and tail. The base of the tail and lower legs are white, with white patches on the throat and chest.

DISTRIBUTION

The species is restricted to seven small areas, five north of the Rift Valley and two south of the Rift Valley, all in Ethiopia.

HABITAT

An extreme specialist, the Ethiopian wolf lives in treeless areas above 9,843 ft (3,000 m), in Afro-alpine habitat.

BEHAVIOR

The species is territorial and monogamous. Young often remain on their natal territory producing small packs of 2–8 members. Females leave their home area sooner than males so packs have more males than females.

FEEDING ECOLOGY AND DIET

Rodents constitute 95% of the diet. The prey include the giant mole rat 10.6–31.7 oz (300–900 g) as well as smaller rats and mice. Hares are caught occasionally. Prey is sighted or heard in the open country. The wolf will stalk until able to make a final dash of 16.4–65.6 ft (5–20 m). Prey may also be dug out of their tunnel systems. Scavenging occurs. Predation on livestock is exceedingly uncommon.

REPRODUCTIVE BIOLOGY

Monogamous. Breeding occurs seasonally with mating in August and September with young born two months later. Litter size is from two to six and all members of the pack bring food to the pups. Only the alpha pair breed. Juveniles will follow the pack at six months but full adult stature is not achieved until two years.

CONSERVATION STATUS

Of the seven populations, only one, in the Bale Mountains, numbers more than 100. The total available habitat is very limited, and humans encroachment is continuing. World population is less than 600. There are none in captivity. Listed as Endangered by the IUCN.

SIGNIFICANCE TO HUMANS

The Oromo people who live among Ethiopian wolves show little or no antagonism towards them, recognizing that they are not a threat to their herds. They are sometimes shot in other parts of their range and their livers are thought to have medicinal properties. ◆

African wild dog

Lycaon pictus

TAXONOMY

Hyaena picta (Temminck, 1820), Mozambique. There is some genetic differentiation between dogs from East and South Africa, but there is also overlap between the types.

OTHER COMMON NAMES

English: Cape hunting dog, painted wolf; French: Lycaon; German: Hyanenhund.

PHYSICAL CHARACTERISTICS

The largest canid in Africa, it weighs 39.7–79.4 lb (18–36 kg). It is 27.6 in (70 cm) at the shoulder. The wild dog has a distinctive spotted coat. Its short hair is divided into irregular yellow, black and white markings with each dog unique. The dark muzzle, large rounded ears and white tail tip are invariable.

DISTRIBUTION

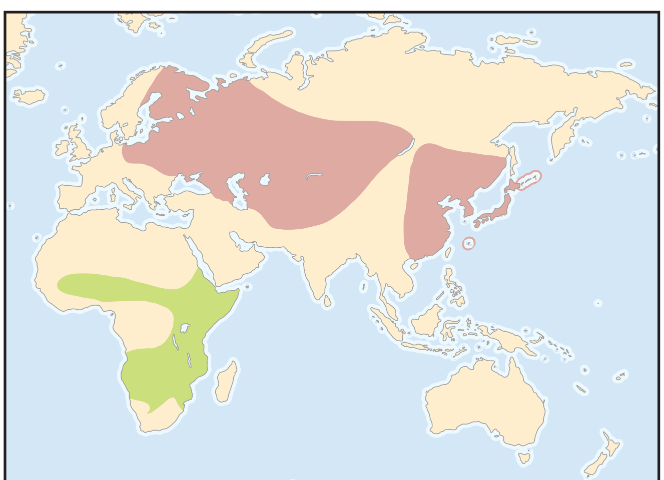
Formerly distributed throughout all of sub-Saharan Africa outside the equatorial forest zone, the species has been extirpated from most of western Africa and southern Africa. The species still survives over much of eastern Africa and parts of the Sahel but the viability of populations outside its strongholds in Tanzania and Botswana is unknown.

HABITAT

The species is most common in savanna and lightly wooded country, but it has the ability to live in a wide range of habitats from desert to mountain forest.

BEHAVIOR

The wild dog is the wolf of Africa but with a more extreme adaptation to pack living. Packs range from two to 30 with an average of six adults and a variable number of pups. Members of a pack spend 95% of their lives in sight or earshot of one another. Resting, which takes 60–85% of their lives, is often done in close contact. Packs are composed of related individuals. Males are more likely then females to stay in the pack where they were born and usually outnumber females in the population.



FEEDING ECOLOGY AND DIET

Predominant prey is small to medium sized antelopes from 22.0–132.3 lb (10–60 kg). Thomson gazelles, *Gazella thomsonii* (44 lb; 20 kg), and young wildebeests (*Connochaetes* spp.) are the chief prey in the open areas of eastern Africa. Impala, *Aepyceros melampus* (110 lb; 50 kg), are the staple food over most of the wooded areas of eastern and southern Africa. The species will take from the size of a hare (4.4 lb; 2 kg) to a zebra (441 lb; 200 kg). Packs hunt mainly in the mornings and evenings. In wooded areas, packs fan out and flush prey. In open areas dogs may slow and lay their ears back as they approach prey. The dogs run after fleeing prey at up to 35 mph (56 kph) for 3.5 mi (5.6 km). However, most chases are much shorter. Sick and gravid prey are vulnerable. The lead dog in the chase attempts to grab the hind leg of the prey. Once the animal is on the ground, it is quickly eaten.

REPRODUCTIVE BIOLOGY

Polyganorous, though there is a pair bond between the alpha male and alpha female in each pack. They rest together and are the only dogs to mark using a cocked leg. The alpha female produces pups annually with some seasonality especially in southern Africa. Subordinate adult females sometimes breed, but are seldom successful unless the pups of the dominant female die. Females produce an average of ten pups in an underground den after a gestation of 70–72 days. All members of the pack raise the pups; they regurgitate food while the young are still close to the den and later relinquish kills to the pups when the latter are able to follow the pack. Pups are not efficient hunters until 14–18 months. Survival through the first year is very low but larger packs tend to be more successful.

CONSERVATION STATUS

African wild dogs still have a wide distribution, but their population density is often very low. The total world population probably does not exceed 7,000. They do not survive well in competition with lions and hyenas and are susceptible to several diseases probably transmitted by domestic dogs. However, they are able to survive on very low prey densities in arid habitats. They are listed as Endangered by IUCN but much is unknown about their population status.

SIGNIFICANCE TO HUMANS

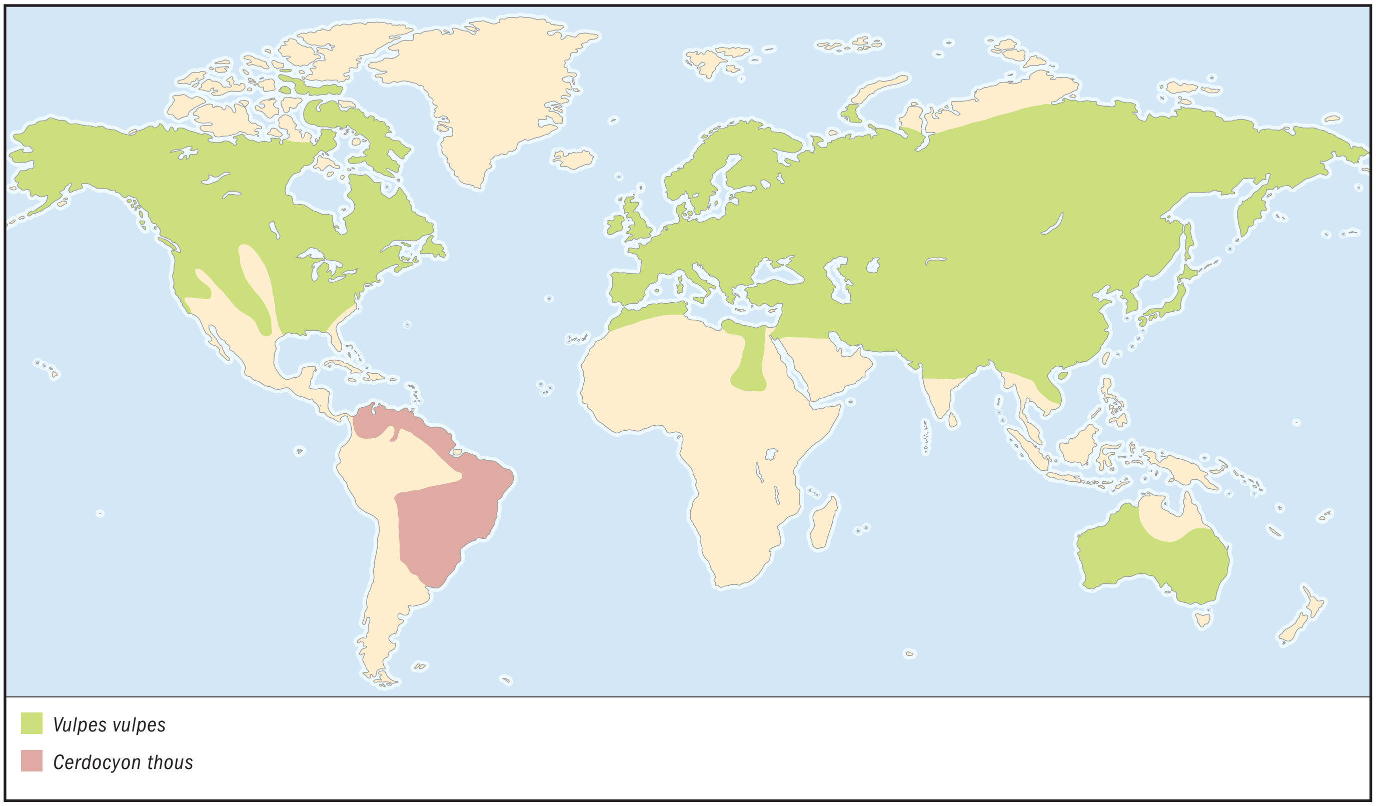
Wild dogs appear very rarely in rock paintings or folk tales suggesting that the species has never been common or an important part of the cultural landscape. In this century they have suffered the same fate as the wolf and been exterminated as a killer both of livestock and innocent prey populations. This attitude is changing although a wild dog extermination officer was employed by Namibia into the 1970s and pastoral people in many areas will kill the species on sight. In the Western world, its status as the wolf of Africa is providing kudos and protection. ◆

Red fox

Vulpes vulpes

TAXONOMY

Canis vulpes Linnaeus, 1758, Sweden. Forty-six races or subspecies have been recognized over the species' immense range.



However, much variation appears due to climate, with smaller, paler animals in the south, e.g. Egypt and larger, darker foxes in places like Alaska.

OTHER COMMON NAMES

English: Silver fox (a color morph used in the fur trade), cross fox (a dark, naturally occurring color morph); French: Renard; German: Fuchs; Spanish: Zorro.

PHYSICAL CHARACTERISTICS

The largest of the true foxes, the genus *Vulpes*, red foxes can weigh up to 24.3 lb (11 kg) but males in Europe average 14.8 lb (6.7 kg) while females weigh 11.9 lb (5.4 kg). The shoulder height is 13.8–15.7 (35–40 cm). The body color is almost always some shade of red but it can vary from bright to grayish. The belly is paler and the muzzle, legs and backs of the ears are black. The snout is long and the canines long and pointed, but the molars are not very large.

DISTRIBUTION

The red fox occurs across Europe and Asia as far south as the Himalayas. It is found in Egypt and Algeria in Africa, and in northern North America extending along the Rockies and to the Gulf Coast in the United States. It has been introduced into Australia and occupies all but the northern parts. It was also introduced in the eastern section of North America.

HABITAT

Red foxes are uncommon in densely wooded habitats, but otherwise show great flexibility in their habitats. They can live in semi-desert scrub in Africa and on the tundra in Alaska. They have adapted well to humans, foraging in towns and hunting in the areas cleared for agriculture.

BEHAVIOR

Red foxes are mainly monogamous and territorial. Often cubs will remain on the parental territory. These non-dispersers are usually female and may help with raising the next litter. Like most canids, red foxes remain playful for most of their lives and there are boisterous games of chasing and mock fighting among the pups, with the adults sometimes joining in.

FEEDING ECOLOGY AND DIET

Mammals, mainly rodents and rabbits, are the mainstay of the diet in most places. However, a wide range of vertebrate and invertebrate food is eaten including earthworms, beetles, the young of ground nesting birds, and human scraps. Lambs are found around red fox dens, but in many cases the victims are known to be sickly or stillborn. Red foxes use their ears to locate the rustle of a mouse in the grass and then launch themselves in a pounce to land on their prey. Other food items appear to picked up opportunistically as they traverse their territories at night.

REPRODUCTIVE BIOLOGY

Monogamous. Cubs are born after a 50 day gestation in an underground den, usually at the end of winter. Litter size is from three to 12 with seven typical in western Europe. The mother nurses the litter for four weeks. The cubs start to eat solid food regurgitated by the group starting at about three weeks. At 10–12 weeks, the young will start to forage on their own but their hunting skills will take nine to 12 months to develop. Most young disperse from six to 12 months.

CONSERVATION STATUS

Although persecuted for predation on game birds and livestock and hunted for fur, red foxes have continued to flourish and have colonized the urban habitat, often without the knowledge of the human inhabitants.

SIGNIFICANCE TO HUMANS

The fox is the sly trickster in the folklore of the Old World. The term "sour grapes" comes from Aesop's anthropomorphic fox. Predation of chickens has probably been going on for several thousand years, but the nineteenth century brought more conflict as game birds and lambs born in the fields provided food. Foxes have been persecuted by guns, hounds, and poison, but have seldom been exterminated. The sport of fox-hunting in England has ensured the survival of the quarry, and now that the sport is close to banned, the fox's range may contract. A vigorous campaign to control foxes in western Europe so as to limit the spread of rabies, has not eliminated the species. ◆

Blanford's fox

Vulpes cana

TAXONOMY

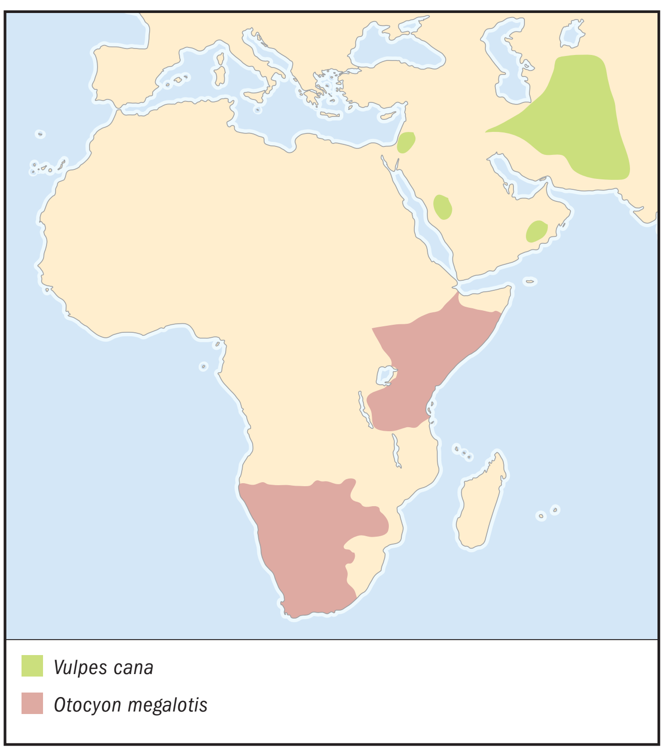
Vulpes cana Blanford, 1877, Pakistan. No subspecies recognized. Blanford's fox is a small but otherwise probably typical member of the desert foxes, a group of nine species all in the genus *Vulpes*, which live in the deserts of the Old World and North America. Genetic evidence shows that the fennec fox is Blanford fox's closest relative.

OTHER COMMON NAMES

English: Afghan fox.

PHYSICAL CHARACTERISTICS

The second smallest of the canids after the fennec, Blanford's fox weighs 2.2–3.3 lb (1–1.5 kg) and stands 10.6–11.8 in (27–30 cm) at the shoulder. Its bushy tail is 70% the length of the head and body, second only to Rueppell's fox in this category among the canids. The coat is a uniform sandy-gray with paler undersides and a dark band along the back. The tail tip is black. Shoulder height is 11.0–11.8 in (28–30 cm). The teeth are small but otherwise typical for the family with a shearing carnassial and grinding back molars.



DISTRIBUTION

The central part of the species range is in the central Asian steppes including Pakistan, northern Iran, Afghanistan, and parts of Turmenia. Since 1970 three outlying populations have been discovered in the Negev desert of southern Israel, in southwest Saudi Arabia and in Oman. With its small size and nocturnal habits, it is possible that other populations will be found in the deserts of the Middle East.

HABITAT

In the area where the species has been studied in Israel, it has a very precise habitat. It lives on rocky hillsides. It does not venture above 6,560 ft (2,000 m) and usually avoids the flat, flood plains of lower elevations.

BEHAVIOR

In Israel, pairs live in small territories averaging 0.6 mi^2 (1.6 km^2). A female from the previous litter often shares her parents' range. The species is strictly nocturnal, traveling about 5.6 mi (9 km) per night during eight hours of foraging.

FEEDING ECOLOGY AND DIET

The species eats mainly insects and fruits. In the Negev of Israel, beetles, ants, termites and grasshoppers were all snapped up together with dates and the fruits of other palms. In central Asia, olives are a staple food. Rats and mice are taken when encountered but constitute less than 10% of the diet. The species can survive without drinking water. Its fluid comes from its food and it has been calculated that the water provided by food may often be more important than the calories. Foraging is almost always solitary and consists of slow and systematic investigation stones and bushes in search on insects. The foxes dash after small vertebrates when flushed.

REPRODUCTIVE BIOLOGY

Monogamous. The species does not try to dig dens in its rocky habitat and the young are born in piles of boulders. The young survive on their mother's milk alone for the first two months of life. Although the male may be present at the den, there is no evidence that he regurgitates or regularly carries food to the young. An insectivorous diet does not make regurgitation practical. At eight weeks, the young start to forage with their parents and at three months they forage on their own.

CONSERVATION STATUS

Blanford's fox is seldom seen and has been considered one of the rare carnivores of central Asia. However is not clear if it is rare or just secretive. It appears to exist over a large range of at least 772 mi^2 (2,000 km^2), and is known to live close to humans. It is hunted in several areas. It is listed by IUCN as Data Deficient.

SIGNIFICANCE TO HUMANS

Blanford's fox is hunted for its fur in parts of Asia, but is often inconspicuous to humans. ◆

Bat-eared fox

Otocyon megalotis

TAXONOMY

Canis megalotis (Desmarest, 1822), South Africa. Two subspecies, *O. m. megalotis* from southwest Africa and *O. m. virgatus* from northeast Africa.

OTHER COMMON NAMES

French: L'otocyon; German: Loffelhund.

PHYSICAL CHARACTERISTICS

The bat-eared fox is a typically sized fox weighing from 4.9–9.9 lb (2.2–4.5 kg) and standing 11.8–15.7 in (30–40 cm) at the shoulder. The body is ash gray, paler below, with black at the extremities. The tail is bushy and the ears large. Its teeth are unique in the canids with a series of 32 cheek teeth, all with high cusps for puncturing insect exoskeletons.

DISTRIBUTION

The species exists in two separate areas, the southwest and northeast of Africa. These two areas of the continent have remained dry even during the wettest periods of the Pleistocene.

HABITAT

Bat-eared foxes prefer open short-grass habitat. They need soil in which they can dig holes for refuge and for breeding. They occur at lower densities in savannah woodlands and desert areas.

BEHAVIOR

Pairs or groups often rest in the vicinity of one another, and get together to play and groom each other at dusk. Almost all foraging occurs at night, and is done solitarily. Bat-eared foxes are preyed upon by eagles and mammals such as jackals and cheetahs. When above ground in the day, they keep a look out for raptors. Against mammalian predators they use a zig-zag run in which their large tail acts as a rudder. They seek refuge underground.

FEEDING ECOLOGY AND DIET

Termites and beetles (adults and larvae) are the principal food. Insect food is often detected by sound. The grazing termite, Hodotermes, makes a noise as it chews grass stems, and bat-eared foxes can hear the sound of termites foraging on the underside of ungulate dung and the noise of beetle larvae in a dung beetle ball. Mice and other small vertebrate prey will be snapped up if encountered and may be common in the diet when young pups are present.

REPRODUCTIVE BIOLOGY

The species is typically monogamous but dens with two breeding females are not uncommon. In some of these cases, it is known that a female pup from the previous year bred at her parents' den. Gestation is long for a fox, 60–75 days, and lactation is very long, from 14 to 15 weeks. Both of these modifications are related to an insect diet that provides a low but constant level of nutrition. Males do not regurgitate insects and hence play a small part in feeding pups. They do play a major role in guarding the pups, thus allowing the female a chance to forage so that she can produce milk. In another difference from other canids, bat-eared foxes are often non-territorial, with dens clustered in areas of suitable soil. Groups mingle on the foraging grounds. It seems that it is not worth expending energy keeping conspecifics from insect resources.

CONSERVATION STATUS

The bat-eared fox remains an inconspicuous but widespread inhabitant of dry areas in southwest and northeast Africa. It is not persecuted and has benefited from cattle ranching in southern Africa which creates short grass habitat, and grazing termites. Disease epidemics sometimes decimate local populations.

SIGNIFICANCE TO HUMANS

Together with all canids, bat-eared foxes can carry rabies but otherwise have no significant interactions with humans.

Raccoon dog

Nyctereutes procyonoides

TAXONOMY

Canis procyonoides (Gray, 1834), Canton, China. The raccoon dogs from the islands of Japan are consistently smaller than those of the mainland and have a different chromosome count as well as other genetic differences. Genetic analysis shows that the raccoon dog is an early independent offshoot from the main canid line.

OTHER COMMON NAMES

French: Chien viverrin; German: Marderhund.

PHYSICAL CHARACTERISTICS

The raccoon dog is a medium-sized canid. Its weight fluctuates markedly through the year. An average summer weight is 11.0 lb (5 kg) increasing to 16.5 lb (7.5 kg) before winter hibernation. It stands 7.9–9.8 in (20–25 cm) at the shoulder. The distinctive mask with a black muzzle and a broad white stripe across the forehead gives the species its common name. The very long coat makes the animal look stocky and barrel-like. Although its legs are not long in proportion to its body, they are not as short as those of several South American canids. The teeth are relatively small.

DISTRIBUTION

The original range of the species is the temperate lands of eastern Asia including China, Siberia, and Manchuria. It also inhabits the Japanese island chain. It was introduced to the USSR for fur farming in the 1920s and has spread widely. It is now found from Finland to Germany and east to the Himalayas.

HABITAT

The species lives in a variety of wooded and forested habitats. It prefers mixed woodlands and often uses water courses. It can tolerate some human encroachment.

BEHAVIOR

At high latitudes, the raccoon dog goes into a deep torpor during the winter, the only canid to hibernate. Groups of the animals sometimes occupy the same den for the winter. Individuals gain up to 50% of their body weight in the late summer and autumn. Males are usually the first to reach their hibernation weight with breeding females and young taking an extra month. Pairs occupy a common range although the degree of territoriality is not clear. Groups of raccoon dogs regularly gather at food sources, and breeding dens are sometimes clumped. The main source of mortality recorded for the species is predation by wolves and, less commonly, red foxes.

FEEDING ECOLOGY AND DIET
The species has a varied diet, although insects and mice are often the most common items. Like the raccoon (*Procyon spp.*), they regularly eat fish and other aquatic foods like frogs, snails, and crabs. In the summer they may eat berries and fruits.

REPRODUCTIVE BIOLOGY
Monogamous. Breeding occurs in the early spring. After a gestation period of 59–64 days, three to eight pups are born in an underground burrow, often an old badger den. The male plays a very active role in raising the pups both provisioning his mate and young and staying at the den to protect the family. The pups reach maturity at about a year.

CONSERVATION STATUS
Not threatened. The species appears to be continuing to expand its range in Europe. It has colonized much of the forested lands of Russia. In its native range it is still common in much of Japan. Information from other areas is sketchy, but it is known to be uncommon from areas of northern China that are now under industrial agriculture.

SIGNIFICANCE TO HUMANS
No fewer than 200,000 raccoon dogs are hunted annually for their fur and a large number are harvested on fur farms. It has been considered an omnivorous pest, like its namesake, the raccoon, as it has spread across Asia. However, even in densely populated Japan, it has remained largely inconspicuous. ◆

Maned wolf
Chrysocyon brachyurus

TAXONOMY
Canis brachyurus (Illiger, 1815), Paraguay. No subspecies are recognized. The maned wolf is genetically distinct from most of the other South American canids.

OTHER COMMON NAMES
German: Mahned wolf; Spanish: Lobo de crin, lobo guara.

PHYSICAL CHARACTERISTICS
Maned wolves, at 29.1–34.2 in (74–87 cm) at the shoulder, stand taller than all but the largest gray wolves, but at 44.1–50.7 lb (20–23 kg), they weigh less than half that of most wolves. They have the longest legs in proportion to their spine of any canid. Their skulls and teeth are not dissimilar from those of coyotes with long, fine canines. Their coat color is a distinctive golden red with dark hairs on the back of the neck creating a small mane. The lower legs are black and the throat and often much of tail is white.

DISTRIBUTION
The species occurs in the southern two-thirds of Brazil, extending south and west into Uruguay, Paraguay, eastern Bolivia, and northern Argentina.

HABITAT
The species can live in a variety of habitats outside the rainforest. However, it appears that its long legs evolved for life in the grasslands and pampas. It can survive in areas of mixed farming and will forage in lightly wooded areas.

BEHAVIOR
The maned wolf is probably the most solitary of the canids. Males and females appear to share a defended territory of up to 12 mi^2 (30 km^2), but interactions between the pair are said to be very uncommon. Their bold white markings on the tail and throat allow visual signals to be communicated at a distance as does the harsh bark and typical patterns of marking by urine and feces. Maned wolves may leave feces high up on rocks and termite mounds.

FEEDING ECOLOGY AND DIET
The only comprehensive study of diet showed that most abundant food was the fruit of a bush related to the tomato. Overall plant and animal material were equally common with rats and mice, birds and lizards also taken. The species has a reputation for eating chickens. Almost all foraging is done from dusk to dawn.

REPRODUCTIVE BIOLOGY
Monogamous. Breeding is very seasonal with a small litter size of 2–6 young. The pups are born in a protected site above ground, in a rock crevice or thick bush. The species long legs may make it hard to dig. The role of the male in helping to raise the young in the wild is still not clear. Usually only a single animal is seen with the young. In captivity however, male maned wolves will provision young. It takes about a year for the young to develop to their full height.

CONSERVATION STATUS
Although the range of the species is large, it seems that they live at very low population densities. With an estimate of only one wolf per 116 mi^2 (300 km^2), the world population may be under 3,000. The species is persecuted for raiding hen houses, and does not live in areas of intensive settled agriculture. On the positive side, it has been able to colonize areas where forests have been recently cleared. Although officially protected and recognized as endangered in its native lands, it is listed only as Lower Risk/Near Threatened by the IUCN.

SIGNIFICANCE TO HUMANS
The maned wolf is usually uncommon with only minor significance to humans. ◆

Crab-eating fox
Cerdocyon thous

TAXONOMY
Canis thous (Linnaeus, 1766), Surinam. This species is quite similar to the more widespread genus of South American canids, *Dusicyon*, and has been included in the latter genus on several occasions. Molecular evidence is needed to resolve this issue. Fossil *Cerdocyon* from North America probably represent a colonization from South America. Five subspecies have been erected but are not well defined.

OTHER COMMON NAMES
English: Common fox, forest fox; Spanish: Zorro comun, zorro sabanero, zorro perro.

PHYSICAL CHARACTERISTICS
A medium sized canid weighing about 11.0 lb (5 kg) (range: 6.6–19.8 lb [3–9 kg]), *Cerdocyon* has relatively short legs (second only to the bush dog amongst the canids in its ratio of forelimb to body length). The hair is pale gray with black hair tips. A reddish tinge on the belly and flanks is also common. The skull dimensions best represent the average skull for the family falling in the middle of a multi-variate plot.

DISTRIBUTION
Crab-eating foxes occupy a large area of eastern South America from Venezuela in the north to northern Argentina in the south. They do not occur in the densest parts of the Amazon forests.

HABITAT
The species occupies a wide range of habitats. They are most common in "edge" habitats with a mixture of woodlands and open country. They can also survive in closed-canopy forests and grassland. However, they do not occupy more open country if *Dusicyon gymnocercus*, Azara's fox, is present in that habitat. They live in the seasonally flooded areas of Amazonia but not the thick forests.

BEHAVIOR
The species is monogamous and pairs live in territories, which are marked by the pair with urine and feces. Territories can be as small as 0.2 mi^2 (0.5 km^2) and as large as 3.9 mi^2 (10 km^2) in less productive areas. In the seasonally flooded Llanos ranges shift and are less rigorously defended in the wet season when food is abundant. Pairs use a loud whistling vocalization to reunite.

FEEDING ECOLOGY AND DIET
The species forages at night and solitarily. They are omnivorous with a very varied diet. During the dry season in Venezuela 48% of the diet is vertebrates with 31% land crabs. During the wet season 54% of the diet is invertebrates, mainly beetles and grasshoppers, and small mammals make up 20%. Fruit and carrion form the remainder of the food. Frogs, lizards, mushrooms, and snails have also been found in stomachs.

REPRODUCTIVE BIOLOGY
Monogamous. Breeding occurs once a year in the wild, but is not strictly seasonal. (In captivity females can produce a litter every eight months, and reproduction does not seem to be tightly linked to patterns of daylight length.) Litter size varies from two to six with an average of four after a gestation of 52–59 days. Both parents provision the young and pups start to forage on their own around four months. Dispersal occurs from six to nine months.

CONSERVATION STATUS
The species remains widespread. It can colonize areas of cleared forest and can live close to human settlement. Like almost all canids it is hunted, but its fur is not useful.

SIGNIFICANCE TO HUMANS
The crab-eating fox is usually inconspicuous. It may kill chickens but is not of great significance to humans. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Arctic fox *Alopex lagopus* Spanish: Zorro polar	Two color phases, white and blue. Head and body length 18–26.6 in (45.8–67.5 cm), tail length 10–16.7 in (25.5–42.5 cm).	Mainly in alpineand arctic tundra, usually in coastal areas. Makes den in low mounds with 4 to 12 entrances. Seasonal movements associated with food availability.	Circumpolar, entire tundra zone of the Holarctic, including most of the Arctic islands.	Any human food, dead or alive, carrion, marine mammals, invertebrates, sea birds, and fish. Predator of the ringed seal in winter and lemmings when on land.	Not threatened
Short-eared dog *Atelocynus microtis* Spanish: Zorro de orejas cortas	Upperparts dark gray to black, underparts rufous mixed with gray and black. Thickly haired, black tail. Head and body length 28.3–39.4 in (72–100 cm), tail length 9.8–13.8 in (25–35 cm).	Tropical forests from sea level to about 3,280 ft (1,000 m). Males dominant in most activities.	Amazon, upper Orinoco, upper Parana basins in Brazil, Peru, Ecuador, Colombia, and probably Venezuala.	Nothing is known about the food habits of this species in the wild. Observations suggest a carnivorous diet, although may eat fruit in the wild if prey is scarce.	Data Deficient
Side-striped jackal *Canis adustus* Spanish: Chacal de dorso franjeado	Coat is long, soft, partially mottled gray. Each side of body is lined with white hair, followed by line of dark hair. Underparts and tip of tail are white. Head and body length 25.6–31.9 in (65–81 cm), tail length 11.8–16.1 in (30–41 cm).	Moister parts of savannas, thickets, forest edge, cultivated areas, and rough country up to 8,860 ft (2,700 m) in elevation. Strictly nocturnal. Social groups are well spaced. Litters consist of 3 to 6 young.	Open woodland and semi-arid grassland from Senegal to Ethiopia, south to northern Namibia, northern Botswana, Zimbabwe, Mozambique, and northern South Africa.	Consists of various types of invertebrates, small vertebrates, carrion, and plant material.	Not threatened
Black-backed jackal *Canis mesomelas* Spanish: Chacal de lomo negro	Dark saddle on length of back to tip of tail. Sides, head, limbs, and ears are rufous. Underparts pale ginger. Slender build, very large ears. Head and body length 26.8–29.3 in (68–74.5 cm), tail length 11.8–15 in (30–38 cm).	Dry grassland, brushland, and open woodland. Basic social unit is mated pair and their young. About four young per litter.	Africa, south of the tropical rainforest in the west and as far north as Ethiopia and Sudan in the east.	An important predator of sheep.	Not threatened
Dhole *Cuon alpinus* Spanish: Dolo	Upperparts are rusty red, underparts pale, tail tipped with black. Head and body length 34.6–44.5 in (88–113 cm), tail length 15.7–19.7 in (40–50 cm).	Many types of habitat, but avoids deserts. Alpine areas, dense forest, and thick scrub jungles are a few. Hunts in packs. Five to 10 individuals within a pack.	Southern Siberia and central Asia to India and the Malay Peninsula, and on the islands of Sumatra and Java, but not Sri Lanka.	Mainly mammals larger than itself, including deer, wild pigs, mountain sheep, gaur, and antelope.	Vulnerable

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Falkland Island wolf *Dusicyon australis* Spanish: Zorro de las Malvinas	Upperparts are brown, some rufous and speckles of white. Underparts pale brown. Coat is soft and thick. Tail is short, bushy, tipped with white. Head and body length 38.2 in (97 cm), tail length 11.2 in (28.5 cm).	Found 250 mi (400 km) away from mainland, on islands. Very tame toward humans. Little is known.	Falkland Islands.	Consists mainly of birds, especially geese and penguins, as well as pinnipeds.	Extinct
Pampas fox *Pseudalopex gymnocercus* Spanish: Zorro gris mayor	Coloration is pale yellow, underparts and back are gray. Head, neck, and large ears are reddish. Muzzle is black. Long, bushy tail with two black spots. Throat and belly are whitish. Head and body length 24.4 in (62 cm), tail length 13.4 in (34 cm).	Pampas grasslands, hills, and deserts. They prefer plains and fields with tall grass, sierras, small narrow woods, and areas along streams.	Argentina, north of Rio Negro, Paraguay, Uruguay, southern Brazil, and eastern Bolivia.	Rodents of all kinds, birds, rabbits, frogs, lizards, fruit, and other vegetable matter like sugar cane stalks.	Not threatened
Culpeo *Pseudalopex culpaeus* German: Andenschakal; Spanish: Zorro colorado	Size increases the farther south the range is. Males are larger than females. Coloration is brownish tawny, underparts are paler. Back is gray, tail is tipped with black.	Pampas grasslands and deciduous forests of their range. Hierarchical matriarchal society. Mating period is from August to October. Strong hierarchical sense in social groups.	From Tierra del Fuego through the Andes of Chile and Argentina to the highlands of Bolivia, Peru, Ecuador, and Colombia.	Rodents and lagomorphs (rabbits and hares), as well as lambs a week old and younger.	Not threatened
Bush dog *Speothos venaticus* Spanish: Perro vinagre	Coloration is ochraceous fawn or tawny into dark brown or black on back and tail. Underparts are dark with a light patch on chin and throat. Stocky body, short, with broad muzzle. Tail is short. Head and body length 22.6–29.5 in (57.5–75 cm), tail length 4.9–5.9 in (12.5–15 cm).	Forests and wet savannas, often near water. Mainly diurnal, semi-aquatic. Litter of two to three individuals are produced during the rainy seasons.	Forested areas of Bolivia, Paraguay, and Brazil (except the semiarid northeast), eastern Peru, Ecuador, Colombia, Venezuela, Guyana, French Guiana, Suriname, and Panama.	Mainly large rodents.	Vulnerable
Gray fox *Urocyon cinereoargenteus* Spanish: Zorro gris plateado	Underparts are gray or white, ventral parts are rusty. Tail is tipped in black and the pelage is coarse. Head and body length 19–27 in (48.3–68.5 cm), tail length 10.8–17.5 in (27.53–44.5 cm).	Wooded and brushy country, often in rocky or broken terrain. Prefer pine-oak woodland bordering fields. Frequently climbs trees. Mostly nocturnal.	North America from Oregon, Nevada, Utah, and Colorado in the West and the USA-Canadian border in the East through Central America to northern Colombia and Venezuela.	Many kinds of small vertebrates, insects, and vegetable matter.	Not threatened
Island fox *Urocyon littoralis* Spanish: Zorro gris isleño	Underparts are gray, ventral parts are rusty. Head and body length 18.9–19.7 in (48–50 cm), tail length 4.3–11.4 in (11–29 cm).	Wooded and brushy country, often in rocky or broken terrain. Prefer pine-oak woodland bordering fields. Frequently climbs trees. Mostly nocturnal.	Islands off the Pacific Coast of southern California, United States.	Many kinds of small vertebrates, insects, and vegetable matter.	Lower Risk/ Conservation Dependent
Tibetan fox *Vulpes ferrilata* English: Tibetan sand fox; Spanish: Zorro tibetaño	General coloration of upperparts is gray or sandy, underparts pale. Tip of tail is white. Head and body length 22.6–27.6 in (57.5–70 cm), tail length 15.7–18.7 in (40–47.5 cm).	Barren slopes and in stream beds at 9,840–13,120 ft (3,000–4,000 m) in the Mustang District of Nepal. Dens are made of boulders. Two to five young born a year.	China, in Tibet, Tsinghai, Kansu, and Yunnan; and Nepal.	Consists of rodents, lagomorphs, and ground birds.	Not threatened
Corsac fox *Vulpes corsac* Spanish: Zorro corsac	Fur is thick, soft, generally pale reddish gray, underparts are white or yellow. Head and body length 19.7–23.6 in (50–60 cm), tail length 9.8–13.8 in (25–35 cm).	Steppes and semi-desert. Lives in a burrow. Mainly nocturnal activity, but has been seen by day. Nomadic, does not keep fixed home range. Very social.	Kazakhstan, Russia, central Asia, Mongolia, Transbaikalia, northeastern China, and northern Afghanistan.	Consists mostly of small rodents, but also pikas, birds, insects, and plant material.	Data Deficient
Swift fox *Vulpes velox* English: Kit fox; Spanish: Zorro veloz	Coloration of upperparts is dark buffy gray, underparts are buff to pure white. Coat is redder in summer. Head and body length 14.8–20.7 in (37.5–52.5 cm), tail length 8.9–13.8 in (22.5–35 cm).	Prairies, especially those with grasses of short and medium height. Builds burrows for shelter. Primarily nocturnal.	Central North America from southeastern British Columbia, south-central Alberta and southwestern Saskatchewan (Canada) to northwest Texas (panhandle) and eastern New Mexico, east of Rockies (United States).	Consists mostly of lagomorphs, as well as rodents, birds, lizards, and insects.	Lower Risk/ Conservation Dependent

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James Malcolm, PhD

Dogs and cats

Dogs

Wolves, the ancestors of today's domestic dog, are social creatures who cooperate with each other to hunt down prey. These social and hunting skills of course proved useful for eventual cohabitation with humans. *Canis familiaris*, the domestic dog, has been living with humans for a long time: longer than cats, longer than horses, longer than any other animal. While some might argue that the dog is no longer man's best friend, having been supplanted in popularity by the cat, it's a safe bet that dogs are man's oldest friends.

The domestication of the dog

But just when and where were dogs first domesticated? A series of three articles published in *Science* (November 2002) shed a great deal of light on the domestication of dogs. One of these studies, by Peter Savolainen and his Swedish and Chinese coworkers, suggest that dogs were first domesticated somewhere in east Asia about 15,000 years ago. Savolainen and his co-researchers compared mitochondrial DNA samples taken from over 600 domestic dogs throughout the world. It takes time for variability to develop in DNA samples. Therefore, the greater the DNA variability, the longer that type of animal has existed. Although all of the sampled dogs shared a common gene pool indicating a common ancestry, East Asian dogs exhibited the greatest variability in DNA, suggesting that dogs have lived there longer than anywhere else in the world.

By estimating how long it would take for these changes in DNA to occur, Savolainen theorized that dogs became domesticated about 15,000 years ago. Although this seems like quite a long time, other researchers had estimated that domestication had occurred as far back as 135,000 years ago. Savolainen admits that a different interpretation of his data could lead to the conclusion that domestication of dogs in east Asia occurred 40,000 years ago, a much longer time frame, but still much less than 135,000 years.

A second study focused on DNA samples taken from domestic dogs who lived in the Old and New World, including samples taken from dog bones of canids that had died before the arrival of Europeans in the Western hemisphere. Based on their results, Jennifer Leonard and her colleagues concluded that New World dogs are not the descendants of local wild species but are instead related to Old World wolves and arrived in the Western Hemisphere 10,000 to 15,000 years ago, when they traveled together with humans over the Bering Strait land bridge.

Interestingly, DNA taken from contemporary New World species, such as the Mexican hairless, show that modern New World dogs are descended from canines that traveled over from Europe, not from pre-Columbian New World dogs. Leonard did not find why the descendants of the dogs that crossed the Bering Strait apparently died out within the last 500 years and were supplanted by the descendants of more recent immigrant European dogs.

The third of the studies reveals that domestic dogs have evolved in their abilities to understand human cues. Brian Hare and his colleagues compared the ability of adult domestic dogs, domestic puppies, adult wolves, and chimpanzees to interpret signs given by humans to communicate the location of food. In one experiment, for example, a human would indicate which one of two containers had food by reaching for, looking at, or putting a wooden block on the full container. (It was ensured that the dogs were not tipped off by scent.) Nine of the 11 dogs picked up the hint, but only two of the eleven chimpanzees.

Another experiment focused on the ability of domestic puppies who were nine to 26 weeks old to read human cues. Even those puppies who had been raised in litters and had only been exposed to humans for a few minutes daily were able to pick up on human cues as to where food had been hidden.

Other research from Siberia suggests that the transformation from wild canid to domestic dog may have taken far less time than originally thought. Since 1959, researchers have selectively bred *Vulpes vulpes*, the silver fox, to produce tame animals. Although it has been conducted for less than 50 years, this study has already produced impressive results. The foxes not only are tamer, but 70–80% lick and smell the human experimenters just like domesticated dogs, and will even whimper for attention.

The behavior of these foxes is not the only thing that has changed. They also are starting to develop different physical characteristics. Their tails are shorter, their ears more droopy, and they have white splotches of fur. These types of physical

This retriever has been trained to retrieve birds shot by hunters. (Photo by J. E. Swedberg. Bruce Coleman, Inc. Reproduced by permission.)

variations have also occurred in domestic dogs. Another interesting characteristic has been noted in these tamed foxes that may be related to change in behavior: their brains have higher levels of serotonin, a neurotransmitter which may be linked to reduced aggression.

Some of these fox pups have been taken out of the study and raised in the experimenters' homes. One describes these pets as being "good-tempered creatures, as devoted as dogs but as independent as cats, capable of forming deep-rooted pair bonds with human beings."

The spread of dogs over the world

Relatively little is known about the spread of dogs throughout the world although, as mentioned above, many researchers now theorize that dogs spread through the New World by following humans over the Bering Strait land bridge and then across North and South America. The earliest physical indication that dogs lived with humans has been found in Israel, where the 12,000-year-old remains of a woman holding a puppy in her hands has been found. Whether it's a dog or wolf pup is not known, but it does suggest that some sort of relationship existed between humans and canines.

Dogs and humans

In spite of their usefulness as work animals, dogs have not been universally valued to the same degree. Ancient Greeks and Romans sometimes sacrificed dogs, and dogs are still used as a food source in the Far East. The Bible mentions dogs about thirty times, but only two of these references are not derogatory. Islam also takes a dim view of them as being unclean. Work dogs do exist in Arabic countries but are typically viewed as animals to be used for a specific function, not as pets or companions.

Hinduism, on the other hand, perhaps because reincarnation is an integral component of its core beliefs, offers a more positive view of dogs. A delightful story in the *Mahabharata*, a 2000-year-old classic of Indian spirituality, relates the attempted entry of Dharmaputra into heaven. Dharmaputra, one of the main characters in this epic, wants to take his dog with him. Heaven's gatekeeper refuses to let the dog enter into heaven. Dharmaputra then refuses to go in without his dog. At this point, the dog turns into the Lord Krishna who had only been pretending to be an animal, an ending with which many dog lovers could identify.

Dog breeds

Although most of the breeds currently in existence are relatively new, dating back a few centuries at most, the initial differentiation into breeds evidently occurred thousands of years ago. Fossil remains indicate five different types of dog dating back to approximately 4500 B.C.: hunting dogs, sheepdogs, wolfish guard dogs, mastiff-type draft and guard dogs, and greyhound-type sight dogs.

Today, the variety of dogs is staggering. A Yorkshire terrier weighs only about 4–7 lb (1.8–3.2 kg), is 9 in (23 cm) tall, and is smaller than many cats. Mastiffs, however, typically weigh up to 190 lb (86 kg) and are 30 in (76 cm) tall.

Interestingly, both breeds originated as work dogs. The Yorkshire terrier was developed by English miners in Yorkshire who wanted a dog that would attack rats but was small enough to be carried in a pocket. Mastiffs, on other hand, go back about 2,000 years and were used by militaries.

Today, of course, dogs are extremely popular throughout much of the world. The increasing number of dog breeds is a reflection of this popularity. Out of an estimated 400 breeds of dog, the American Kennel Club recognizes about 150, forming eight groups of dog breeds: sporting, hunting, working, terrier, toy, nonsporting, herding, and miscellaneous.

Some of these groups are related to the roles that dogs have played in human society. Sporting dogs, such as pointers and retrievers, have been used to help in hunting and are still used for this purpose. These dogs are energetic and need regular exercise. Hounds have also been used for hunting. Some breeds have been used for their sense of smell in following the trail of their quarry, others for their ability to run down prey, and all have a unique vocalization (baying). Beagles and Afghans are two types of hounds.

Herding dogs, as their name indicates, have been used to herd animals. Border collies and German shepherds are two

Dogs have been trained as helpers to assist humans, such as this man in a wheelchair. (Photo by Carolyn A. McKeone/Photo Researchers, Inc. Reproduced by permission.)

popular breeds. Working dogs tend to be large animals and have been used to help humans by performing tasks other than hunting. Some are guard dogs, others have pulled sleds. Doberman pinschers, great Danes, and Siberian huskies are working dogs.

Toys are at the other end of the size continuum. Pekinese, poodles, and Yorkshire terriers all belong to the toy group. While some of these animals have been work animals, such as ratters, others have been bred as companion animals. Terriers were bred to control rodents, somewhat like a canine version of the cat. There are about two dozen or so recognized breeds.

The nonsporting group includes recognized breeds that do not fit into any of the above groups. They range from the Bichon frise, which weighs about 10 lb (4.5 kg), to the Dalmatian, which weighs in at about 50 lb (23 kg). Their backgrounds are similarly varied. The bichon frise started out as a pet of European royalty and became a circus performer after it fell out of favor, while Dalmatians have been used for everything from guarding and shepherding to being the mascot of fire fighters. The miscellaneous group currently consists of seven breeds which do not quite as yet meet the American Kennel Club's requirements for fully recognized breeds.

Cats

The domestication of cats

Although cats have not been domesticated for as long as dogs, felines have lived with humans for thousands of years. The earliest indication that cats may have lived with people dates back approximately 10,000 years. A cat's tooth from 9000 B.C. was found in the remains of a settlement in Jericho, Israel.

The next oldest remain dates back to about 5000–6000 B.C. in Cyprus, where the remains of cats and humans have been found in the same area. Since cats are not native to this Mediterranean island, it is assumed that humans brought cats there. Not surprisingly, the remains of rodents were also found at this site, suggesting that humans were using cats to control pest populations at that time.

The domestic cat's (*Felis catus*) whiskers are extremely sensitive, which enables it to easily locate prey. (Photo by © Pete Saloutos/Corbis. Reproduced by permission.)

It is not definitively known which species of wild cat is the ancestor of *Felis catus*, the domestic cat. *Felis silvestris libyca*, the Libyan wild cat, lived in Egypt and many experts have suggested that this wild cat is the ancestor of *F. catus*. A few others, however, have suggested that domestic cats are descended from *Felis chaus*, a jungle cat, or from cats native to Persia or Nubia. However, many experts agree that *F. silvestris* is the ancestor of today's domestic cats, and most come down on the side of *F. silvestris libyca*.

The ever closer relationship between humans and cats seems to have been an accidental offshoot of a mutually beneficial relationship. There was apparently no conscious attempt at breeding the domestic cat, but wild cats were encouraged to live in and around human settlements. Humans would deliberately leave out food for them and sometimes raised kittens, resulting in cats that were less afraid of humans than their wild parents.

Over a period of time, cats became incorporated into Egyptian life and were given the onomatopoeic name (a name that sounds like the sound an animal makes) *miu*. Eventually, cats and humans coexisted along the Nile River, but it is hard to decipher when cats became completely domesticated, and some might argue that cats are not completely domesticated even today.

While cats initially performed a strictly functional role in Egyptian society as mousers, Egyptians gradually started to become more emotionally attached to cats, and even reverential toward them. Many statues and drawings of cats have been unearthed, suggesting their importance to ancient Egyptians. Some of these relics even feature cats adorned with jewelry.

Along with human and other animals, cat mummies have been found in Egyptian tombs. The evidence indicates that these cats were ritualistically killed, sometimes by breaking their necks, and then embalmed. By the fifth century B.C., Egyptians were so attached to their cats that the Greek scholar Herodotus wrote that they would pluck their eyebrows in mourning when a household cat died of natural causes. Eventually, Egyptians viewed cats as being sacred creatures. Cats were associated with the goddess Bastet. Bastet sometimes was depicted as wholly feline but often had the body of a woman and the head of a cat. She was associated with fertility, joy, and beauty. Many cats lived at her largest temple in the city of Bubastis and thousands of mummies of cats have been unearthed in excavations around this ancient city.

Killing cats (outside of ritualistic events which produced the afore-mentioned mummies) eventually became a capital crime in Egypt. The historian Diodorus Siculus recorded one such incident, which resulted in a lynching.

> "Whoever kills a cat in Egypt is condemned to death, whether he committed this crime deliberately or not. The people gather and kill him. An unfortunate Roman, who had accidentally killed a cat, could not be saved, either by King Ptolemy of Egypt or by the fear which Rome inspired."

Although Egypt tried to prevent the export of cats to other countries, their usefulness as mousers led to their spread elsewhere around the Mediterranean and, eventually, throughout the world. The two great epics of Hinduism, the *Ramayana* and the *Mahabharata*, which were written about 300 B.C., both mention cats, indicating that cats came to India well over 2,000 years ago.

It is not clear when cats first arrived in Europe, although they spread throughout the continent during the time of the Roman Empire, reaching into northern Europe by about A.D. 100.

It took a while for domestic cats to become established in North America, although at least one cat traveled on the Mayflower with the Pilgrims in 1620 and Jesuits brought some cats with them to Quebec back in the sixteenth century. However, cats did not become popular in the Americas until the eighteenth century, when they were imported into Pennsylvania for the very same reason they had become popular in Egypt thousands of years earlier—to control rodents.

While humans have primarily developed a relationship with domestic cats, their ability to hunt rodents and other pests resulted in the use of wild cats as work animals. Cheetahs, for example, have been used as hunting companions in parts of Africa and Asia, in a role similar to what falcons performed in European countries. Sometimes, however, wild cats were used in particularly gruesome situations. The use of lions and other wild cats as a public means of execution in ancient Rome is well-known.

The evolution of the domestic cat

Cats have gradually changed as they became domesticated. Obviously, they are tamer. They are also more tolerant, not just of people, but of other cats. That is why a household can have more than one cat, although anyone who shares a home with multiple cats can vouch that even domestic cats can still be quite territorial. Still, while it may take some coaxing, domestic cats can learn to live together, which is not the case for their wild cousins.

Not dependent on hunting to stay alive, domestic cats have also developed smaller bodies, teeth, and jaws than their wild cousins. Their senses of smell, hearing, and sight are not as well developed. And as camouflage in the natural environment became unimportant for an animal living with humans, the color of cats' coats changed, typically into either a solid coat of one color or a combination of solid colors and/or stripes. One breed of domestic cat, the Egyptian mau, is spotted. Also, while many cat lovers may disagree, there is evidence that domestic cats have a smaller brain capacity than their wild cousins.

The typical adult domestic cat is rather small, weighing 8–25 lb (3.6–11 kg). As domesticated cats spread over the globe, they eventually developed into different breeds. Cats, however, lack the great variety of breeds found in dogs and have never been bred to fill distinct working roles (e.g., hunting, guarding, herding) as is true for dogs. The number of cat breeds is increasing and as of 2003, The Cat Fanciers' Association recognizes 39 breeds of domestic cat ranging from the Abyssinian to the Turkish van.

Cats and humans

While always valued for their usefulness in hunting rodents and other pests, cats have not been viewed with affection in all societies. For example, during the Middle Ages, cats became associated with witchcraft, first in Christian countries in Europe and then in America. In 1494, Pope Innocent VIII declared that witches could take the form of animals such as cats.

Islamic countries, however, have traditionally viewed cats in a positive light. Mohammed is reported to have been particularly fond of cats. One popular story relates that when a cat fell asleep while lying on Mohammed's garment, the Prophet cut off the sleeve so he would not disturb the sleeping cat when he had to stand up.

Cats and wildlife

Domestic cats are hunters. They will prey upon wildlife even when they are fed and cared for by humans. If not controlled, cats can have a disastrous effect on local birds. For example, their introduction to the California Channel Islands and northwestern Baja California resulted in the elimination of three local populations of seabirds and the extinction of the Guadalupe storm-petrel (*Oceanodroma macrodactyla*). One researcher has estimated that cats kill approximately 39 million birds—just in the state of Wisconsin—each year.

Control is difficult. While "belling the cat" is a traditional strategy, cats can eventually figure out how to move without making the bell ring out. It is possible that an electronic alarm will be developed that would intermittently go off as a warning to potential prey.

Popular pets

According to the American Pet Products Manufacturers Association 2001–2002 National Pet Owners Survey, there are an estimated 73 million pet cats in the United States. About one out of every three households has at least one cat and, on average, have two cats. Males and females are equally popular and about 80% of all household cats are spayed or neutered.

Dogs currently are just slightly less popular than cats. Although more households (four out every ten) have a dog than a cat, most households have only one dog, resulting in about 63 million pet dogs in the United States. Dogs are slightly less likely to be spayed or neutered than cats.

The importance of spaying and neutering is emphasized by some statistics provided by the Humane Society of the United States. A female cat can have an average of three litters every year, with an average of four to six kittens per litter. Cats typically live up to 15 years and become sexually mature by the time they are a year old. Theoretically, under ideal conditions, a single female and all of her offspring could produce 420,000 cats in just seven years. Even under normal conditions, unspayed and unneutered cats can produce a huge number of kittens with nowhere to go but the local animal shelter.

Pets used in conjunction with treatment can reduce the length of time in the hospital. (Photo by © Tom & Dee Ann McCarthy/Corbis. Reproduced by permission.)

These dogs scent out the quarry and lead the chase for a hunting party. (Photo by Ernest A. Janes. Bruce Coleman, Inc. Reproduced by permission.)

Dogs are not as prolific as cats, but they still can easily overbreed. A dog can have two litters every year and there are typically six to eight puppies per litter. So one female and her offspring could, theoretically, produce 67,000 dogs in six years.

Of course, cats and dogs do not have anywhere near that many offspring, but pet overpopulation is a serious problem. It has been estimated that there are 30 million feral cats in the United States and that six to eight million cats and dogs are dropped off at shelters every year. Approximately three to four million of these animals are euthanized.

Although cats still know how to hunt, life is much more difficult for feral cats than it is for pets. It has been estimated that the typical feral cat lives for only three years and that 42% of feral kittens die before they are two months old.

Organizations have sprung up in various parts of the country to trap, sterilize, and then release feral cats in order to reduce euthanasia of cats and to protect local wildlife. One such group, the Feral Cat Coalition of San Diego, California, claims that the number of cats euthanized at local shelters decreased by almost 50% between the start of its trap-neuter-release program in 1992.

Dogs, cats and people: an evolving relationship

Dogs and cats have been used as work animals ever since they first associated with humans. While cats have primarily been used exclusively to hunt rodents and pests, dogs have filled a much wider variety of roles in human society.

Sighthounds, dogs that hunt prey primarily by using their sense of sight, have existed for thousands of years. The saluki has been bred in the Middle East for at least 5,000 years and mummified salukis have been found in Egypt. Unlike other dogs, salukis are not viewed as being "unclean" in the Arabic world.

Scenthounds also are hunters but are used for their well-developed sense of smell. These dogs were bred to find prey, but some have no interest in catching quarry once they have found it. Scenthounds often have other characteristics, such as droopy, long ears which form air currents, making it easier for these dogs to pick up scents.

Terriers are a specialized form of hunting dog. Small and low to the ground, terriers have been used to hunt small mammals, such as foxes, and to keep down the pest population around homes and farms.

Herding is another traditional job for dogs. Some herding breeds have been around for millennia. The corgi, for example, is estimated to have arrived in Great Britain anywhere from 1,000 to 3,000 years ago. Many other breeds, such as the giant schnauzer and the Old English sheepdog, were herding animals hundreds of years ago.

Although it is not known how these older breeds were created, some of the more recently developed herding breeds involved a careful mix of breeds to produce just the right characteristics needed for herding animals under specific situations. Ancestors of the Australian cattle dog, for example, include collies, dingos, Dalmatians, and kelpies, resulting in a dog that could herd cattle under the often harsh conditions found in Australia.

Guard dogs have a similarly long association with humans. The Portuguese watchdog guarded sheep in Portugal back in the Middle Ages. Today, dogs such as the rottweiler are still used as guard dogs but are frequently used to protect people and property in homes and businesses, instead of livestock on ranches and farms.

Siberian huskies have been used for centuries to pull sleds across the snow. (Photo by © James Marshall/Corbis. Reproduced by permission.)

Unfortunately, these dogs sometimes also had another role, especially when times were tough for their human companions. In addition to guarding livestock, they were sometimes viewed as livestock themselves. The chow chow, for example, was considered to be a particularly tasty breed.

Draft dogs worked as miniature horses, pulling carts and sleds. These dogs, not surprisingly, tend to be large. However, size is not the only asset needed to fill this role. The Siberian husky, weighing between 35 and 60 lb (16 and 27 kg), is one of the smaller draft breeds, yet it is the dog of choice for sled races due to its stamina.

Dogs have also been used as search animals for centuries. The Saint Bernard breed is particularly well known. Raised by monks in the Alps, Saint Bernards were originally bred as watchdogs and companions but eventually became legendary for saving travelers trapped in the snow during harsh European winters. The ability of dogs to be used as search animals has been refined over the last few decades. In addition to finding people by tracking their odors, dogs can be trained to detect other scents, including illegal drugs. They have been trained to recognize the smell of explosives and can be used detect minefields. Dogs have also been used in arson investigations because they can detect traces of gas and flammable liquids.

Some roles are relatively new for dogs. Formally trained seeing-eye dogs, for example, originated in Germany after World War I. Dorothy Harrison Eustis became interested in the concept and wrote a popular article about it for the Saturday Evening Post in 1927. She was approached by Morris Frank, a young man who had recently lost his sight, and she agreed to train a dog for him. Mr. Frank, in turn, helped to establish the first seeing-eye dog school in the United States.

The use of seeing-eye dogs grew in popularity and eventually included other species of animals and other tasks. According to the Americans with Disabilities Act of 1990, a service animal is "any animal individually trained to do work or perform tasks for the benefit of a person with a disability," which can range from helping a blind person walk across a busy street to picking up dropped items for a person who cannot bend over.

While it is not surprising that service dogs have a beneficial effect on their eventual owners, they also can produce beneficial effects in their trainers. For example, some prison inmates at a maximum-security prison in Washington State train service dogs. One hundred percent of the trainers are reported to have found jobs when released from jail and none of them returned to prison within a three-year period, a much better success rate than that of the average released inmate.

Animal-assisted therapy (AAT) and animal-assisted activities (AAA) are two other new ways that animals such as dogs and cats have been used to help humans. While AAT and AAA both involve animals, their uses and goals are different. AAT has specific goals and must be directed by someone who has been trained in its use. It produces measurable results, such as improved range of motion or decreased anxiety. AAA has a more general purpose and doesn't require a measurable goal. Volunteers taking dogs and cats to nursing homes to promote social interaction among the elderly residents and taking these animals to pediatric hospitals to cheer up sick children are two examples of AAA.

Guide dogs have been trained to assist people with visual disabilities, including navigating city streets. (Photo by Peter Skinner/Science Source/Photo Researchers, Inc. Reproduced by permission.)

Animal welfare and rights movement

Dogs and cats have given a great deal to humans—work, companionship, and affection—and people have responded to this relationship. Although animals have sometimes been viewed as nothing more than useful tools, countless humans have developed a very affectionate relationship with dogs and cats. Eventually, the affection and empathy that some people felt toward animals led to the development of organizations devoted to animal welfare and even to what is referred to as the "animal rights movement." Although most of these organizations are concerned with many species of animals, cats and dogs are typically a major focus of their efforts.

The American for the Prevention of Cruelty to Animals (ASPCA), for example, was established in 1866 by Henry Bergh. This wealthy philanthropist was appalled by the abuse some people inflicted on horses, dogs, and cats, and he and the ASPCA worked to reduce these abuses. One of the first successes of the ASPCA was the enactment of an animal anti-cruelty law by the state of New York. Today, it's readily accepted that animals should not be abused and anti-cruelty legislation has been passed throughout the United States.

Some animal rights groups are more controversial. People for the Ethical Treatment of Animals (PETA), for example, proposes that “animals are not ours to eat, wear, experiment on, or use for entertainment.” Since its inception in 1980, PETA has influenced consumers and businesses in various ways: by working against wearing fur, hunting, and experimenting on animals; and advocating the adoption of a vegetarian diet. Some of its projects, such as the “I’d Rather Go Naked Than Wear Fur” campaign, have garnered huge amounts of publicity. Others, however, such as comparing animal suffering to the Holocaust, have garnered accusations of being insensitive and excessively reactive.

Other animal protection groups, such as the Humane Society of the United States (HSUS), founded in 1954, are more widely accepted. Indeed, the HSUS states that it is “the world’s largest animal-protection organization,” with seven million members and constituents and 250 employees. The HSUS envisions a world in which people satisfy the physical and emotional needs of domestic animals; protect wild animals and their environments; and change their relationships with all animals, evolving from exploitation and harm to respect and compassion. As evidenced by these groups, the relationship among cats, dogs, and humans is still evolving in many ways. Originally viewed as four-legged workers, today domesticated cats and dogs are increasingly valued for their productive roles in human society.

Resources

Books

Fogle, Bruce. *The New Encyclopedia of the Cat.* London: Dorling Kindersley, 2001.

Fogle, Bruce. *The New Encyclopedia of the Dog.* London: Dorling Kindersley, 2000.

Periodicals

Hare, et al. “The Domestication of Social Cognition in Dogs.” *Science* 298 (2002): 1634–1636.

Leonard, Jennifer, et al. “Ancient DNA Evidence for Old World Origin of New World Dogs.” *Science* 298 (2002): 1613–1616.

Savolainen, Peter, et al. “Genetic Evidence of an East Asian Origin of Domestic Dogs.” *Science* 298 (2002): 1610–1613.

Trut, Lyudmila. “Early Canid Domestication: The Farm-Fox Experiment.” *American Scientist* 87 (1999): 160–165.

Organizations

American Kennel Club. 260 Madison Avenue, New York, NY 10016 United States. Phone: (212) 696-8200. Web site: <http://www.akc.org>

American Society for the Prevention of Cruelty to Animals. 424 E. 92nd St., New York, NY 10128 United States. Phone: (212) 876-7700. Web site: <http://www.aspca.org>

Cat Fanciers Association. P.O. Box 1055, Manasquan, NJ 08736 United States. Phone: (732) 528-9797. Fax: (732) 528-7391. E-mail: cfa@cfainc.org Web site: <http://www.cfainc.org>

Delta Society. 585 Naches Avenue, SW, Suite 101, Renton, WA 98055 United States. Phone: (425) 226-7357. Fax: (425) 235-1076. E-mail: info@deltasociety.org Web site: <http://www.deltasociety.org>

The Humane Society of the United States. 2100 L Street, NW, Washington, DC 20037 United States. Phone: (202) 452-1100. Web site: <http://www.hsus.org>

People for the Ethical Treatment of Animals. 501 Front Street, Norfolk, VA 23510 United States. Phone: (757) 622-7382. Fax: (757) 622-0457. E-mail: info@peta.org Web site: <http://www.peta.org>

The Seeing Eye. P.O. Box 375, Morristown, NJ 07963 United States. Phone: (973) 539-4425. Fax: (973) 539-0922. Web site: <http://www.seeingeye.org>

Sue Wallace

▲
Bears
(Ursidae)

Class Mammalia
Order Carnivora
Suborder Fissipedia
Family Ursidae

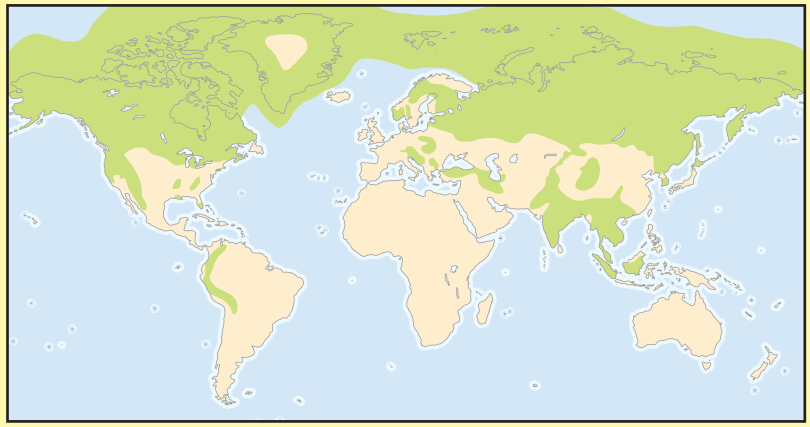
Thumbnail description
Medium to large, stocky mammals with fur that may be black, brown, reddish, or white

Size
Adults average 4–5 ft (1.2–1.5 m) and 60–150 lbs (27–70 kg) in body length for sun bears to 8–9 ft (2.4–2.7 m) and 900–1,300 lbs (400–590 kg) for polar bears

Number of genera, species
3–6 genera; 8 (or more) species

Habitat
Wide ranging, including forests, rainforests, tundra, deserts, and swamps

Conservation status
Endangered: 1 species; Vulnerable: 3 species; Lower Risk/Conservation Dependent: 1 species; Data Deficient: 1 species



Distribution
On every continent except Africa and Antarctica, but mainly in the Northern Hemisphere

Evolution and systematics

Although this family has a small number of genera and species, it still has a good share of controversy when it comes to classification. For example, some systematists over the years have placed the giant panda in a subfamily of Ursidae, as it is in this chapter, or in its own family, called Ailuropodidae. The Malayan sun bear, sloth bear, and polar bear are often grouped under the *Ursus* genus, but sometimes fall under the genera *Helarctos*, *Melursus*, and *Thalarctos*, respectively. Subspecies of the brown bear (*U. arctos*) are often listed as separate species, including the Alaskan brown bear (*U. middendorffi*) and the grizzly bear (*U. horribilis*). In addition, the red panda (*Ailurus fulgens*) was once listed with the ursids, but is now considered a to be a member of its own family, the Ailuridae, or a subfamily of the Procyonidae, which includes the raccoons.

This chapter uses the following classification:

- giant panda, *Ailuropoda melanoleuca*
- Malayan sun bear, *Helarctos malayanus*
- sloth bear, *Melursus ursinus*
- spectacled bear, *Tremarctos ornatus*
- American black bear, *Ursus americanus*
- brown bear, *U. arctos*
- polar bear, *U. maritimus*
- Asiatic black bear, *U. thibetanus*

The family Ursidae is believed to have originated in Asia, and is closely related to the canids (dogs and relatives), procyonids (raccoons and relatives), and ailurids (lesser panda). The giant panda is considered to be the most primitive of the bears. Various evolutionary studies have attempted to determine the relationships of the other bears. Fossil studies seem to indicate that the spectacled bear, which is in the subfamily Tremarctinae, diverged from the remaining bears, which are in the subfamily Ursinae. The fossil record also points to a very close relationship between the Asiatic black and American black bears, and places brown and polar bears close to

A brown bear (*Ursus arctos*) fishes for salmon. (Photo by Jeff Foott. Bruce Coleman, Inc. Reproduced by permission.)

A polar bear (*Ursus maritimus*) mother and cub. Polar bears give birth to one or two cubs and wean them at two or three years of age. (Photo by John Swedberg. Bruce Coleman, Inc. Reproduced by permission.)

them evolutionarily. Other studies using mitochondrial DNA and cytochrone-b sequence data have provided clarification, and sometimes challenged, previous conclusions. For example, mtDNA data have indicated that polar bears and spectacled bears are very closely related, and diverged from the ursinids about 2 million years ago. Cytochrome-b data appear to show that the sun bear and American black bear are sister taxa, and are somewhat separated from the Asiatic black bear.

Physical characteristics

Bears are medium to large, powerful mammals with rather short tails and plantigrade feet on stocky limbs. Many bears are dark brown to black, but the fur color is often variable within the species and sometimes even among siblings. Among the American black bear, for instance, black, brown, reddish, and even whitish individuals exist. Some species have distinctive white patches or lines on the face, throat, and/or chest. An example is the spectacled bear, which has whitish rings around its eyes. The polar bear is the only species that consists of all white-furred individuals, although the skin is black to make the best use of the heat from the arctic sun, and the individual outer (or guard) hairs are actually clear rather than white. Some species, such as the brown bear, have longer hair on the shoulders that forms a mane. A few, like the sloth bear, have long fur over much of their bodies.

Their heads are rather large, particularly in some species like the panda, and they have small, forward-facing eyes, and noticeable but usually modest round ears. Their teeth include premolars and molars designed for crushing, and long canines, which together assist their omnivorous diet. The giant panda and spectacled bear have flattened molars suited to their strongly herbivorous diets. The sloth bear, which is particularly fond of termites, has no incisors in its upper jaw. The gap, combined with protrusible and naked lips, allows the bear to suck up the insects. Sun bears have especially long tongues to assist them in attaining honey, a frequent item in their diet.

Bear claws, which are non-retractile, differ in length in separate species. In the brown bear, for example, the light-colored claws stand out from the typically brown fur, and range from 2–4 in (5–10 cm) long. The Asiatic black bear, on the other hand, has comparatively short claws, typically measuring less than 2 in (4–5 cm) in length.

In overall size, bears have a fairly wide range. In all species, males are larger than females. The smallest ursid is the Malayan sun bear, with a body length of 4–5 ft (1.2–1.5 m), and a typical male weight of 60–150 lb (27–70 kg). Polar and brown bears are at the opposite end of the spectrum, with male polar bears averaging 8–9 ft (2.4–2.7 m) in body length and 900–1,300 lb (400–590 kg), and male brown bears 5–8 ft (1.5–2.4 m) and about 350–850 lb (160–385 kg).

Distribution

Bears have a wide distribution in the Northern Hemisphere. Here, the most widely distributed species include the polar bears, which inhabit the circumpolar ice pack; the brown bears, which live throughout northern North American and north to north-central Eurasia; and the American black bear, which stretches from northern Mexico well into Canada. Both the sun bear and sloth bear reside in Southeast Asia. The range of the Asiatic black bear is somewhat larger, extending from Afghanistan to southeastern Russia. The giant panda has the smallest range of all bears, with six small populations known from the Tibetan plateau in southwestern China. The spectacled bear, the only ursid that inhabits in the Southern Hemisphere, lives around the Andes in South America, including sites in Bolivia, Colombia, Ecuador, Peru, and Venezuela.

Habitat

Bears' habitats vary from species to species. The polar bear thrives on the arctic ice pack, a sharp contrast to the tropical rainforests of southeast Asia, where the Malayan sun bear resides. The American black bear's habitat spreads from the woods in western U.S. mountains to wetlands in southeastern

An American black bear (*Ursus americanus*) and North American beaver (*Castor canadensis*) fighting in a stream in Wyoming, USA. (Photo by J. Wright. Bruce Coleman, Inc. Reproduced by permission.)

states, and to the northern tundra in Canada. In contrast, the shaggy-looking sloth bear opts for grasslands and dry forests from lowlands in India to the foothills of the Himalayas.

The brown bear, also known in parts of North America as the grizzly or kodiak, ranges from thickly forested areas into grasslands and tundra in the Northern Hemisphere, while the spectacled bear prefers lush mountain forests in South America. The giant panda lives in the bamboo forests of China, and the Asiatic black bear in primarily moist forests throughout southern Asia.

Home ranges for bears also vary. Pandas keep to about 2–3 mi^2, but brown bears are known to range over 800–1,000 mi^2 if the habitat is poor and food is scarce.

Behavior

Little is known about the behavior in the wild of half of the ursid species, mostly due to their remote geographical distribution. These include the spectacled bear, Asiatic black bear, sun bear, and sloth bear. In general, however, bears overall are solitary animals except during mating season or in mother-cub groupings. Occasionally among brown bears, siblings will stay near one another for a year or two after they leave their mother. Although additional research is needed for substantiation, some reports indicate that sloth bears may form social units, and that male sun bears may remain with the mother after she gives birth.

Bears generally maintain home ranges, with the males' ranges frequently overlapping with those of the females. Black bears mark their territories with scent markings or long scratches clawed into trees. Unusually, male panda bears sometimes do their scent marking while standing on their hands. In black bears and several other species, the ranges of male bears may also overlap, but since the ranges are often very large and bears rarely see one another, the overlaps present little opportunity for territorial conflicts. Even when bears come together at one feeding site, such as brown or black bears at a salmon stream, individual bears maintain their personal space and share the resource. When bears approach one another too closely, temporary dominance hierarchies may form, with the largest males mounting short-lived aggressive displays, including growls, and occasional charges to maintain a small feeding territory. During breeding season, males generally compete for females, but the male-female bonds typically only last one or two weeks.

The giant panda (*Ailuropoda melanoleuca*) bases 99% of its diet on bamboo. (Photo by Hans Reinhard/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)

A sun bear (*Helarctos malayanus*) showing its long tongue, in Cambodia. (Photo by Terry Whittaker/Photo Researchers, Inc. Reproduced by permission.)

Kodiak bears (*Ursus arctos middendorffi*) fight over a fishing site at McNeil River, Alaska, USA. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

With their large, plantigrade feet and stout limbs, bears are often pictured as lumbering animals that always move slowly and deliberately. They can, however, move very quickly when necessary. Black bears, for example, can run at speeds of 30 mph (50 kph), and polar bears are fast enough to catch caribou on the Arctic tundra. Even the somewhat awkward-moving sloth bear can outrun a human over short distances. Most bears are also accomplished tree climbers. The sun bear has perfected climbing, quickly scaling trees in search of honey and other food items, and even fashioning resting/feeding platforms out of broken branches high up in the trees. Polar bears and adult brown bears (with the exception of some populations in Europe) do not climb, but both are good swimmers. Other bears, like the Asiatic black bear, can also swim. With their large and slightly webbed front feet, polar bears are particularly adept swimmers and divers, and reportedly are able to swim across open-water expanses of up to 100 mi (65 km).

Ursids tend to be crepuscular (mainly active at dawn and dusk) or nocturnal animals, although some extend their active periods into the daytime. Polar bears are an example. While they are most active at night and at dawn, they are frequently seen hunting during the day.

Although ursids do not technically hibernate, many cooler-climate bears do enter winter dormancy, during which the respiratory and heart rates drop, but the body temperature dips only slightly. In the black bear, for instance, their body temperature drops from about 100°F (38°C) to 88–93°F (31–34°C). The Asiatic black bear is an exception: Its body temperature declines precipitously to just 37–45°F (3–7°C). It is during the winter dormancy that female ursids give birth. As she sleeps, the young suckle and grow. Among the cooler-climate species, both males and females become dormant, except in the polar bears, where only pregnant females enter winter sleep. During the winter, bears are capable of awakening, and occasionally leave their winter dens, which may be burrows, hollow logs, or tunnels in the snow and ice. Warm-climate bears, including sun, sloth, and spectacled bears, do not enter winter sleep. Although most brown bears and Asiatic black bears "hibernate," those from warmer climates frequently skip winter dormancy and remain active all year.

Feeding ecology and diet

Bears are omnivores, often eating whatever is available. The polar bear tends heavily toward a carnivorous diet, existing primarily on ringed seals (*Phoca hispida*), although it will eat berries and vegetation in the summer. Hunting is accomplished either by ambush or active stalking. In the former, the polar bear will simply wait at an ice hole for a seal to surface, then overpower it with one whack of its mighty paw. It reverts to stalking either on land or in the water if it happens to see a seal on the ice or another animal, such as an elk, in the open. With the polar bear's cryptic coloration, it can approach closely enough on land to give chase and sometimes overtake the animal.

Other ursids tend to prefer a greater amount of vegetation than the polar bear, eating fruits, tender stems, and roots most of the time, and supplementing the diet with insects, fish, an occasional small mammal, or carrion. The larger bears, like the brown bear, will sporadically hunt moose, or elk (*Alces alces*), and other ungulates. The giant panda, on the other hand, is almost exclusively an herbivore, eating little but bamboo leaves, stems and shoots. Sloth bears are unusual in their strong reliance on termites for food, although other bears also eat termites to some extent. Sloth bears, along with the sun bear in particular, are also fond of honey. In both cases, the bears use their claws to rip open termite and bees nests, and get at the reward.

A spectacled bear (*Tremarctos ornatus*) showing the ring around its eye from which its name is derived. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Reproductive biology

Bears' mating systems vary by species; some, such as the spectacled bear, are monogamous. Others, such as the polar bear, are polygamous. Most bears mate in the spring or summer, but the fertilized eggs do not implant in the uterus and begin developing until fall. After this so-called delayed implantation, the eggs begin to develop and the females give birth in the winter. Some species, including the sloth bear, apparently mate year-round in especially warm climates, but due to delayed implantation, all give birth in the winter. Sun bears appear to have delayed implantation, but individuals in zoos have given birth at different times of the year.

An American black bear (*Ursus americanus*) nursing cubs in the Smoky Mountains, North Carolina, USA. (Photo by Animals Animals ©Zig Leszcznski. Reproduced by permission.)

Cubs are born small, naked and blind, having developed in the womb for only two to three months. Birth weight ranges from about 11 oz (325 g) in sun bears to 21 oz (600 g) in brown and polar bears. In most cases, females give birth from one to five cubs, although two is the most common litter size among ursids. Panda mothers generally rear only one cub, regardless of the litter size, and the others die. Among cooler-climate bears, the young are born while the mother is in winter dormancy. In warmer-climate species, such as the sun bear, the mother chooses a concealed site, perhaps under branches or thick vegetation, to make a nest for the cubs. Cubs are generally weaned within the first two to five months (pandas wean at about nine months), but remain with the family unit for two to four years, during which the cubs learn to find their own food and hunt while under the protective eye of their mother.

Sexual maturity generally occurs from four to seven years old, but the timing varies among species.

Conservation status

Only one ursid, the panda bear, has been listed as Endangered by the IUCN. Habitat destruction is a major reason for this species' decline. A recent study indicated that not only human population magnitude, but the increasing number of households as family units decrease in size, have contributed to intensifying habitat destruction, particularly for this bear. As the number of households have risen, deforestation and fragmentation of panda habitat have accelerated. Estimates place the total number of pandas in the wild at below 1,000.

Other bears have also experienced decreased suitable habitat and habitat fragmentation. The brown bear, for instance, is now found in only 2% of its former range within the continental United States. The lessened range is blamed in part on habitat destruction and fragmentation. In addition, individual populations of various species have experienced declines, even if the overall species numbers are relatively high. The American black bear is an example. Several subspecies, including *Ursus americanus floridanus*, are considered threatened locally. To counteract the declines, various hunting bans or regulations, habitat preservation programs, and educational efforts are under way worldwide.

The sloth bear, spectacled bear, and Asiatic black bear are listed as Vulnerable; the polar bear is Lower Risk/Conservation Dependent; and the Malayan sun bear is listed as Data Deficient by the IUCN.

Significance to humans

Various bears are hunted for meat, fur, and trophy mounts. In addition, body parts, such as the gall bladder of sun and American black bears, are also harvested for medicinal purposes, particularly in China. Bears have also become important as attractions at zoos.

While many bears are assumed to be dangerous to humans, bear attacks are few and fatalities are rare.

1. Spectacled bear (*Tremarctos ornatus*); 2. Giant panda (*Ailuropoda melanoleuca*); 3. Brown bear (*Ursus arctos*); 4. American black bear (*Ursus americanus*); 5. Polar bear (*Ursus maritimus*). (Illustration by John Megahan)

Species accounts

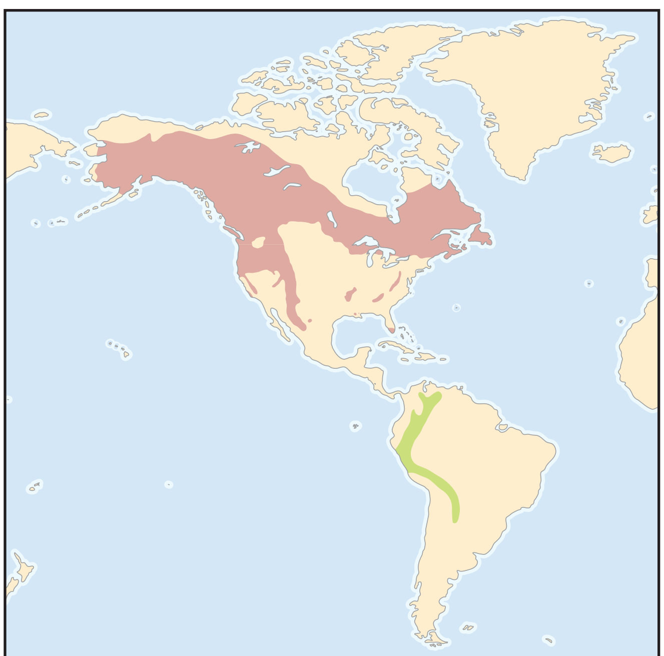
American black bear
Ursus americanus

SUBFAMILY
Ursinae

TAXONOMY
Ursus americanus Pallas, 1780, type locality not given but assumed to be eastern North America. Up to 18 subspecies.

OTHER COMMON NAMES
English: North American black bear, cinnamon bear, kermode bear, glacier bear; French: L'ours noir; German: Amerikanischer Schwarzbär; Spanish: Oso negro, oso varibal, oso negro americano.

PHYSICAL CHARACTERISTICS
A relatively short-haired bear with curved claws; rather short tail; conspicuous, but not overly large ears; and fairly long, often tawny snout. Somewhat similar to the brown bear, but the American black bear's shoulders are lower than its rump when walking. Fur coloration can vary from brown to black, sometimes reddish, bluish black, and occasionally white, with geographically distinct subspecies typically tending toward one color pelage, although color can vary even among brothers and sisters. They often have a bit of white fur on the chest. Head and body length runs from about 5–6 ft (1.5–1.8 m), and shoulder height at about 2–3 ft (60–90 cm). Standing, a typical adult reaches about 5 ft (1.5 m). Weight differs among the sexes, with the males averaging 250–350 lb (110–160 kg), almost twice the female's average weight of about 150–175 lb (70–80 kg). The largest males can reach up to 800–900 lb (360–400 kg) when they are at their heaviest just before hibernation, although these extreme weights are rare.



DISTRIBUTION
Northernmost Mexico, all but north-central Canada, and about half of the United States, especially Alaska and the western and eastern states, and the upper Great Lakes region.

HABITAT
Commonly woods with thick undergrowth, but also wetland areas, meadows, tundra particularly in Labrador, and sometimes disturbed sites near human activity.

BEHAVIOR
American black bears are commonly crepuscular and spend most of the day and night resting in a clump of leaves on the ground, although they may shift this schedule and become active during the day. Despite their typically lumbering gait, they can break into short 30 mph (48 kph) runs if necessary. They are also good swimmers and expert tree climbers, using their front claws to scale a trunk in very short order.

American black bears spend much of the winter dormant, but scientists do not consider them true hibernators, because they frequently awaken from deep sleep to leave their winter dens for short periods. Their dens may be caves; hollow, standing or fallen trees; or burrows.

American black bears are typically solitary, except for females with cubs, and maintain feeding territories of 8–15 mi^2 (20–40 km^2) throughout much of the year. At sites where food is abundant, such as garbage dumps, however, several adult males and females may share a small area. Males and females pair up for breeding for only a few days at most.

FEEDING ECOLOGY AND DIET
These omnivores eat almost anything, and are most frequently seen by humans scavenging for leftovers at campsites and garbage dumps. In the wild, they tend toward a vegetarian diet, eating everything from berries and nuts to grasses and roots, but will also dine on honey, salmon, ants and other insects, rodents, an occasional young ungulate, livestock, and carrion when the opportunities arise.

REPRODUCTIVE BIOLOGY
Polygynous. Mating occurs from late spring to early summer, but implantation of the embryo is delayed until late fall. Birth follows in mid-winter with typically two blind and naked cubs, although litters may range from one to four, rarely five, young. The young nurse while the female continues her winter rest and then leave the den in the spring. The family remains together with the mother providing milk until late summer or early fall, sometimes longer. After weaning, the cubs stay with the mother for one or two years. American black bears become sexually mature at about 3–6 years of age, with the females maturing on average about a year earlier than the males.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Hunted for meat, trophies, and hides, as well as various body organs and parts for cultural medicinal uses. American black bears are not normally aggressive, and only very rarely harm humans. They do, however, occasionally become pests to campers, beekeepers, farmers, and others who usually unintentionally furnish food sources. ◆

Brown bear
Ursus arctos

SUBFAMILY
Ursinae

TAXONOMY
Ursus arctos Linnaeus, 1758, "sylvis Europaelig frigidaelig" assumed to be northern Sweden. Five subspecies.

OTHER COMMON NAMES
English: Grizzly, kodiak, coastal brown bear, Alaskan brown bear, Asiatic brown bear, Russian brown bear, European brown bear, Himalayan snow bear, Syrian bear; French: L'ours brun; German: Braunbär; Spanish: Oso pardo.

PHYSICAL CHARACTERISTICS
A large bear that varies in color from its typical brown to light tan or black. Large muscles create a noticeable shoulder hump that is further exaggerated in some geographic areas, particularly in North America, by a mane of long hairs with whitish-gray highlights. Its snout protrudes from a concave or "hollow" face. Females average from 250–450 lb (110–200 kg), and males from 350–850 lb (160–385 kg), although brown bears from some areas, including parts of Alaska, often reach 1,000 lb (450 kg) or more. Average adult size is about 3–4 ft (0.9–1.2 m) at the shoulder and 6–7 ft (1.8–2.1 m) when standing on the hind legs. Large bears may stand more than 8 ft (2.4 m) tall.

DISTRIBUTION
Widely distributed globally, with populations in North America from Alaska and northern Canada as far south as Wyoming, in Europe, in northern Asia, and in Japan.

HABITAT
Found in diverse habitats, particularly heavily wooded forests in Eurasia, and more open areas and tundra in North America.

BEHAVIOR
Other than females with their cubs, brown bears are mostly solitary animals. If food is plentiful, however, they will share one area. For example, it is not uncommon to see several brown bears along a shallow river during a salmon run. Brown bears are usually most active at dawn and dusk, but may be active at any time. A hierarchy of sorts often forms, with the largest males keeping smaller individuals from approaching them too closely.

FEEDING ECOLOGY AND DIET
Omnivores, brown bears mainly subsist on grasses and plant roots, but will also dig up and eat ants, catch fish using their jaws and paws, and take both small and large mammals, including moose, caribou, and even American black bears. They also occasionally eat carrion.

REPRODUCTIVE BIOLOGY
Polygamous. Breeding season is an occasion when bears abandon their solitary ways, with pairs forming for up to two weeks. However, a female may mate with more than one male, and have cubs in the same litter with different fathers. Mating occurs from mid-spring to mid-summer, with implantation of the embryo following in the fall. Females typically have two cubs, although a litter may range from one to four. Births occur in the winter. Weaned at about 5 months of age, the cubs stay under the protective care of their mother for at least two-and-a-half years, at which point she may breed again. Sexual maturity is attained at about 4–7 years of age, although competition for females may prevent a younger male from breeding as early as that.

CONSERVATION STATUS
Not listed by the IUCN, although it has diminished greatly from its historical range.

SIGNIFICANCE TO HUMANS
Hunted primarily as trophies, but once hunted for their meat and hides. Various organs and body parts are also currently sought by Asian markets. Brown bears can be aggressive and have been known to attack humans, although this is rare. ◆

Giant panda
Ailuropoda melanoleuca

SUBFAMILY
Ailuropodinae

TAXONOMY
Ailuropoda melanoleuca (David, 1869), "Mou-pin."

OTHER COMMON NAMES
English: Cat bear, black and white bear; French: Le grand panda; German: Großer Panda; Spanish: Oso panda.


Ursus arctos

Ailuropoda melanoleuca

PHYSICAL CHARACTERISTICS
Striking black-and-white bear with black fur around the eyes, on the ears, on all four legs, and across the back from shoulder to shoulder. Sometimes the black fur is replaced with reddish black or brownish fur. Unusually, it has six digits on each front foot, with the sixth digit actually an extension of the sesamoid bone and serving as an opposable thumb, thus giving the panda additional dexterity. This stocky bear reaches about 5.5–6 ft (1.7–1.8 m) in body length and weighs about 175–280 lb (80–125 kg), with the females about 10–15 percent lighter than the males.

DISTRIBUTION
Narrowly distributed in small parts of the Tibetan plateau in southwestern China.

HABITAT
Bamboo jungles 4,000–12,000 ft (1,200–3,600 m) above sea level.

BEHAVIOR
These are mainly solitary animals, except for female-and-cub groupings. Males and females have home ranges. A male's range excludes other males, but may overlap with the range(s) of one or more females. Territories are maintained by scent markings on trees or other surfaces, and by tree scratches. Males and females vocalize, with females doing most of their sound-making during the breeding season. Males may compete for females.

FEEDING ECOLOGY AND DIET
Primarily eat bamboo, including the leaves, stems, and shoots. They are the most vegetarian of the bears, eating little other than bamboo. They have flattened molars and a specialized digestive system to handle the tough plant material.

REPRODUCTIVE BIOLOGY
Polygynous and promiscuous. Mating occurs in spring, with litters of one to three cubs born in late summer to early fall. Despite the size of the litter, the mother commonly only rears one of her cubs. The cub weans at about nine months, and stays with their mother for about one-and-a-half years. Sexual maturity is attained at about 5–7 years of age, although competition for females may prevent a younger male from breeding that early.

CONSERVATION STATUS
Listed as Endangered by the IUCN.

SIGNIFICANCE TO HUMANS
Particularly important to the tourism industry. Panda bears are a major attraction in zoos, and a symbol of species conservation efforts. ◆

Polar bear
Ursus maritimus

SUBFAMILY
Ursinae

TAXONOMY
Ursus maritimus Phipps, 1774, Norway.

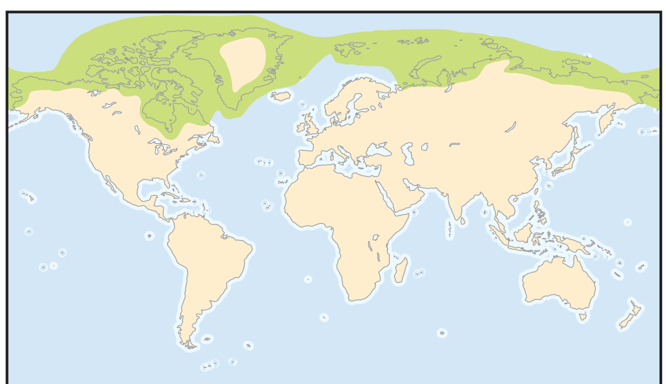
OTHER COMMON NAMES
English: Sea bear; French: L'ours blanc, l'ours polaire; German: Eisbär; Spanish: Oso polar.

PHYSICAL CHARACTERISTICS
A large, white to yellowish bear with a black nose, small eyes, fairly small ears, and a neck that is long compared to other bears. Under the "white" fur (actually made up of clear, hollow hairs), it has black skin. A marine animal, polar bears also have webbed front paws to aid in swimming. The largest of the terrestrial carnivores, male polar bears can reach 8–9 ft (2.4–2.7 m) in body length, 4 ft (1.2 m) at the shoulder, and more than 10 ft (3 m) when standing on their hind legs. Males commonly weigh 900–1,300 lb (400–590 kg), although very large males have been recorded that weighed in excess of 2,000 lb. (907 kg) and stood more than 12 ft (3.6 m). The average female body length ranges from about 6–7 ft (1.8–2.1 m), and they weigh 450–600 lb (200–270 kg).

DISTRIBUTION
Circumpolar distribution, ranging to the edge of the Arctic Ocean ice pack. They are found well into northern Canada, Europe and Asia in warmer months, and as far south as Newfoundland, Canada, and the northern Bering Sea in the winter.

HABITAT
Arctic snow and ice fields, with southern populations sometimes summering on land. Because they spend a considerable time on the ice pack or in the water, they are sometimes considered a marine mammal.

BEHAVIOR
Not territorial animals, polar bears normally live alone on large home ranges. Females and cubs are the only social unit. Males



Ursus maritimus

compete for receptive females during mating season. Pregnant females spend much of the winter in dens burrowed in the permafrost, but other polar bears generally do not enter winter dormancy, instead remaining active all year. Some of the females' dens go back many years, with the successive generations clawing farther down to make ever-deepening caverns.

FEEDING ECOLOGY AND DIET
Typically designated as carnivores because the vast majority of their diet is meat, particularly seals and fish. Ambush is a favored hunting method, with the polar bears waiting at holes in the ice for a seal to surface, then delivering a fatal blow with their clawed paws. The bears will also occasionally attack and eat other marine animals, including walruses and even beluga whales. During the summer, polar bears will subsist on berries, grasses and other vegetation, and carrion.

REPRODUCTIVE BIOLOGY
Polygamous. Mating occurs in the spring, with implantation of the embryo following in late fall. Females typically have two cubs, although a litter may range from one to three, rarely four. Births occur in early winter. The cubs stay with their mother for at least two-and-a-half years, at which point she may breed again. Sexual maturity is attained at 3–6 years of age.

CONSERVATION STATUS
Listed as Lower Risk/Conservation Dependent by the IUCN, although some scientists believe they could face extinction within the century if global warming continues to melt arctic ice.

SIGNIFICANCE TO HUMANS
Now protected, they were once widely hunted for their fur, meat, and trophy value. Polar bears can be aggressive, and have been known to attack humans, although this is very rare. ◆

Spectacled bear
Tremarctos ornatus

SUBFAMILY
Tremarctinae

TAXONOMY
Tremarctos ornatus (F. G. Cuvier, 1825), Chile.

OTHER COMMON NAMES
French: L'ours à lunettes; German: Brillenbär; Spanish: Oso de anteojos, oso frontino o andino.

PHYSICAL CHARACTERISTICS
A smaller, black, brown or slightly reddish bear with whitish fur "spectacles" completely or partially encircling the eyes. Small, whitish stripes and patches typically run along on the sides of the face, the neck and chest. Body length is about 5–6 ft (1.5–1.8 m), with males weighing 220–340 lb (100–150 kg) and females 140–180 lb (65–80 kg).

DISTRIBUTION
South America, including parts of Bolivia, Colombia, Ecuador, Peru, and Venezuela.

HABITAT
Variable, but commonly in thick, lush forests of mountainous areas ranging from 6,000–9,000 ft (1,800–2,750 m). Also found as low as 600 ft (180 m) and as high as 14,000 ft (4,300 m), and in drier, open areas.

BEHAVIOR
Active at dawn, dusk, and through the night, these bears spend much of their time on platforms, which they build of broken branches in trees, typically among fruiting branches. Between naps on the platform, they spend their time harvesting and eating the fruit. During mating season, males and females come together for one or two weeks, beginning by mock fighting apparently to stimulate the female for mating, and then copulating multiple times. Some communicative vocalizations have been documented between captive mothers and cubs.

FEEDING ECOLOGY AND DIET
These omnivorous bears prefer fruits and various parts of bromeliads, but also will eat orchid bulbs, grasses, small mammals, and birds.

REPRODUCTIVE BIOLOGY
Monogamous. Mating occurs from spring to early summer, followed by delayed implantation, then birth in late fall to mid-winter with one to three cubs, although three is rare. The cubs remain with the mother, often riding on her back as she moves through the forest. Spectacled bears become sexually mature at about 4–7 years of age.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Hunted for meat and fur, also for their fat, which is used for medicinal purposes. Due to their large fruit diet, spectacled bears are also important seed dispersers. Farmers and ranchers sometimes view the bears as a threat to their crops and livestock. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Malayan sun bear *Helarctos malayanus* Spanish: Oso malayo	Short, sleek black fur covers body. White colored crescent shape on chest, muzzle, and eyes. Muzzle is short, ears are small and very round. Large paws with naked soles, claws are long, curved, and very pointed. Body length 48–60 in (122–152 cm), weight 60–145 lb (27–66 kg).	Prefers lowland tropical rainforests. They are quite arboreal and are believed to sleep in trees. Cubs can be born throughout the year.	Myanmar, China (Yunnan and Szechwan), India, Indonesia (Sumatra, Borneo), Laos, Taiwan, Malaysia, Thailand, and Vietnam.	Consists of birds, small mammals, termites, the young tips of palm trees, and the nests of wild bees.	Data Deficient
Sloth bear *Melursus ursinus* Spanish: Oso labiado	Coat is black, shaggy, with gray and brown mixed in. Chest, muzzle, and eye area is white or cream colored. Body length 60–75 in (122–191 cm), weight 175–310 lb (79–41 kg).	Prefers grasslands and forested area at predominantly lower altitudes. They are more often found in drier forests and areas with rock outcroppings. Live mainly as solitary individuals, except when mother is with cubs. Cubs stay with mothers for 2 to 3 years.	Sri Lanka; India, north to the Indian desert and to the foothills of the Himalayas.	Mainly termites, as well as fruit and other plant matter, eggs, insects, honeycomb, and carrion.	Vulnerable
Asiatic black bear *Ursus thibetanus* Spanish: Oso negro asiático	Mainly black coloration with light muzzle and ears. Distinct white patch on chest and on chin. Brown color phase does occur. Total length 51–75 in (130–190 cm), weight for adult male 220–440 lb (100–200 kg), adult female 110–275 lb (50–125 kg).	Can be found predominantly in forested areas, especially in hills and mountainous areas. In summer, they can be found mainly at altitudes over 9,840 ft (3,000 m), descending to lower elevations during winter. Mainly nocturnal.	Afghanistan, China, India, Indochina, Japan, Korea, Laos, Nepal, Pakistan, Taiwan, Thailand, Russia (southeast Primorski Krai), and Vietnam.	Consists of fruits, bees' nests, insects, invertebrates, small vertebrates, and carrion.	Vulnerable

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Organizations

American Bear Association. P.O. Box 77, Orr, MN 55771 United States. Phone: (218) 757-0172. E-mail: admin@americanbear.org Web site: <http://www.americanbear.org/>

Great Bear Foundation. P.O. Box 9383, Missoula, MT 59807 United States. Phone: (406) 829-9378. Fax: (406) 829-9379. E-mail: gbf@greatbear.org Web site: <http://www.greatbear.org>

IUCN/SSC Bear Specialist Group. Harry V. Reynolds, Alaska Dept. of Fish and Game - Fairbanks, 1300 College Rd., Fairbanks, AK 99701 United States. Phone: (907) 459-7238. Fax: (907) 459-9723. E-mail: harry_reynolds@fishgame.state.ak.us Web site: <http://www.iucn.org/themes/ssc/pubs/bears511.htm>

Ursus International Conservation Institute. P.O. Box 832, Pincher Creek, Alberta T0K 1W0 Canada. E-mail: info@ursusinternational.org Web site: <http://www.ursusinternational.org/>

Other

Animal Diversity Web. University of Michigan Museum of Zoology. <http://animaldiversity.ummz.umich.edu/chordata/mammalia/carnivora/ursidae.html>

The Bear Den. <http://www.bearden.org/blkbear.html>

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Leslie Ann Mertz, PhD

▲
Raccoons and relatives
(Procyonidae)

Class Mammalia
Order Carnivora
Family Procyonidae

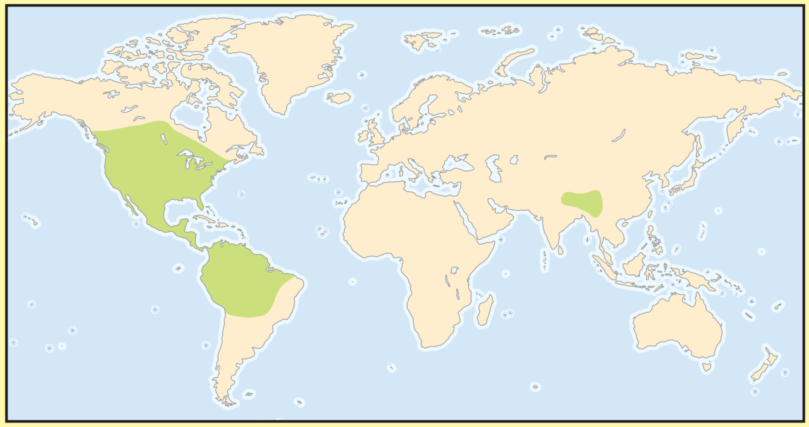
Thumbnail description
Medium-sized carnivores with dexterous digits and long tails, most with dark bands

Size
Body 1.0–2.5 ft (30–70 cm); tail 0.8–2.0 ft (20–70 cm); mass 2–40 lb (0.8–18 kg)

Number of genera, species
7 genera; 16 species

Habitat
Forests, farmland, and cities

Conservation status
Endangered: 5 species and 1 subspecies; Lower Risk/Near Threatened: 3 species; Data Deficient: 1 species



Distribution
South and Central America, North America, and Asia

Evolution and systematics

Procyonids evolved in the tropical environments of South and Central America. Their morphology and habits reveal numerous adaptations for warm climates including naked soles, long digits, diet relying heavily on fruits and berries, and tree climbing skills. Several aspects of their phylogeny (origin) remain unresolved. First, the position of the red panda, *Ailurus fulgens*, with the Procyonidae (but the giant panda *Ailuropoda melanoleuca* in the Ursidae) is not universally accepted. In the past, the red panda has been considered under a separate family Ailuridae with the giant panda. Second, the number of species of raccoons (genus *Procyon*) seems to vary as many previously recognized island species such as Bahaman raccoon (*Procyon maynardi*), Guadeloupe raccoon (*Procyon minor*), and the extinct Barbados raccoon (*Procyon gloveralleni*) have recently been reconsidered variants of the northern raccoon (*Procyon lotor*). Similarly, five species of olingos (genus *Bassaricyon*) are currently recognized, but are probably variants (subspecies) of the same species.

Physical characteristics

Procyonidae have a rounded head and ears, short snouts (genus *Potos*) or long snouts (generas *Nasua* and *Procyon*), most have long banded tails except kinkajous (*Potos flavus*), which have unbanded tails. Pelage varies from pale brown in *Bassariscus* to dark red in *Ailurus*, and is variable from yellowish to silver, brown, or even black in some color morphs of *Procyon lotor*. Facial markings often occur, and are most pronounced in raccoons and red pandas, yet absent in kinkajous. Limbs have five digits, with short, recurved claws. Mass ranges from 2 lbs (1 kg) in *Bassariscus* to close to 40 lbs (18 kg) in *Procyon lotor*. Males are slightly larger than females, and have a baculum (penis).

Distribution

Procyonids (except the red panda) occur throughout Central American and the northern half of South America, but the northern raccoon occurs in North America, and now in Germany following introductions. Red pandas occur in the

Northern raccoons (*Procyon lotor*) in their tree den. (Photo by Leonard Lee Rue III. Bruce Coleman, Inc. Reproduced by permission.)

The ringtail (*Bassariscus astutus*) is a nocturnal hunter. (Photo by Bob & Clara Calhoun. Bruce Coleman, Inc. Reproduced by permission.)

Kinkajous (*Potos flavus*) eat mostly fruit. (Photo by Tom Brakefield/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)

temperate forests of the Himalayas from Nepal through to provinces of Sichuan and Yunnan in China.

Habitat

Procyonidae are extremely adaptable and occur in all habitats except possibly desertic habitats. Most species probably occur in tropical forests except for the northern raccoon that inhabits farmland, mixed forests and urban areas throughout the United States and Canada. Red pandas inhabit bamboo forests of Asia.

Behavior

With the exception of the coatis, the procyonids are nocturnal species. All species are capable climbers. Some species such as *Bassariscus* are solitary, others such as *Procyon* have variable degrees of sociality, and *Nasua* is highly gregarious. Solitary species such as *Bassariscus* or *Nasua* do not defend territories, but home ranges typically overlap more intersexually than intra-sexually. Only red pandas are truly territorial. Some species such as *Potos flavus* and *Ailurus fulgens* scent mark.

A white-nosed coati (*Nasua narica*) searching for grubs. (Photo by James H. Charmichael. Bruce Coleman, Inc. Reproduced by permission.)

Feeding ecology and diet

Procyonidae are omnivorous. Some specialization occurs from the ring-tailed cats (mostly carnivores) to kinkajous (frugivore) or red pandas (mostly herbivore), but all species consume plant or animal matter, depending on season or availability.

Reproductive biology

Most species are promiscuous and breed in the spring or throughout the year in southern latitudes. Females bear young once a year after a gestation period of 60–118 days. Males do not provide care for the young.

Conservation status

Twelve species plus one subspecies are listed on the IUCN Red List of Threatened Species. However, listing of two raccoons as Endangered (*Procyon minor*, *Procyon maynardi*) and one as Extinct (*Procyon gloveralleni*) may be invalid as they are forms of the northern raccoon. Among extant species, five are Endangered (*Ailurus fulgens*, *Procyon pygmaeus*, *Procyon insularis*, *Bassaricyon lasius*, and *Bassaricyon pauli*), three are listed as Near Threatened (*Bassaricyon beddardi*, *Bassaricyon gabbii*, and *Bassariscus sumichrasti*), and one species as Data Deficient (*Nasuella olivacea*). The red panda is currently endangered be-

The red panda (*Ailurus fulgens*) lives in the mountain forests of Bhutan, India, and China. (Photo by Harald Schütz. Reproduced by permission.)

cause of deforestation, killing for its pelt, illegal trade of live animals, and predation by domestic dogs. Estimates suggest that less than 2,500 animals remain. One species of raccoon,

A northern raccoon (*Procyon lotor*) eats a crayfish. (Photo by Joe McDonald. Bruce Coleman, Inc. Reproduced by permission.)

The olingo (*Bassaricyon gabbii*) is mostly aboreal. (Photo by Art Wolfe/Photo Researchers, Inc. Reproduced by permission.)

the Cozumel Island raccoon (*Procyon pygmaeus*) is threatened by urbanization and persecution as pests by orchard owners.

Significance to humans

Procyonids are hunted for their meat and fur, or killed as pests. The northern raccoon has the greatest importance to humans, either as a furbearer, for meat, as a carrier of rabies, or as a pest. Other procyonids such as coatis or kinkajous may also be harvested for their meat or fur, although none to the extent of the northern raccoon.

1. Ringtail (*Bassariscus astutus*); 2. Kinkajou (*Potos flavus*); 3. Red panda (*Ailurus fulgens*); 4. White-nosed coati (*Nasua narica*); 5. Northern raccoon (*Procyon lotor*). (Illustration by Brian Cressman)

Species accounts

Northern raccoon
Procyon lotor

SUBFAMILY
Procyoninae

TAXONOMY
Ursus lotor (Linnaeus, 1758), Americae maritimis (Pennsylvania).

OTHER COMMON NAMES
English: Raccoon, coon; French: Raton laveur; German: Waschbär; Spanish: Mapache.

PHYSICAL CHARACTERISTICS
Body length 18–25 in (50–65 cm), tail 8–12 in (20–30 cm), mass 10–35 lb (4–16 kg). Large rounded head, round ears, black mask across face, long digits and naked feet, long, thick fur, and long tail with numerous concentric dark bands.

DISTRIBUTION
Southern Panama north to the fringe of the boreal forests in Canada. Introduced into Russia and Germany.

HABITAT
Raccoons thrive in a variety of habitats including forests to mixed forests, prairies, and urban areas.

BEHAVIOR
Nocturnal, raccoons spend the day sheltered in abandoned houses, barns, culverts, hollow trees, brush piles, or dens of other animals. Home ranges vary according to food abundance, and range from 12 to 6,000 acres (0.5–25 km^2). Densities range from one to 600 individuals per mi^2 (0.5–300 per km^2), and highest densities occur in urban areas. In northern environments, raccoons accumulate large amounts of fat during late summer and autumn in preparation for an extended period of sleep (up to six months) during winter. Longevity up to 17 years in captivity, but rarely reaches five years in the wild. Main predators are coyotes, bobcats, and alligators.

FEEDING ECOLOGY AND DIET
Raccoons are opportunistic and consume whatever foods they encounter. Most often, diet consists of fruits, berries, cereal grains, hard mast, crayfish, frogs, and bird eggs. Although historically believed to wash their food before eating, this habit is a myth and simply the result of raccoons often searching for and handling aquatic food with their dexterous forepaws.

REPRODUCTIVE BIOLOGY
Promiscuous. Mating in February or March. Gestation 63 days, litter size is one to seven. Males do not provide care for the young.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
The raccoon is important to humans for meat, fur, as a pest and as a carrier of rabies. The meat is consumed mostly in southern United States and Central America. The raccoon is also an important furbearer across the United States and Canada. Raccoons are sometimes killed as pests, especially for damage caused to crops (corn), for consuming and spreading garbage in urban areas, or for perceived threats to domestic animals (chicken) or wild game birds, especially ducks. In the eastern United States, the raccoon is of significant concern as a carrier of rabies. The ability of raccoons to thrive in the presence of humans is a major factor leading to its importance as a pest: currently, the highest densities of raccoons anywhere are found in large cities such as Chicago (USA), Cincinnati (USA), and Toronto (Canada). ◆

Kinkajou
Potos flavus

SUBFAMILY
Potosinae

TAXONOMY
Lemur flavus (Schreber, 1774), Surinam.

OTHER COMMON NAMES
English: Honey bear; French: Kinkajou; German: Wickelbär; Spanish: Marta.

PHYSICAL CHARACTERISTICS
Body length 16–30 in (40–75 cm), tail 16–24 in (40–60 cm), mass 3–10 lb (1.4–4.6 kg). Tawny olive pelage with large rounded head and ears, short snout, prehensile tail, and large protruding eyes.

DISTRIBUTION
Southeast Mexico through Central America into Brazil.

HABITAT
Southern tropical forests.

BEHAVIOR
Solitary and arboreal, kinkajous rest in hollow trees during the day. They scent mark, possibly to communicate or advertise sexual status. Kinkajous are not territorial, and animals may aggregate near good food sources. Density may reach 30–75/mi^2 (12–30/km^2). Longevity may reach 23 years in captivity.

FEEDING ECOLOGY AND DIET
Fruits, honey, insects, bird eggs and nestlings, and rarely small mammals.

REPRODUCTIVE BIOLOGY
Promiscuous. Breeding throughout the year. Gestation 112–118 days, litter size typically one, but rarely two.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
May be eaten in some localities. ◆

White-nosed coati
Nasua narica

SUBFAMILY
Procyoninae

TAXONOMY
Viverra narica (Linnaeus, 1766), America (Vera Cruz).

OTHER COMMON NAMES
English: Coatimundi; French: Coati à nez blanc; German: Nasenbär; Spanish: Tejón.

PHYSICAL CHARACTERISTICS
Body length 16–30 in (40–67 cm), tail 13–18 in (32–69 cm), mass 6–13 lb (3–6 kg). Reddish brown pelage above and yellow to dark brown below. White muzzle, chin and throat. Movable, trunk-like snout, and long, banded tail.

DISTRIBUTION
Southwestern United States south to Panama.

HABITAT
Mostly in wooded areas.

BEHAVIOR
Diurnal and highly gregarious. Females with young often form large bands of up to 25 individuals, whereas males are mostly solitary. Gregariousness of females with young likely is an adaptation to reduce predation of young by males or other predators. Animals usually carry the tail erect, except for the curled tip. Longevity up to 14 years. Predators include big cats and large snakes.

FEEDING ECOLOGY AND DIET
Invertebrates, fruits, lizards, and small rodents. Individuals do not share or cache food.

REPRODUCTIVE BIOLOGY
Promiscuous. Gestation 74 days, litter size is one to six.

CONSERVATION STATUS
One subspecies, sometimes considered a separate species, the Cozumel Island coati (*N. n. nelsoni*) is Endangered.

SIGNIFICANCE TO HUMANS
Coatis are hunted for their meat and fur. ◆

Ringtail
Bassariscus astutus

SUBFAMILY
Procyoninae

TAXONOMY
Bassaris astuta (Lichtenstein, 1830), Mexico City.

OTHER COMMON NAMES
English: Ring-tailed cat, cacomistle, miner's cat; German: Nordamerikanisches Katzenfrett; Spanish: Mico de noche.

PHYSICAL CHARACTERISTICS
The smallest procyonid. Body length 12–16 in (30–42 cm), tail 12–18 in (30–45 cm), mass 1.8–3.0 lb (800–1400 g). Long banded tail, flat head, large ears, and long, tapered snout.

DISTRIBUTION
Southern Oregon, southwest United States into Mexico (including Baja California) and south to Veracruz and Oaxaca.

HABITAT
Rocky, semi-desertic areas, often near water.

BEHAVIOR
Nocturnal, it shelters in rock crevices during the day. Agile climber.

FEEDING ECOLOGY AND DIET
Rodents, insects, birds and bird eggs, reptiles, fruits, vegetable matter.

REPRODUCTIVE BIOLOGY
Promiscuous. Gestation is 60 days, litter size 2–4, parturition from March to June.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Ringtails are harvested as furbearers in southern United States. ◆

Red panda
Ailurus fulgens

SUBFAMILY
Ailurinae

TAXONOMY
Ailurus fulgens F. G. Cuvier, 1825, East Indies.

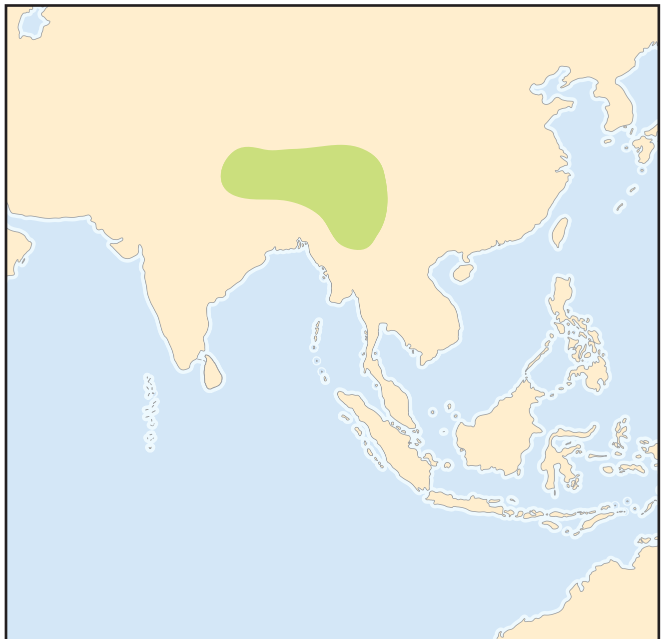
OTHER COMMON NAMES
English: Lesser panda; French: Petit panda; German: Kleiner Panda, Katzenbär; Spanish: Panda rojo.

PHYSICAL CHARACTERISTICS
Body length 20–24 in (50–60 cm), tail 12–20 in (30–50 cm), mass 6.5–11 lb (3–5 kg). Overall pelage reddish, with well furred and banded tail. Large round ears with white fringe, two black stripes from the eyes down on the cheeks.

DISTRIBUTION
Nepal, India, Bhutan, Myanmar, and south central China, possibly also in Tibet and Assam.

HABITAT
Occupies bamboo forests.

BEHAVIOR
Mostly nocturnal. Capable climber but forages mostly on the ground. Red pandas are territorial, and territorial boundaries are scent marked. Territories occupy 0.4–1.5 mi^2 (1–3.5 km^2). Density is roughly one animal/mi^2 (0.4/km^2).



FEEDING ECOLOGY AND DIET
Bamboo sprouts, grasses, roots, fruits, acorns, and rarely animal prey.

REPRODUCTIVE BIOLOGY
Promiscuous. Mating occurs in July and August. Gestation lasts 134 days, litter size is one to four.

CONSERVATION STATUS
Endangered.

SIGNIFICANCE TO HUMANS
Red pandas are not harvested for their fur or meat, and are popular zoo animals. They are threatened by deforestation and increased agriculture.◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Crab-eating raccoon *Procyon cancrivorus* Spanish: Mapache cangrejero	Upperparts are brown or grayish in color. Underparts are lighter. Mask of black on eyes and rings on tail. Very short hair, large. Head and body length 21.7–29.9 in (55–76 cm), tail length 3.9–5.9 in (10–15 in).	Marshy and jungle areas of Central and South America. Solitary animal, active during evening and at night.	Argentina, Bolivia, Brazil, Colombia, Costa Rica, Guyana, Panama, Peru, Suriname, Trinidad and Tobago, and Venezuela.	Frogs, toads, crabs, shrimp, turtle eggs, fruits, and seeds.	Not listed by IUCN
Bahaman raccoon *Procyon maynardi* Spanish: Mapache de las Bahamas	Coloration is gray to black, 5 to 10 rings on well-furred tail. Head and body length 16.3–23.6 in (41.5–60 cm), tail length 7.9–15.9 in (20–40.5 cm). Males generally larger than females.	Timbered and brushy areas, usually near water. More nocturnal than diurnal. Build dens for shelter and do not hibernate.	New Providence Island, Bahamas.	Crayfish, crabs, other arthropods, frogs, fish nuts, seeds, acorns, and berries.	Endangered
Cozumel Island raccoon *Procyon pygmaeus* Spanish: Mapache pigmeo	Coloration is gray to black, 5 to 10 rings on well-furred tail. Head and body length 16.3–23.6 in (41.5–60 cm), tail length 7.9–15.9 in (20–40.5 cm). Males generally larger than females.	Timbered and brushy areas, usually near water. More nocturnal than diurnal. Build dens for shelter and do not hibernate.	Cozumel Island off northeastern Yucatán, Mexico.	Crayfish, crabs, other arthropods, frogs, fish nuts, seeds, acorns, and berries.	Endangered

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Guadeloupe raccoon *Procyon minor* Spanish: Mapache de Guadalupe	Coloration is gray to black, 5 to 10 rings on well-furred tail. Head and body length 16.3–23.6 in (41.5–60 cm), tail length 7.9–15.9 in (20–40.5 cm). Males generally larger than females.	Timbered and brushy areas, usually near water. More nocturnal than diurnal. Build dens for shelter and do not hibernate.	Guadeloupe Island, Lesser Antilles.	Crayfish, crabs, other arthropods, frogs, fish, nuts, seeds, acorns, and berries.	Endangered
Cozumel Island coati *Nasua nelsoni*	Short, fairly soft hair. Coloration is generally reddish brown to black. Muzzle, chin, and throat whitish and feet blackish. Striped tail. Head and body length 16.1–23.4 in (41–67 cm), tail length 12.6–27.2 in (32–69 cm).	Mainly in wooded areas. Use tail as balancing organ, primarily diurnal. Loose band of to 20 individuals. Single reproductive season.	Cozumel Island off north-eastern Yucatán, Mexico.	Fruits, other plant matter, large rodents.	Endangered
Ring-tailed coati *Nasua nasua* Spanish: Coatí isleño	Tawny red with black face; a small white spot above and below each eye and a large one on each cheek; white throat, belly; black feet, black rings on tail. Head and body length 31.5–51.2 in (80–130 cm).	Mainly in wooded areas. Use tail as balancing organ, primarily diurnal. Loose band of 4 to 20 individuals. Single reproductive season.	Arizona, United States, to Argentina.	Fruits, other plant matter, large rodents.	Not threatened
Cacomistle *Bassariscus sumichrasti* French: Bassarai rusé; Spanish: Babisuri	Color is buffy gray to brownish, tail is ringed with buff and black. Ears are pointed, tail is long. Head and body length 15–18.5 in (38–47 cm), tail length 15.4–20.9 in (39–53 cm).	Tropical forests and is very arboreal. Enters estrus in winter, spring, or summer. Late winter is main breeding season.	Southern Mexico to western Panama.	Insects, rodents, birds, fruits, and other vegetable matter.	Lower Risk/Near Threatened
Allen's olingo *Bassaricyon alleni* Spanish: Olingo leonado	Upperparts are pinkish buff to golden, mixed with black or grayish. Underparts are pale yellowish. Tail is flat and body is elongate. Head and body length 13.8–18.5 in (35–47 cm), tail length 15.7–18.9 in (40–48 cm).	Tropical forests from sea level to 6,560 ft (2,000 m). Primarily aboreal and nocturnal. There is no definite breeding season. Females give birth to one off-spring per year.	Ecuador east of the Andes, and Peru to Cuzco Province; Bolivia; and possibly into Venezuela.	Mainly fruit, but also insects and warm-blooded animals.	Not threatened
Beddard's olingo *Bassaricyon beddardi* Spanish: Olingo de Guayana	Upperparts are pinkish buff to golden, mixed with black or grayish. Underparts are pale yellowish. Tail is flat and body is elongate. Head and body length 13.8–18.5 in (35–47 cm), tail length 15.7–18.9 in (40–48 cm).	Tropical forests from sea level to 6,560 ft (2,000 m). Primarily aboreal and nocturnal. There is no definite breeding season. Females give birth to one off-spring per year.	Guyana, and possibly adjacent Venezuela and Brazil.	Mainly fruit, but also insects and warm-blooded animals.	Lower Risk/Near Threatened
Olingo *Bassaricyon gabbii* Spanish: Olingo grisáceo	Coloration is light brown with cream under-sides and neck. Tail has 11–13 dark brown rings. Long muzzle and no prehensile tail. Head and body length 14–16 in (35.6–40.6 cm), tail length 15–19 in (38.1–48.3 cm).	Rainforests of Central America and northwestern South America, at elevations from sea level to 6,560 ft (2,000 m). Arboreal, nocturnal, and solitary. There is no particular breeding season. Females give birth to one offspring per year.	Central Nicaragua, Costa Rica, Panama, western Colombia, and western Ecuador.	Mostly fruits, nectar, insects, small mammals, and birds.	Lower Risk/Near Threatened
Harris's olingo *Bassaricyon lasius* Spanish: Olingo costarricense	Upperparts are pinkish buff to golden, mixed with black or grayish. Underparts are pale yellowish. Tail is flat and body is elongate. Head and body length 13.8–18.5 in (35–47 cm), tail length 15.7–18.9 in (40–48 cm).	Tropical forests from sea level to 6,560 ft (2,000 m). Primarily arboreal and nocturnal. Spends day in nest. Lives alone or in pairs.	Known only from type locality: 6–8 mi (9.7–12.9 km) south of Cartago, Costa Rica, near the source of the Rio Estrella, at an altitude of about 4,500 ft (1,370 m).	Mainly fruit, but also insects and warm-blooded animals.	Endangered

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Serge Larivière, PhD

Weasels, badgers, skunks, and otters
(Mustelidae)

Class Mammalia
Order Carnivora
Family Mustelidae

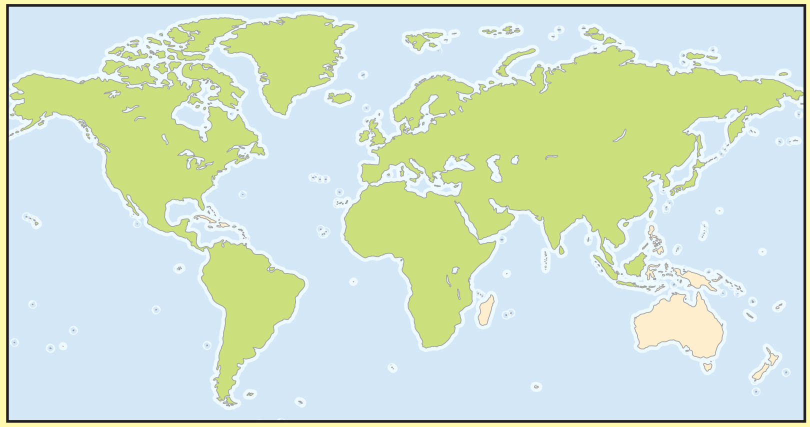
Thumbnail description
Small-to-medium carnivores characterized by long tubular shape or stocky build, short limbs, large necks, small heads, and habits that are either terrestrial or semi-aquatic

Size
4–60 in (0.1–1.5 m), 0.5–100 lb (0.25–45 kg)

Number of genera, species
25 genera; 65 species

Habitat
Forests, prairie, steppes, tundra, waterways, and seashore

Conservation status
Extinct in the Wild: 1 species; Endangered: 7 species; Vulnerable: 8 species; Lower Risk/Near Threatened: 1 species; Data Deficient: 4 species



Distribution
North and South America, Europe, Asia, Africa, and introduced in New Zealand

Evolution and systematics

The first Mustelidae appeared in the late Eocene to Oligocene from Europe and North America. Migrations to southern continents occurred first in Africa during the early Miocene, and then in South America in the Quarternary. Mustelids were among the first carnivore families to enter South America from the Panamanian land bridge, and they diversified in South America to 14 extant species.

Considered the most successful of the small carnivores, mustelids never evolved large body forms (less than 200 lbs or 100 kg), or cursorial open-country predators. Instead, mustelids are small to medium-sized, and dominate densely vegetated habitats where they occupy terrestrial, arboreal, and aquatic environments. The extant family Mustelidae includes five subfamilies: the Mustelinae (weasels, mink, polecats, and martens); the Mellivorinae (honey badgers), the Melinae (badgers), the Mephitinae (skunks), and the Lutrinae (otters). Skunks (genera *Conepatus*, *Mephitis*, and *Spilogale*) and stink badgers (genus *Mydaus*) have been suggested as belonging to their own family, the Mephitidae, based on genetic analyses. However, this classification proposed in 1997 has not yet been uniformly accepted.

European badgers (*Meles meles*) are nocturnal and live together in large underground catacombs called "setts." (Photo by Hans Reinhard. Bruce Coleman, Inc. Reproduced by permission.)

Physical characteristics

The body may be either long and slender with a long tail (weasels, mink, martens, andotters), or compact with a short tail (badgers and wolverines); there are five fingers and toes with non-retractile claws. Otters have fully webbed hind feet, and most also have webbed front feet (*Pteronura*, *Lutra*, and

Spraying defense of the western spotted shunk (*Spilogale gracilis*). 1. After noticing the threat, the skunk pulls up its tail and fluffs its fur to accentuate its warning markings. It may stamp its feet. 2. The skunk handstands, sometimes moving toward the threat. 3. If the threat does not withdraw, the skunk makes eye contact, moves into position, and sprays. (Illustration by Gillian Harris)

An American marten (Martes americana) in its forest habitat. (Illustration by Gillian Harris)

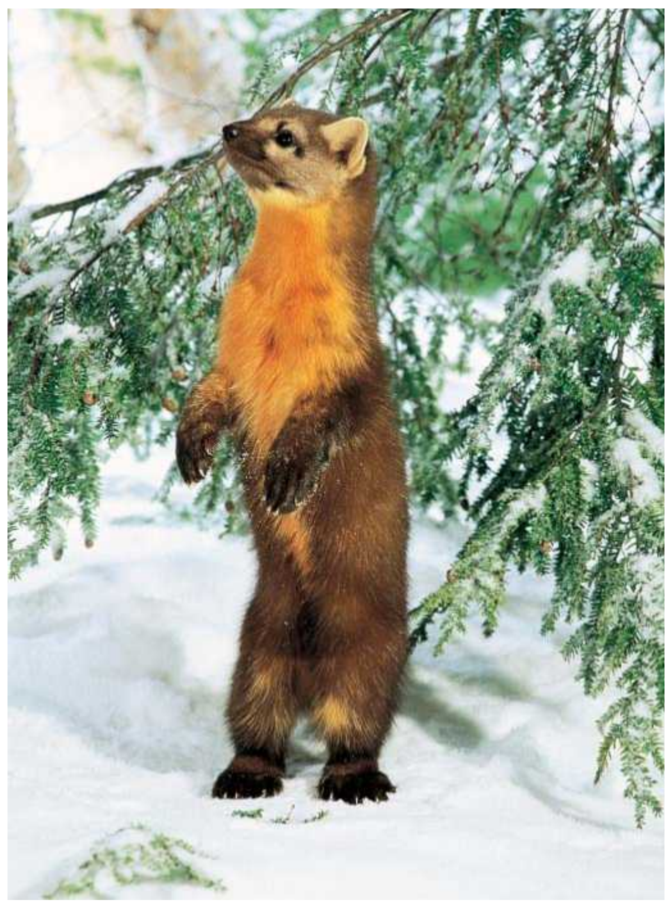
The yellow-throated marten (*Martes flavigula*) comes to the ground to feed. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

A juvenile striped skunk (*Mephitis mephitis*) foraging for insects. (Photo by E & P Bauer. Bruce Coleman, Inc. Reproduced by permission.)

Lontra) but one genus has long, dexterous, and unwebbed forefeet (*Aonyx*). Size varies from 4–10 in (11–26 cm) in the least weasel (*Mustela nivalis*), which is both the smallest mustelid and the smallest carnivore, to 40–60 in (100–150 cm) in the giant otter (*Pteronura brasiliensis*), the largest mustelid. Depend-

An ermine (*Mustela erminea*) turns from summer brown to winter white. (Photo by E & P Bauer. Bruce Coleman, Inc. Reproduced by permission.)

A spotted skunk (*Spilogale putorius*) in a hollow log. (Photo by Jeff Foott. Bruce Coleman, Inc. Reproduced by permission.)



The American marten (*Martes americana*) is found in coniferous forests in northern North America south to the Rocky Mountains and east into New England. (Photo by Malsowski/Photo Researchers, Inc. Reproduced by permission.)

Northern river otters (*Lontra canadensis*) run on the ice at the edge of a river in Wyoming, USA. (Photo by Bob & Clara Calhoun. Bruce Coleman, Inc. Reproduced by permission.)

A honey badger (*Mellivora capensis*) with the python it has killed. (Photo by J & D Bartlett. Bruce Coleman, Inc. Reproduced by permission.)

A badger (*Taxidea taxus*) guards its den in Montana, USA. (Photo by James Allen. Bruce Coleman, Inc. Reproduced by permission.)

A river otter (*Lutra canadensis*) eating trout. (Photo by Joe McDonald. Bruce Coleman, Inc. Reproduced by permission.)

ing on species, males are 10–100% larger than females. All species have strong canine teeth for capturing and killing prey.

Coloration ranges from completely white (winter coloration of least weasels) to silver (badgers *Taxidea taxus* and *Meles meles*), pale to dark brown (mink, fisher *Martes pennanti*, and otters), and black and white (skunks). Pelage is either uniform (mink and otters), spotted or marbled (genera *Spilogale* and *Vormela*), or striped (*Gulo* and *Mephitis*). Many species have facial stripes (skunks and badgers), or marking on the throat (American marten [*Martes americana*], spotted-necked otter [*Lutra maculicollis*], giant otter, and American mink [*Mustela vison*]). All species possess anal glands, and skunks (genera *Conepatus*, *Mephitis*, and *Spilogale*), zorillas (genus *Ictonyx*), and stink badgers (genus *Mydaus*) can spray the liquid secretions to repel aggressors.

Distribution

Mustelids occupy all continents except Antarctica. Mustelids were originally absent from Australia, but stoats (ermine or *Mustela erminea*), least weasels, and ferrets (*Mustela putorius*) were introduced to New Zealand to control rabbits.

Habitat

The Mustelidae are a diverse family that occupies a wide range of habitats from aquatic systems (otters and mink) to prairies (black-footed ferret, *Mustela nigripes*, and North American badger, *Taxidea taxus*), steppes (steppe polecat, *Mustela eversmanni*), treeless tundra (wolverine, *Gulo gulo*), and forests (most mustelids). Some species, such as striped skunk (*Mephitis mephitis*), tolerate humans well and abound in urban areas.

Behavior

Mustelids are mostly nocturnal, terrestrial (most species), or semi-aquatic (mink and otter), and they shelter in burrows, hollow trees, dense vegetation, rock crevices, or abandoned buildings during the day. Many species such as weasels, mink, and ferrets shelter in burrows of their prey. Most mustelids are agile tree climbers and good swimmers. One species, the sea otter (*Enhydra lutris*), is almost entirely aquatic.

Most species are solitary, but group living occurs in otters and European badgers (*Meles meles*). Some species defend exclusive territories (e.g., groups of European badgers), while others (such as striped skunk) use non-exclusive ranges that overlap with both males and females of the same species. Many species, such as otters, use their anal glands for scent marking, and skunks and stink badgers use their anal glands for defense.

Vocalizations are most developed in the Lutrinae (otters), which display a wide range of calls from purring sounds, threatening growls, and alarm calls. Skunks, zorillas (genus *Ictonyx*), and marbled polecats (*Vormela peregusna*) communicate their noxiousness to potential predator species through warning displays, whereas other mustelids may growl (badgers and wolverine) or release musk from their anal glands when threatened (weasels and mink). Most mustelids escape predation by escaping inside burrows (badgers and skunks), climbing trees (weasels, martens and wolverine), or seeking refuge in water (mink and otter). Play behavior occurs mostly in juveniles, and in adults is best known in otters sliding down muddy or snowy banks, or playing with inanimate objects in the water.

Feeding ecology and diet

Mustelids are either true carnivores (weasels, martens, and otters) or omnivores that also consume fruits and plant material (skunks, badgers, and tayra). Most species are proficient predators, killing rodent prey with a bite at the back of the neck. Small mammals such as mice and voles constitute the staple prey for most species; fish, crustaceans, and amphibians dominate the diet of otters. Most species consume reptiles opportunistically. Some species such as wolverines and fishers are opportunistic scavengers.

The long tubular shape of many mustelids allows them access to burrows of their prey. Weasels often hunt in burrows of small rodents, and American mink regularly access burrows of the muskrat (*Ondatra zibethicus*). Similarly, ferrets access the burrows of rabbits and hares.

Some mustelids display feeding specialization or associations with other species. The black-footed ferret depends on prairie dogs (genus *Cynomys*) for both food and shelter. American mink also relies heavily on muskrats as prey and use muskrat burrows and lodges as shelter. In northern Canada and the United States, the northern river otter (*Lontra canadensis*) uses burrows and lodges of beavers (*Castor canadensis*) for daily shelter and as maternity dens. Fishers probably evolved as expert predators of North American porcupines (*Erethizon dorsatum*). Others such as wolverines often associate with larger predators such as wolves (*Canis lupus*) to scavenge remains of their kills.

Reproductive biology

Only one species of mustelid, the giant otter, is monogamous; all other Mustelidae are promiscuous, meaning that individuals of both sexes will mate with numerous members of the other sex. Pair-bonds are typically short, and in some species such as striped skunk, American mink, and wolverine, ovulation is induced by copulation. Females have one litter per year, and males do not provide care for the young.

Implantation of the blastocyst into the uterine wall is delayed in many species such as wolverine, American marten, fisher, and sea otter. However, not all mustelids have delayed implantation, and many species closely related do not share this trait. For example, ermines (*Mustela erminea*) have delayed implantation whereas least weasels do not. Similarly, western spotted skunks (*Spilogale gracilis*) have delayed implantation whereas eastern spotted skunk (*Spilogale putorius*) do not. Delayed implantation likely offers species living in seasonal environments an advantage by allowing decoupling of mating and parturition and allowing parturition to occur at the peak availability of resources.

Conservation status

Many species are threatened because of habitat loss (e.g., black-footed ferret and many otters), or competition from other, non-native mustelids (European mink, *Mustela lutreola*). In contrast, several mustelids are extremely abundant and considered pests: stoats in New Zealand for depredation of native birds, skunks in North American cities for risk of rabies, and American mink in Europe for competition with the declining European mink. In 2003, 21 species of extant mustelids were listed by the IUCN. Among those, the black-footed ferret is listed as Extinct in the Wild, and seven additional species were listed as Endangered: the sea otter, the marine otter (*Lontra felina*), the southern river otter (*Lontra provocax*), the Colombian weasel (*Mustela felipei*), the European mink, the Indonesian mountain weasel (*Mustela lutreolina*), and the giant otter.

Black-footed ferrets, the most endangered of all mustelids, once occurred throughout the Great Plains in 12 states and two Canadian provinces, and possibly portions of northern Mexico. By the 1960s, the only known population of black-footed ferrets was a small colony in southwestern South Dakota, which disappeared in l974 for unknown reasons. In 1981, a black-footed ferret was killed by a ranch dog in northwestern Wyoming, and this event led to the discovery of about 130 ferrets near Meeteetse, Wyoming. However, outbreaks of sylvatic plague and canine distemper killed nearly all of the Meeteetse population. Consequently, the remaining 18 ferrets were taken into captivity between 1985 and 1987 in an effort to save the species. Beginning in Wyoming, reintroduction efforts have since expanded to sites in Montana, South Dakota, and Arizona. The Recovery Plan for the black-footed ferret calls for the establishment of 10 or more separate, self-sustaining wild populations. In 2003, black-footed ferret still occupied less than 2% of its original range.

Significance to humans

Mustelids are of great significance to humans as furbearers. In North America, annual harvest of weasels, mink, martens, fishers, otters, and wolverines significantly contributes to the economy. In Russia, the fur trade is especially strong for sables (*Martes zibellina*).

Few mustelids are consumed for meat. In North America, striped skunks are an important vector of rabies, especially in the midwestern United States and Canada and the southwestern United States. In Europe, the European badger carries bovine tuberculosis, which is a significant concern to European farmers and consequently led to persecution of the badger near farms. Other mustelids also are considered pests on occasion. When near human habitations, skunks damage lawns, consume human refuse, and occasionally spray pets; weasels and ferrets may depredate domestic chickens; and otters may visit commercial fish ponds.

In Asia, species of otters such as Asian small-clawed otters (*Amblonyx cinereus*) and smooth-coated otters (*Lutrogale perspiciallata*) are tamed and used by indigenous people to catch fish. Throughout the world, ferrets are kept as pets. In North America, striped skunks also are kept as pets after their anal glands are surgically removed. Mustelids are popular in zoological gardens, especially otters, because of their playful behavior and underwater agility, and most importantly, willingness to be active during the daytime.

1. Tayra (*Eira barbara*); 2. American mink (*Mustela vison*); 3. European badger (*Meles meles*); 4. Ermine (*Mustela erminea*) white winter phase; 5. Ermine (*M. erminea*) breeding phase; 6. Wolverine (*Gulo gulo*); 7. European otter (*Lutra lutra*); 8. Striped skunk (*Mephitis mephitis*). (Illustration by Gillian Harris)

Species accounts

Ermine

Mustela erminea

SUBFAMILY

Mustelinae

TAXONOMY

Mustela erminea Linnaeus, 1758, Europe and Asia.

OTHER COMMON NAMES

English: Stoat, short-tailed weasel; French: Belette à queue courte, hermine; German: Wiesel, Hermelin; Spanish: Armiño, mostela.

PHYSICAL CHARACTERISTICS

Body length 6–10 in (15–25 cm), tail 2–4 in (3–10 cm), weight 0.3–0.8 lb (125–350 g). Long, tubular-shaped body with short limbs. Pelage brown during summer, white during winter, always with a black-tipped tail.

DISTRIBUTION

The ermine has the greatest distribution of all weasels. It occurs across Europe, Ireland, parts of Asia, into Japan, northern India, Algeria, Mongolia, on Greenland, and across most of North America, and was introduced in New Zealand.

HABITAT

Inhabits farmland, forests, marshes, steppes, river valleys, even human settlements of North America and Europe.

BEHAVIOR

Specialist on mice, weasels often visit rodent burrows when hunting. Active throughout day and night, ermines are solitary and hunt and hide beneath roots, rock crevices, rodent burrows, wood piles, around old barns and buildings—anywhere small rodents may occur. Prey is detected by smell, hearing, or vision, and most are killed by a bite at the back of the neck. Ermines are good climbers and may use trees to rest, search for food, or escape predators.

FEEDING ECOLOGY AND DIET

Mostly rodents, especially mice, voles, and lemmings. On occasion, may kill ground squirrels, rabbits, birds and bird eggs, and insects. Surplus killing may occur, and ermines cache extra food for later use.

REPRODUCTIVE BIOLOGY

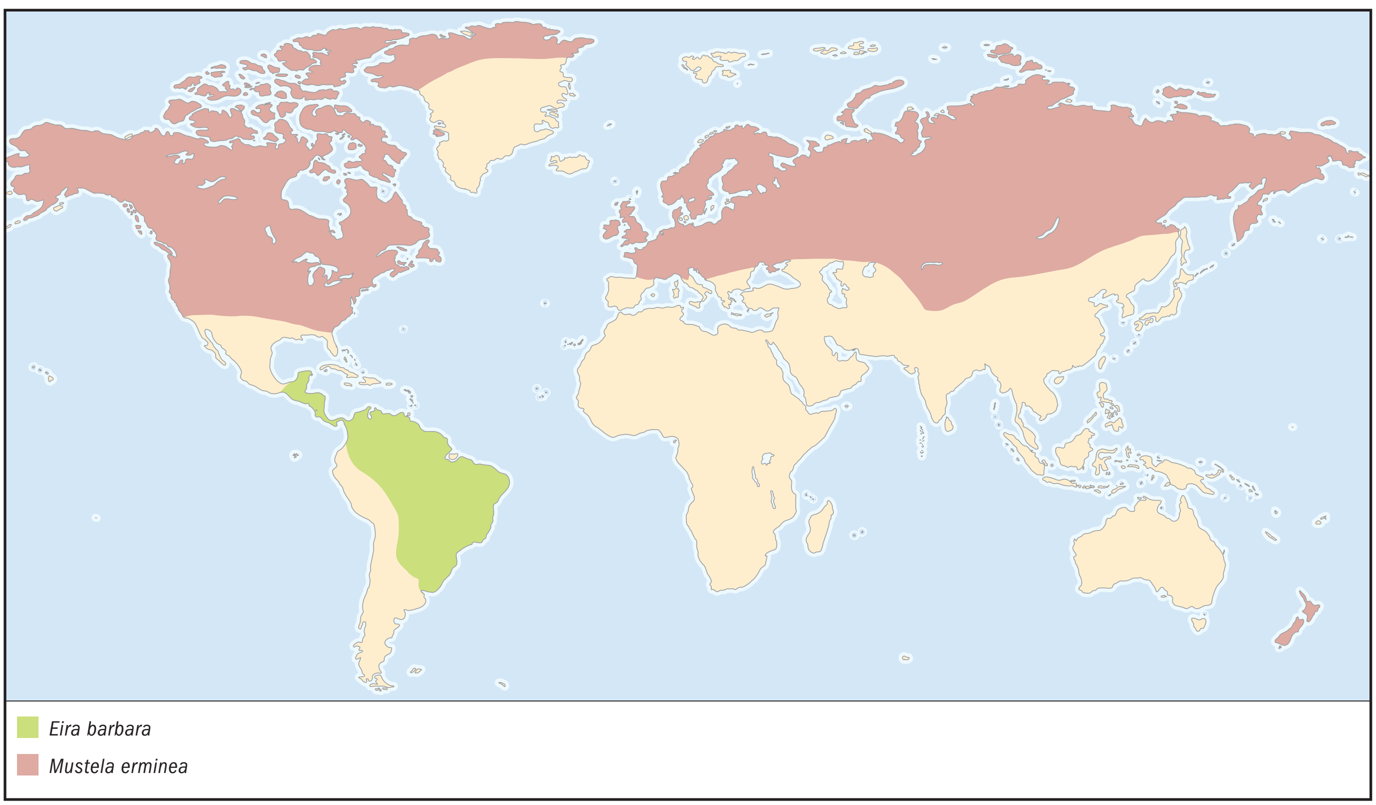
Promiscuous. Mating occurs in summer, and implantation is delayed nine to 10 months. Total gestation is 280 days, and litter size is typically four to eight.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Harvested as a furbearer in Canada and United States. The winter coat of ermine has been used for centuries as an article of clothing. Royalty traditionally wore white ermine capes, with the black tail tips sewed on, during festive occasions.



Around 1885, the stoat or ermine was introduced into New Zealand (from England) to control the expanding rabbit population and the results were disastrous. Stoats depredate local birds and their eggs, and efforts to eradicate stoats require large sums of money. ◆

American mink
Mustela vison

SUBFAMILY
Mustelinae

TAXONOMY
Mustela vison Schreber, 1777, eastern Canada.

OTHER COMMON NAMES
French: Vison américain; German: Amerikanischer Nerz; Spanish: Vison.

PHYSICAL CHARACTERISTICS
Body length 12–20 in (30–50 cm), tail 6–8 in (16–20 cm), weight 1.7–4.0 lb (0.8–1.8 kg). Mink have a long, tubular shape with short limbs, large neck and small head. Pelage is chocolate brown throughout, often with white marking on the chin and chest. Tail is slightly darker than body.

DISTRIBUTION
Occurs throughout North America wherever suitable water bodies occur. American mink have been introduced in many areas following escapes from fur farms and now inhabit South America and most of western Europe.

HABITAT
American mink occur in proximity to water in a wide variety of habitats from farmland to pastures, mixed forests, prairies, and evergreen forests, even north into the tundra.

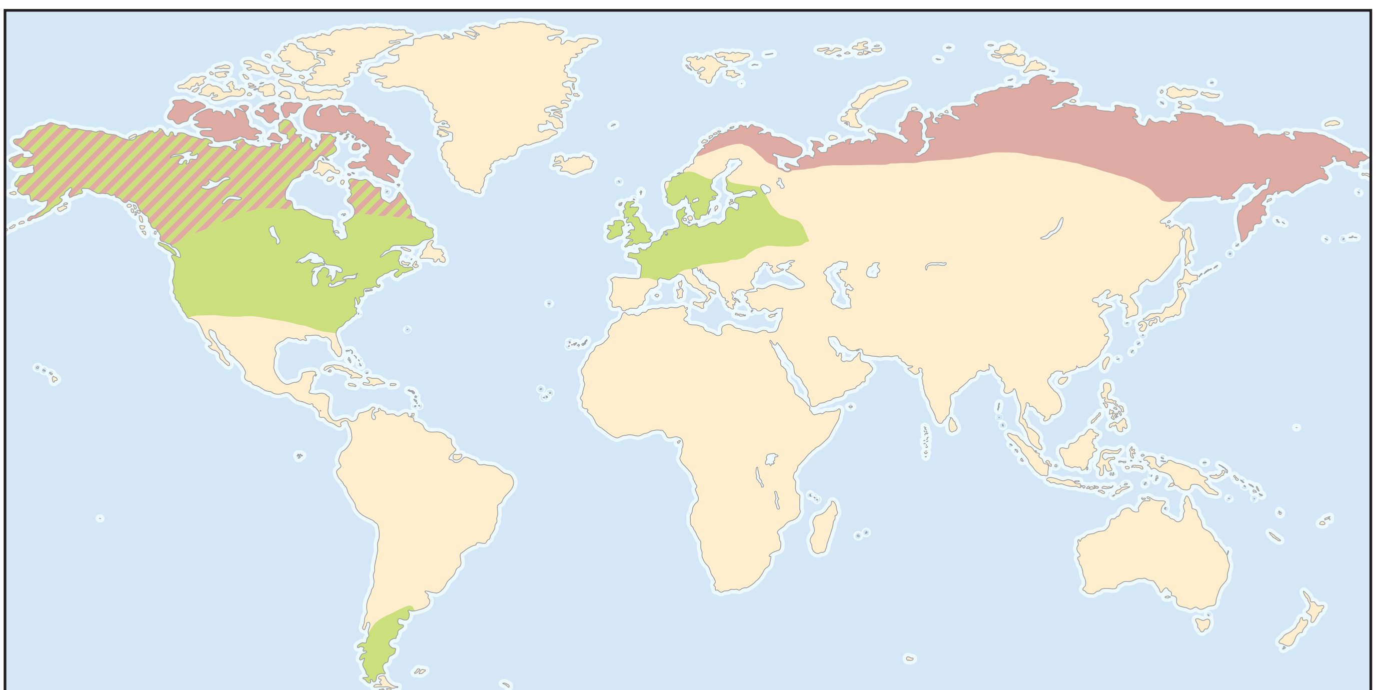
BEHAVIOR
They hunt mostly at night along creeks and waterways, searching for prey in and around water. Mink are skillful swimmers and divers, and can climb trees.

FEEDING ECOLOGY AND DIET
Feeds chiefly on small mammals, muskrats, fish, crayfish, frogs, and rabbits.

REPRODUCTIVE BIOLOGY
Promiscuous. Breeding occurs in the spring, gestation is 51 days, and the litter size is two to eight, typically four. Females raise young alone. Longevity may reach eight years in captivity, but typically is less than three years in the wild.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
The fur trade of the American mink probably is the most popular of all Mustelidae. Since World War I, American mink have been raised on farms where selective breeding can produce color variations such as pure white mink, completely black mink, silver-blue-gray varieties ("platinum"), and blue ones ("sapphire"). Because of their popularity, American mink were introduced into numerous countries of Europe and Asia. Subsequently, escapes from fur farms and releases led to the establishment of numerous feral populations outside of the original range. Impacts on native wildlife soon became appar-



Mustela vision
Gulo gulo

ent and the American mink is now considered a pest for destroying and competing with native animals. ◆

Striped skunk

Mephitis mephitis

SUBFAMILY

Mephitinae

TAXONOMY

Viverra mephitis (Schreber, 1776), eastern Canada.

OTHER COMMON NAMES

French: Moufette rayée; German: Streifenskunk; Spanish: Zorillo, moufetta.

PHYSICAL CHARACTERISTICS

Body length 13–18 in (33–45 cm, tail 7–10 in (18–25 cm), weight 4–18 lb (2–8 kg). Easily recognized by the black pelage contrasting with the two dorsal white stripes that unite on the nape. Tail is bushy and mixed with black and white hairs. Front claws are long for digging.

DISTRIBUTION

Occurs throughout most of the United States and Canada south to northern Mexico.

HABITAT

Occurs in farmland, grasslands and forests, and also in numerous large cities.

BEHAVIOR

Nocturnal, the striped skunk shelters in abandoned buildings or underground burrows during the day. When threatened, striped skunks raise the tail, stomp the feet, do fake charges, and if needed, turn in a U-shape and spray their aggressor with the noxious fluid stored in their anal glands. The liquid is harmless to skin, and can easily be washed off; it irritates the eyes, causing extreme pain and may even result in temporary blindness. The smell is very difficult to remove from clothing. In northern environments, skunks become dormant in winter and must accumulate large amounts of fat to survive the long (sometimes up to six months) winters. Longevity may exceed eight years in captivity, but seldom exceeds three years in the wild.

FEEDING ECOLOGY AND DIET

Opportunistic omnivore that consumes mainly small rodents and insects, but also reptiles, amphibians, bird eggs, fruits, and seeds.

REPRODUCTIVE BIOLOGY

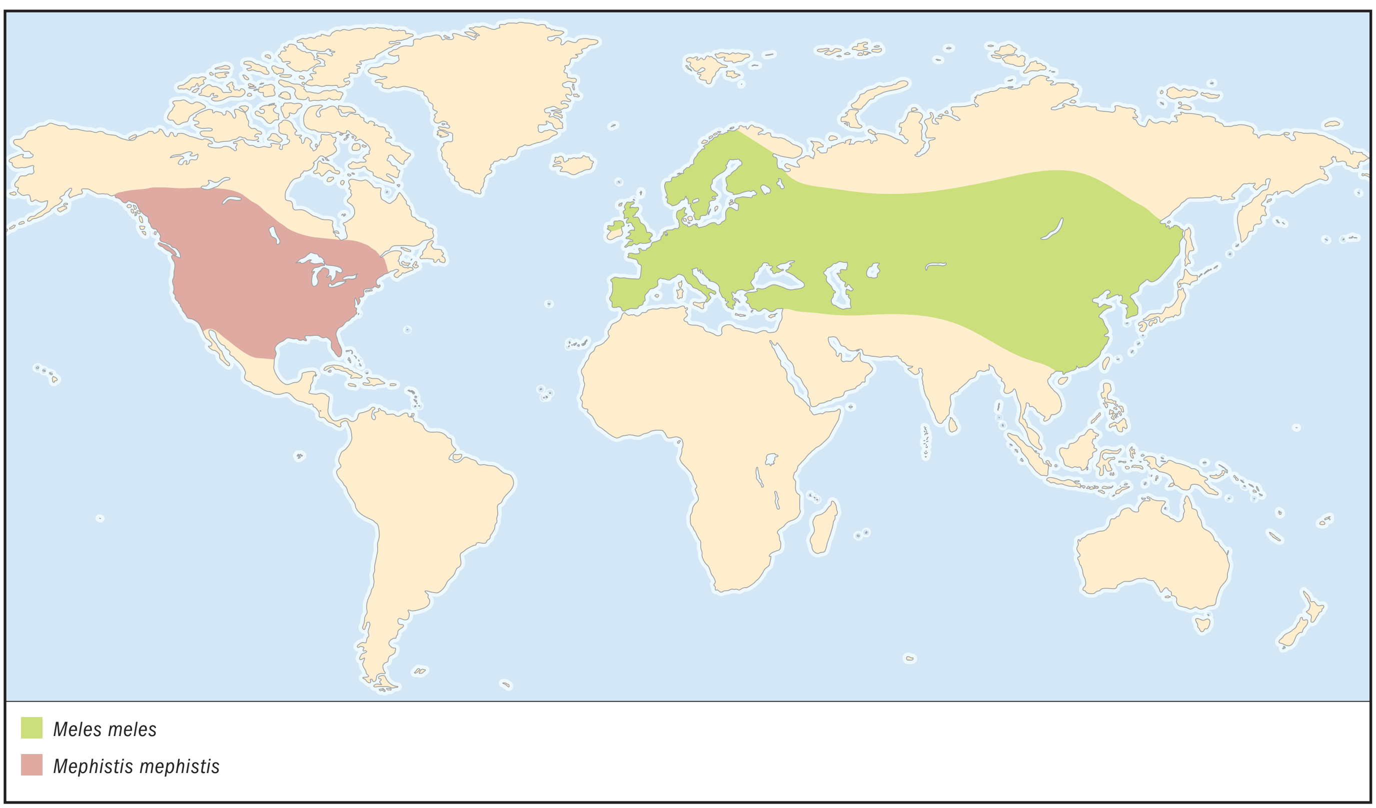
Promiscuous. Mating occurs in spring, implantation delay is short (less than 14 days) and variable, and between four and 10 young are born in April or May.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

The striped skunk is an important vector of rabies in North America, and because of that, is often considered undesirable around human habitations. Also, the noxious smell of skunks typically annoys landowners, who fear their pets may get sprayed. In some areas, striped skunks are important predators of duck eggs. In others, skunks may kill bees or damage beehives and thus are considered pests. ◆



European otter
Lutra lutra

SUBFAMILY
Lutrinae

TAXONOMY
Mustela lutra (Linnaeus, 1758), Sweden.

OTHER COMMON NAMES
French: Loutre d'Europe; German: Otter; Spanish: Nutria.

PHYSICAL CHARACTERISTICS
Body length 25–33 in (65–85 cm), tail 15–20 in (36–52 cm), weight 15–33 lb (7–15 kg). Long, tubular body with large neck, small flat head, small round eyes and ears, short limbs, and long tail flattened dorso-ventrally. All feet are fully webbed with short claws. Pelage is dark brown to black throughout, and fur is short and dense.

DISTRIBUTION
Europe, Asia, and north Africa.

HABITAT
Occupies streams, ponds, rivers, lakes, swamps, and coastal areas.

BEHAVIOR
Travels alone or in groups, remaining in the water but occasionally crossing over land to reach other waterways. Prey are captured by active pursuit underwater, and larger prey are taken to shore for consumption. Longevity may exceed 20 years in captivity.

FEEDING ECOLOGY AND DIET
Fish, frogs, crabs, crayfish, small rodents, and aquatic birds.

REPRODUCTIVE BIOLOGY
Promiscuous. Litter size is two to four born in a waterside hole or crevice in April or June.

CONSERVATION STATUS
Vulnerable.

SIGNIFICANCE TO HUMANS
European otters were historically hunted for their fur but are now protected through most of their distribution. May be considered as pests and killed on occasion for predation of fish in commercial fish ponds. ◆

Wolverine
Gulo gulo

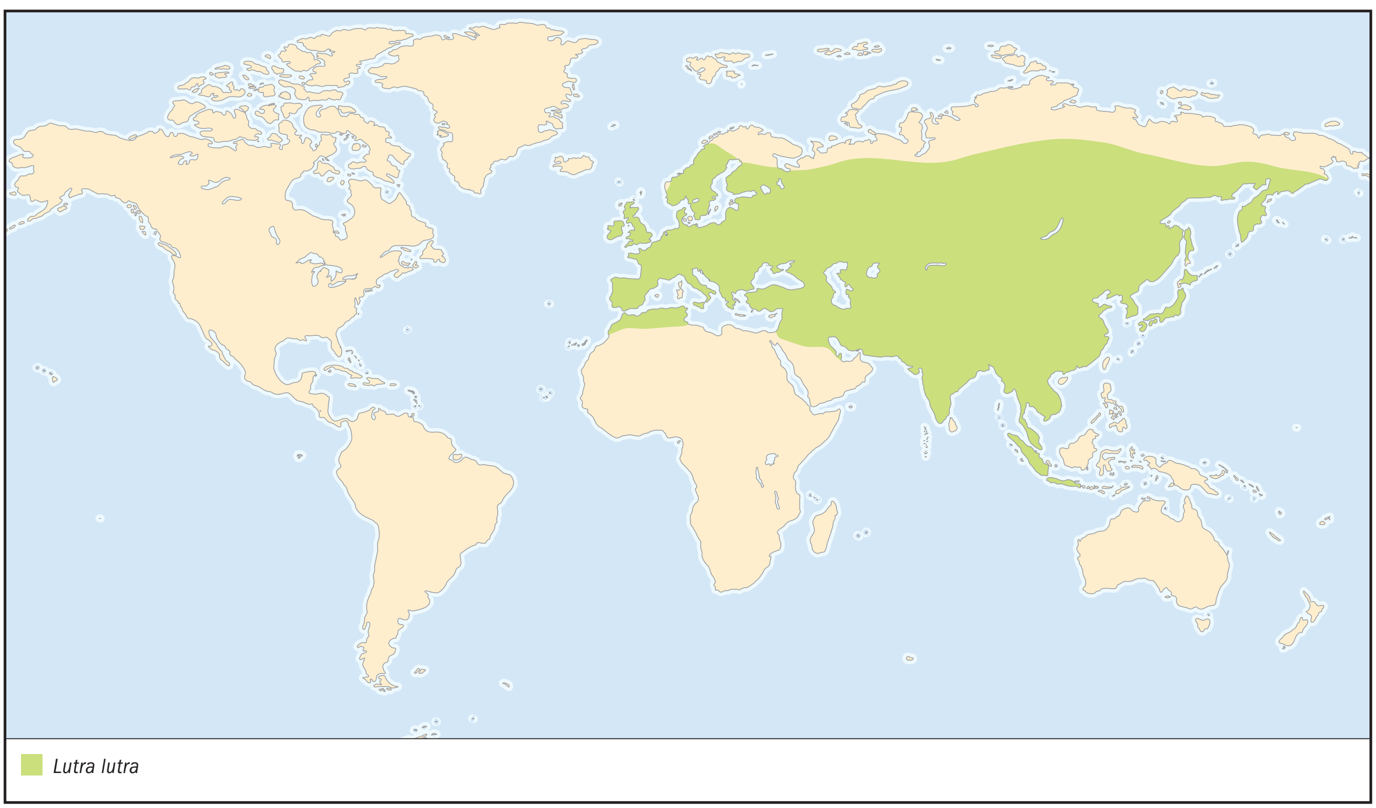
SUBFAMILY
Mustelinae

TAXONOMY
Mustela gulo (Linnaeus, 1758), Sweden.

OTHER COMMON NAMES
French: Carcajou, glouton; German:Vielfraß.

PHYSICAL CHARACTERISTICS
Body length 25–34 in (65–87 cm), tail 7–10 in (17–26 cm), weight 22–55 lb (10–25 kg). Large and stocky. Pelage is brown most often with two yellowish stripes on back. Feet are broad and furred, webbed, and front feet have long, strong claws.

DISTRIBUTION
Throughout the northern part of North America and Asia.



HABITAT
Mostly in boreal forests, taiga, and tundra.

BEHAVIOR
Wolverines are solitary, wide-roaming carnivores that abound where large game such as moose, caribou, or reindeer occur. Wolverines are strong climbers, and may follow wolves to scavenge remains of the prey killed by the pack hunters. Wolverines may be killed by wolves. Longevity may reach 16 years in captivity.

FEEDING ECOLOGY AND DIET
Wolverines are mostly scavengers that consume remains of large game. They may also kill and eat small mammals, birds and bird eggs, and can kill large ungulates or other carnivores such as lynx on occasion.

REPRODUCTIVE BIOLOGY
Promiscuous. Breeding occurs in summer. Gestation is long (215–275 days) because implantation is delayed. Litter size is one to four.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Hunted for its fur, especially in Alaska and Canadian territories. ◆

European badger
Meles meles

SUBFAMILY
Melinae

TAXONOMY
Ursus meles (Linnaeus, 1758), Sweden.

OTHER COMMON NAMES
French: Blaireau d'Europe; German: Dachs; Spanish: Téjon.

PHYSICAL CHARACTERISTICS
Body length 24–33 in (60–85 cm), tail 6–8 in (15–20 cm), weight 22–44 lb (10–20 kg). Head long and slender, stocky build, short limbs. Fur is long, thin, and stiff, and there is little underfur. Pelage is grayish throughout.

DISTRIBUTION
Throughout Europe and Asia south of the Arctic Circle.

HABITAT
Occurs in forests, ravines, and parks.

BEHAVIOR
Active mostly at night, Eurasian badgers are social carnivores that hide in burrows (setts) during the day. May spend winter sleeping in burrows in northern environments. Longevity may reach 15 years in captivity.

FEEDING ECOLOGY AND DIET
Earthworms, snails, insects, small rodents, hedgehogs, fruits, seeds, mushrooms, and roots.

REPRODUCTIVE BIOLOGY
Promiscuous. Breeds in summer, implantation of fertilized egg is delayed, and litter of two to five young is born in February or March.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
European badgers may conflict with humans because of damage to lawns, gardens, or golf courses. They also carry bovine tuberculosis, and programs to control badger abundance near cattle operations are in place, especially in Great Britain. ◆

Tayra
Eira barbara

SUBFAMILY
Mustelinae

TAXONOMY
Mustela barbara (Linnaeus, 1758), Brasilia (Brazil).

OTHER COMMON NAMES
English: Bushdog; French: Taira; German: Tayra; Spanish: Cabeza de viejo, gato negro.

PHYSICAL CHARACTERISTICS
Body length 22–27 in (56–71 cm), tail 15–18 in (37–46 cm), weight 4–15 lb (2–7 kg). Large and slender with long legs and long tail. Pelage dark brown to black, with grayish or pale yellow heads and neck.

DISTRIBUTION
Southern Mexico south to northern Argentina, and across most of South America east of the Andes.

HABITAT
Occurs in tropical or subtropical forested habitats, but also occupies human-altered habitats such as plantations, gardens, orchards.

BEHAVIOR
Solitary and wide ranging, tayras are mostly diurnal.

FEEDING ECOLOGY AND DIET
Fruits, small rodents, carrion, insects, honey, and birds.

REPRODUCTIVE BIOLOGY
Promiscuous. Breeding occurs year-round, gestation 65 days, litter size one to three young.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Locally hunted for their fur. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Western hog-nosed skunk *Conepatus mesoleucus* Spanish: Mofeta de mancha blanca	Coloration is black except for two white stripes, beginning at nape and extending to hips. Long, coarse fur, bushy tail with few black hairs on underside, small eyes and ears. One of the larger skunks. Average male length 22.7 in (57.7 cm), female 21.3 in (54.2 cm), weight 2.4–6 lb (1.1–2.7 kg).	Foothills, partially timbered, or brushy areas. They avoid open desert and heavily wooded areas, and instead choose rocky areas where they make their dens. Breeding season begins in February. Litter consists of up to three young. Mostly nocturnal, groups not common. Powerful musk.	Arizona, Colorado, and Texas, United States, south to Nicaragua.	Species is omnivorous and food depends on season. Consumes mostly insects, arachnids, vegetable matter, some reptiles, and small mammals.	Not threatened
Zorilla *Ictonyx striatus* English: Striped polecat; Spanish: Comadreja rayada	Coloration is black with white dorsal stripes, tail is white, face has white markings. Head and body length 11–15.2 in (28–38.5 cm), tail length 7.9–12 in (20–30.5 cm).	Variety of habitats, but avoid dense forest. Can be found in temperate forest and rainforest, desert, tropical, deciduous forest, tropical scrub forest, tropical savanna, and grasslands. Mating season from early spring to late summer. Usually three young per litter. Extremely solitary.	Africa from Sudan to South Africa.	Small rodents, large insects, eggs, snakes, birds, frogs, small mammals, and reptiles.	Not threatened
Hairy-nosed otter *Lutra sumatrana* French: Loutre de Sumatra; Spanish: Nutria de Sumatra	Upperparts brownish, underparts paler. Lower jaw and throat are whitish, fur is short and dense, head is flattened and round. Small ears and nostrils close in water. Head and body length 18.1–32.3 in (46–82 cm), tail length 11.8–19.7 in (30–50 cm).	All types of inland waterways, estuaries, and marine covers. Excellent swimmers and divers. May shelter in small burrows. Swim by movement of hind legs and tail. May be either diurnal or nocturnal.	Indochina, Thailand, Malay Peninsula, Sumatra, Bangka, Java, and Borneo.	Fish, frogs, crayfish, crabs, and other aquatic invertebrates. May also consume birds and land mammals, such as rodents and rabbits.	Data Deficient
Patagonian weasel *Lyncodon patagonicus* German: Zwerggrison; Spanish: Huroncito patagónico	Coloration is grayish brown with a whitish tinge on back. Top of head is white. Underparts are brown. Head and body length 11.8–13.8 in (30–35 cm), tail length 2.4–3.5 in (6–9 cm).	Pampas. Habits are little known.	Argentina and southern Chile.	Very carnivorous animal, rats are most likely a large part of diet.	Not threatened
European pine marten *Martes martes* Spanish: Marta de los pinares	Coloration is rich brown, thick and silky fur. Complete molt once a year. Tail is long and bushy, ears large and triangular. Head and body length 17.7–22.8 in (45–58 cm), tail length 6.3–11 in (16–28 cm).	Forest habitats, including rainforest, temperate grassland, and deciduous, mixed, and coniferous forest. Old-growth forest is often preferred over young forest. Considered to be habitat specialist. May also show no habitat preference and reside in shrubland. Two to 5 offspring per litter. Mating occurs within 30- to 45-day periods. Mostly active during night and at dusk.	Western Europe to western Siberia and the Caucasus, Ireland, Britain, Corsica, Sardinia, and Sicily.	Mostly carnivorous, relying on small mammals for most of the year. The diet composition and proportion often change according to season and local conditions. Populations respond to the unpredictable cycles of rodents, such as voles, by drastically increasing their consumption of these prey items	Not threatened
Chinese ferret badger *Melogale moschata* Spanish: Tejón chino	Coloration of upperparts is gray brown to brown balck. Underparts are paler. White or reddish dorsal stripe. Head is black with patches of white or yellow. Tail is bushy. Limbs are short, feet are broad. Head and body length 13–16.9 in (33–43 cm), tail length 5.7–9.1 in (14.5–23 cm).	Wooded country and grassland. Species makes burrows and shelters during day, active at night. Usually one to three young per litter.	Assam to southern China and northern Indochina, Taiwan, and Hainan.	Mostly omnivorous animals, but also consume arachnids, insects, small mammals, mollusks, and snails. Diet depends on seasonal availability.	Not threatened
Honey badger *Mellivora capensis* English: Ratel; Spanish: Tejón melívoro	Coloration is black with white strip that runs from above eyes to tip of tail. Head and body length 31.5 in (80 cm), tail length 3.9 in (10 cm).	Temperate climates, and not in overly hot and arid, or wet and dense ones, such as jungles and deserts. Can be found in tropical deciduous forest, temperate forest, and rainforest, temperate grassland, tropical savanna and grasslands. Solitary animal, but groups may consist of three members. Nomadic with large home range, very secretive, nocturnal.	Africa, the Middle East, and India.	Omnivorous. Most often observed consuming small reptiles, rodents, birds, insects and even carrion but also eats fruits, berries, roots, plants, and eggs. Occasionally honey.	Not threatened

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Hooded skunk *Mephitis macroura* Spanish: Mofeta de cola larga	Coloration is black with white stripe from eyes to tip of tail. Long, soft fur, especially on upper neck. Very long tails. Average male length 27.6 in (70 cm). Average male body weight 1.8–2 lb (800–900 g), female 0.9–1.5 lb (400–700 g).	Intermediate elevations, above deserts but below high mountains; desert scrub, closed basin scrub, plains-mesa grassland, desert grassland, and riparian areas. Mostly nocturnal.	Arizona and southwestern Texas, United States, to Nicaragua.	Insects and vertebrates such as shrews and rodents. Also eat plant material such as prickly pear fruit.	Not threatened
Indonesian stink badger *Mydaus javensis* English: Malaysian stink badger; Spanish: Tejón malayo	Coloration varies from dark black to blackish brown with white patch on the top of the head. A white mid-dorsal stripe extends from head and to tip of tail. Neck hair stands nearly erect. Small, squat, heavy, and nearly plantigrade body. Head and body length 14.6–20.1 in (37–51 cm), tail length 2–3 in (5–7.5 cm), weight 3.1–7.9 lb (1.4–3.6 kg).	Elevations often above 7,000 ft (2,130 m), but may occur below 4,000 ft (1,220 m) and even as low as 850 ft (260 m) in West Java. Most inhabit shallow burrows underground. Mainly nocturnal. Two or three offspring per litter.	Indonesian islands of Sumatra, Java, Borneo, and North Natuna Islands.	Forage mainly for insects and worms, but also feed on invertebrates and plant material. Consume bird eggs and carrion as well.	Not threatened
Philippine stink badger *Mydaus marchei* English: Philippine badger, Palawan stink badger; Spanish: Tejón filipino	Upperparts are brown to black, scattering of white hair on back, underparts brown. Head and body length 12.6–18.1 in (32–46 cm), tail length 0.6–1.8 in (1.5–4.5 cm), weight 5.5 lb (2.5 kg)	Elevations often above 7,000 ft (2,130 m). Active during day and night. Leaves track and scent along paths.	Palawan and Calamian Island (Philippines).	Forage mainly for insects and worms, but also feed on invertebrates and plant material. Consume bird eggs and carrion as well.	Vulnerable
Least weasel *Mustela nivalis*	Body is long and slender, long neck, short limbs. Large, black eyes. Mass depends on location, the largest originating from Africa. Coloration is chocolate brown on back side, white with brown spots on under side.	Wide variety of habitats, including open forests, farmlands, meadows, prairies, steppe, and semi-deserts. Avoids deep forests, sandy deserts, and open spaces. Separation of males and females, except during breeding season. Dens are taken from prey.	Western Europe and Asia Minor to northeastern Siberia and Korea, parts of China and possibly Indochina, Britain, several Mediterranean islands, Japan, northwestern Africa, Egypt, Alaska, Canada, and north-central United States.	Small mammals, mainly rodents, birds' eggs, nestlings, insects, and lizards	Not threatened
White-naped weasel *Poecilogale albinucha* Spanish: Comadreja serpiente	Sleek, long body with short legs. Coloration is black with white stripe from top of head to tip of tail and along sides. White stripe may be yellow to deep buff. Head and body length 9.8–14.2 in (25–36 cm), tail length 5.2–9.1 in (13–23 cm).	Forest edge, grassland, and marsh regions. Species is nocturnal and fossorial. Can climb very well, but usually stays on the ground. May be solitary or stay in groups of 2–4 family members. Releases an odor from its anal glands when it is attacked or under stress.	From Zaire and Uganda to South Africa.	Mainly carnivorous and eats small mammals, including rodents, rats, mole rats, and birds, and also snakes and insects.	Not threatened
North African striped weasel *Poecilictis libyca*	Back is white with variable patter of black bands. Tail is white, underparts and limbs are black. Hair on back stands erects. Head and body length 7.9–11.2 in (20–28.5 cm), tail length 3.9–7.1 in (10–18 cm).	Edges of Sahara and contiguous arid zones. Nocturnal, shelters throughout day. Litter contains two or three offspring. Disagreeable smell and aggressive toward humans.	Morocco and Senegal to the Red Sea.	Rodents, young ground birds, eggs, lizards, and insects.	Not threatened
North American badger *Taxidea taxus* Spanish: Tejón norteamericano	Upperparts are grayish to reddish, white stripe extends from neck and shoulder area to rump. Black patches present on face and cheeks. Head and body length 16.5–28.3 in (42–72 cm), tail length 3.9–6.1 in (10–15.5 cm), weight 8.8–26.5 lb (4–12 kg).	Relatively dry, open country. May be active at all hours, but mainly nocturnal. Mating in summer and early autumn.	Northern Alberta and southern British Columbia, Canada, to Ohio, United States, central Mexico, and Baja California.	Mainly prey within foraged dens, but also small mammals, birds, reptiles, and arthropods.	Not threatened
Marbled polecat *Vormela peregusna* Spanish: Turón jaspeado	Back is reddish brown, and white or yellowish, tail is whitish with dark tip. Underparts are dark brown or black, facial mask is dark brown. Head and body length 1.4–15 in (29–38 cm), tail length 5.9–8.6 in (15–21.8 cm), weight 0.8–1.6 lb (370–715 g).	Steppes and foothills. Species is solitary, except during breeding season. Mainly nocturnal, good climber, litter size is 4 to 8 young.	Steppe and subdesert zones from the Balkans and Palestine to Inner Mongolia and Pakistan.	Rodents, birds, reptiles, and other animals.	Not threatened

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Serge Larivière, PhD

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Civets, genets, and linsangs

(Viverridae)

Class Mammalia
Order Carnivora
Family Viverridae

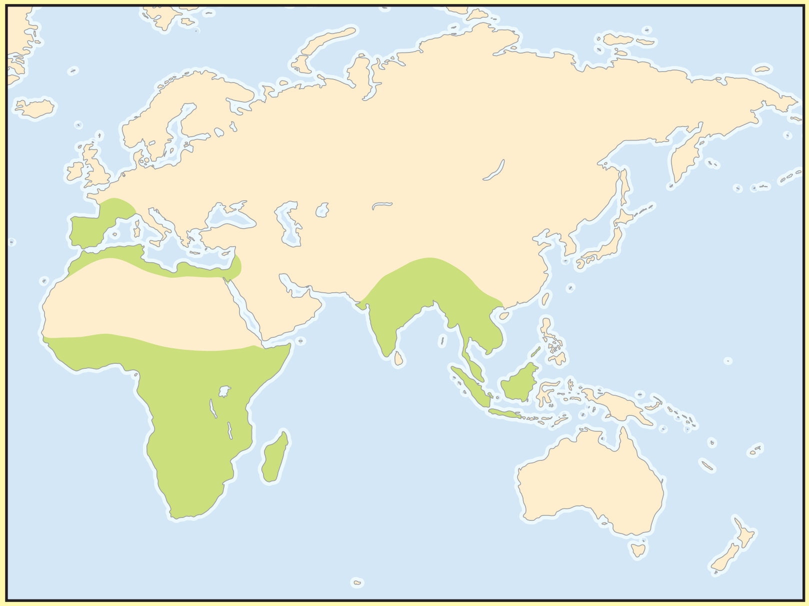
Thumbnail description
Small to medium carnivores resembling the Mustelidae but limited to the Old World; body and tail are long, legs are short, and face is elongated with a pointy nose and conspicuous ears; claws are short and sharp; many species with long, banded tails

Size
13–35 in (33–88 cm), 1.3–30 lb (0.6–13 kg)

Number of genera, species
20 genera; 34 species

Habitat
Forests, steppes, and brushland

Conservation status
Critically Endangered: 1 species; Endangered: 4 species; Vulnerable: 6 species; Data Deficient: 3 species



Distribution
Western Europe, Africa, Arabia, and Southeast Asia

Evolution and systematics

The Viverridae is an old and primitive carnivore family for which the fossil record is scarce. First appearance of Viverridae in Europe and Asia occurs in the early Oligocene and in Africa in the early Miocene. Because of incomplete records, the place of origin of viverrids in the Old World is unknown. Extant species resemble fossil forms, suggesting that skeletal morphology and tooth structure has remained unchanged for 40–50 million years. The diversity within the family is explained by the variety of the niches occupied, from truly terrestrial, partly to mostly arboreal, to aquatic. The mongooses were once considered in the Viverridae under a different subfamily, the Herpestinae. However, most authorities now recognize mongooses under the family Herpestidae.

The current Viverridae is divided into six subfamilies. The Euplerinae consists of two species in two genera, the falanouc (*Eupleres goudotii*) and the Malagasy civet (*Fossa fossana*). The Hemigalinae includes the otter civet (*Cynogale bennettii*) and three species of palm civets. The Nandiniinae has only one species, the African palm civet (*Nandinia binotata*), whereas the Paradoxurinae consists of five genera and seven species of palm civets as well as the binturong (*Arctictis binturong*). Finally, the largest subfamily is the Viverrinae, which consists of seven genera and 20 species of genets (*Genetta* and *Osbornictis*), civets (*Civettictis*, *Viverra*, and *Viverricula*), and linsangs (*Poiana* and *Prionodon*). Authorities are still debating the position of one species, the fossa (*Cryptoprocta ferox*), but it is herein considered with the mongooses in the Herpestidae.

Physical characteristics

Civets, genets, and linsangs are characterized by long, sinewy bodies, short legs with strong, sharp claws, long tails, and elongated heads with pointed snouts. Ears typically are fairly large and erect. Most species have short fur with, a slen-

A common genet (*Genetta genetta*), foraging. (Photo by Harald Schütz. Reproduced by permission.)

Blotched genets (*Genetta tigrina*) are nocturnal tree dwellers. (Photo by © George McCarthy/Corbis. Reproduced by permission.)

der appearance, and a long, non-prehensile tail that may exceed the length of the body. One species, the binturong, differs from most viverrids by having exceptionally long fur, stocky appearance, and a prehensile tail. Viverrids have five fingers and five toes. Perineal glands are present, and well developed in numerous species, especially *Civettictis civetta*, *Viverra zibetha*, and *Viverricula indica*. Pelage color is uniform in the binturong, but most species have dark spots, bands, or stripes, and many have banded tails.

Viverrids display adaptations based on the niche they occupy. Terrestrial species such as *Civettictis civetta*, *Viverra zibetha*, and *Eupleres goudotii* have digitigrade feet, non or semi-retractile claws, short tails, and fur with spots or stripes. Arboreal or semi-arboreal species can be separated into two groups, agile species that leap or jump (e.g., *Genetta servalina*) or less-agile species that grasp branches and move more slowly (*Arctictis binturong*, *Paguma larvata*, and *Paradoxurus* sp.). Agile arboreal species have digitigrade feet, long tails, and spotted fur, whereas less agile species have plantigrade feet, long tails, but uniform fur. Long tails occur in all arboreal species

This young African civet (*Civettictis civetta*) is on its way back to its lair in the rocks. (Photo by Cyril C. Laubscher. Bruce Coleman, Inc. Reproduced by permission.)

and help animal maintain their balance. Aquatic species have bare soles, plantigrade feet, uniform pelage, and long tails.

Distribution

The Viverridae are confined to the Old World, and occupy parts of western Europe, most of Africa including Madagascar, Southeast Asia, and Malaysia.

The banded linsang (*Prionodon linsang*) uses its tail to help keep its feet warm. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

The banded palm civet (*Hemigalus derbyanus*) is mostly terrestrial but has the ability to climb trees. (Photo by Art Wolfe/Photo Researchers, Inc. Reproduced by permission.)

Habitat

The Viverridae occupy tropical forests and densely vegetated areas. Possibly the most flexible species is the common genet (*Genetta genetta*), which can be found in deciduous forests, plantations, steppes, and parks.

Behavior

The Viverridae are shy animals that are primarily nocturnal. They are solitary, or live in pairs or small groups. Most species are good climbers, some are almost exlusively arboreal (*Paradoxurus hermaphroditus* and *Poiana richardsonii*, for example), and two species, the otter civet and the aquatic genet (*Osbornictis piscivora*), are aquatic. Many species such as *Genetta genetta* use secretions from their anal glands to scent mark their territories. Scent marks are deposited either passively when moving through vegetation, or actively by squatting and rubbing the anal region on the ground or on prominent objects. Scent marks likely allow assessment of social status, individual recognition, kin recognition, and sexual receptiveness. Vocalizations are well developed in some species.

The behavior and ecology of most species of Viverridae are poorly known, and the family is probably the least known of all carnivores. Most species are nocturnal and shy, and occupy dense vegetation. Because few species are of commercial value to humans, and because most are secretive, few studies have been devoted to gaining a better understanding of this group. Knowledge of spacing patterns and population estimates are unavailable for most species, and much current knowledge arises from opportunistic observations or specimen collections for museums, or from captive animals kept as pets or in zoological gardens.

Feeding ecology and diet

All species are opportunistic feeders, although some specialization occurs toward frugivory in palm civets, to a mostly carnivorous diet in genets. The Viverridae are excellent predators and mostly use their sense of sight and hearing to find prey.

A common genet (*Genetta genetta*) sitting in a tree. (Photo by © Peter Johnson/Corbis. Reproduced by permission.)

An African civet (*Civettictis civetta*), foraging. (Photo by Harald Schütz. Reproduced by permission.)

Reproductive biology

Breeding occurs seasonally or throughout the year. Some groups may bear two litters per year, and litter size is one to six. Young are born blind but furred. Little else is known of their reproduction or mating system.

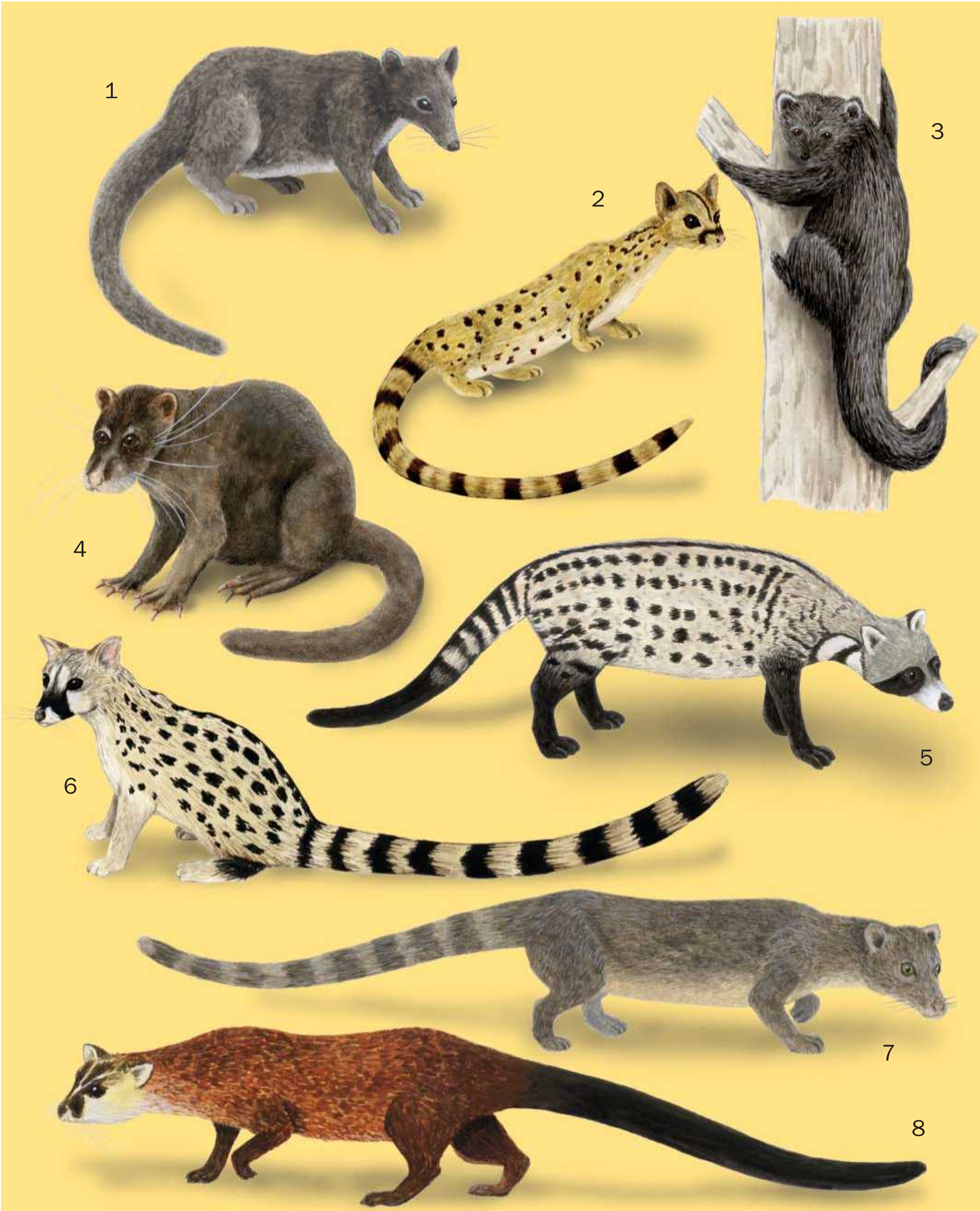
Conservation status

Of the fourteen species of Viverridae listed on the IUCN Red List, one species, the Malabar civet (*Viverra civettina*) is listed as Critically Endangered, and two species (otter civet and falanouc) as Endangered, mostly because of habitat destruction, predation, and illegal hunting. Many species such as Owston's palm civet (*Chrotogale owstoni*), Sulawesi palm civet (*Macrogalidia musschenbroekii*), and Jerdon's palm civet (*Paradoxurus jerdoni*) are listed as Vulnerable. Three additional species, the Johnston's genet (*Genetta johnstoni*), Abyssinian genet (*Genetta abyssinica*), and the aquatic genet (*Osbornictis piscivora*) are listed as Data Deficient because of lack of information on their abundance and population trends.

Significance to humans

The main importance of this carnivore family to humans is in the production of civet oil, the product from the anal glands of species in at least three genera (*Civettictis*, *Viverra*, and *Viverricula*). The musk, often referred to as "civet," has a sweet smell and is used mostly for the perfume industry and for medicinal purposes. In the seventeenth and eighteenth century, civet was highly sought after for the perfume industry. Today, synthetic replacements have caused the market to decline, but captive civets are still held for civet production. Most of the production originates in Ethiopia. The civet is removed from captive animals by squeezing the protruding anal pockets. Males produce a stronger and better quality civet, and production from individual animals averages 0.14–0.67 oz (4–19 g) per week.

Some species of Viverridae are considered pests in some areas for depredation of poultry. Many species are kept as pets to control rodents and insects around households. Skins of some animals may be used locally by indigenous people, but no species are harvested commercially for their pelts.



1. Falanouc (*Eupleres goudotii*); 2. African linsang (*Poiana richardsonii*); 3. Binturong (*Arctictis binturong*); 4. Otter civet (*Cynogale bennettii*); 5. African civet (*Civettictis civetta*); 6. Common genet (*Genetta genetta*); 7. African palm civet (*Nandinia binotata*); 8. Aquatic genet (*Osbornictis piscivora*). (Illustration by Dan Erickson)

Species accounts

African civet
Civettictis civetta

SUBFAMILY
Viverrinae

TAXONOMY
Viverra civetta (Schreber, 1776), Guinea.

OTHER COMMON NAMES
English: Civet cat; French: Civette africaine; German: Afrika Zibetkatze; Spanish: Cibeta.

PHYSICAL CHARACTERISTICS
Body length 27–33 in (67–84 cm), tail 13–19 in (34–47 cm), weight 22–38 lb (10–17 kg). It has medium-length legs and a rather long, erectile dorsal mane. The ash-gray to yellowish basic coloration has numerous black-brown spots on the sides of the body.

DISTRIBUTION
Sub-Saharan Africa.

HABITAT
Forests and open grassy areas.

BEHAVIOR
Solitary, territorial, and predominantly nocturnal, African civets rest in dense vegetation during the day. Scent marking is common with secretions from the perineal glands, but vocal communication is limited. Longevity may reach 14 years.

FEEDING ECOLOGY AND DIET
Opportunistic omnivore. African civets consume mainly fruits, rodents, insects, reptiles, birds, amphibians, and carrion.

REPRODUCTIVE BIOLOGY
Breeding occurs year round, gestation is 60–81 days, litter size one to four young. Young are born fully furred, and eyes open at birth or shortly thereafter. Weaning occurs at 14–16 weeks, and sexual maturity is reached after one year. Mating system is not known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
African civets are easily tamed, and probably are the most popular animal for the production of civet. ◆

Common genet
Genetta genetta

SUBFAMILY
Viverrinae

TAXONOMY
Viverra genetta (Linnaeus, 1758), Spain.

OTHER COMMON NAMES
English: European genet, small-spotted genet; French: Genette commune, genette européenne; German: Ginsterkatze; Spanish: Genetta.

PHYSICAL CHARACTERISTICS
Body length 17–22 in (43–55 cm), tail 13–16 in (33–51 cm), weight 3–6 lb (1.5–2.5 kg). The body is elongated, with a long tail. The head is small and has a long snout and medium-sized ears. Legs are short. The fur has a light basic coloration and dark spots, and the tail is banded.

DISTRIBUTION
Spain, Portugal, France, Arabia, north Africa, and in sub-Saharan savannas.

HABITAT
Forests, savannas, shrublands.

BEHAVIOR
European genets are probably the best known of all Viverridae. Nocturnal and solitary, common genets shelter in dense vegetation and hollow trees during the day. Genets are excellent climbers, and often climb down head first. Home ranges vary in size from 1–3 mi^2 (2–8 km^2), and overlap. Genets scent mark with the secretion from their perineal glands, and marks allow assessment of social status and individual recognition. Several different vocalizations are used.

FEEDING ECOLOGY AND DIET
Opportunistic, genets consume mainly rodents, birds, amphibians, fruits, reptiles and insects.

REPRODUCTIVE BIOLOGY
Mating occurs from January to September, but peaks in February or March. Gestation lasts 10–11 weeks, litter size is one to four. Young are born with hair, but belly is naked. Eyes open after eight days. Sexual maturity is reached after two years, and longevity may exceed 16 years. Mating system is not known.

CONSERVATION STATUS
Only one subspecies, *G. g. isabelae*, is rare and listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. Genets are easily tamed, and readily breed in captivity. ◆

Aquatic genet
Osbornictis piscivora

SUBFAMILY
Viverrinae

TAXONOMY
Osbornictis piscivora J. A. Allen, 1919, Zaire.

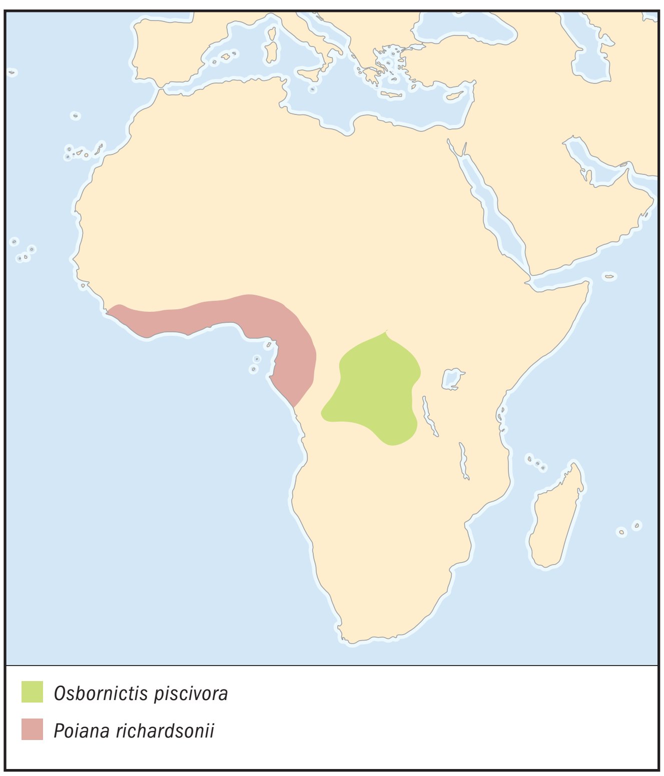
OTHER COMMON NAMES
English: Congo water civet, fishing genet; French: Genette aquatique; German: Wasser-Schleichkatze.

PHYSICAL CHARACTERISTICS
Body length 18–20 in (44–50 cm), tail 13–16 in (34–41 cm), weight 3 lb (1.5 kg).

DISTRIBUTION
Democratic Republic of the Congo (Zaire).

HABITAT
Heavily forested areas in proximity to water.

BEHAVIOR
Solitary.



FEEDING ECOLOGY AND DIET
Mainly fish, possibly amphibians and crustaceans.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Listed by the IUCN as Data Deficient.

SIGNIFICANCE TO HUMANS
Meat may be consumed by local people. ◆

African linsang
Poiana richardsonii

SUBFAMILY
Viverrinae

TAXONOMY
Genetta richardsonii (Thomson, 1842), Fernando Po (Equatorial Guinea).

OTHER COMMON NAMES
English: Oyan; French: Linsang africain, poiana; German: Pojana.

PHYSICAL CHARACTERISTICS
Body length 13–15 in (33–38 cm), tail 14–15 in (36–38 cm), weight 1.4 lb (650 g). The tail is longer than the body and is covered by a thick fur; it has 12 dark rings and a dark tip. The yellow basic coloration is covered by numerous small, black spots.

DISTRIBUTION
Sierra Leone, Ivory Coast, Gabon, Cameroon, Congo, and Fernando Po.

HABITAT
Forests.

BEHAVIOR
Nocturnal, rests on tree limbs or in deserted squirrel nests during the day.

FEEDING ECOLOGY AND DIET
Nuts, insects, and birds.

REPRODUCTIVE BIOLOGY
Litter size two to three. Mating system is not known.

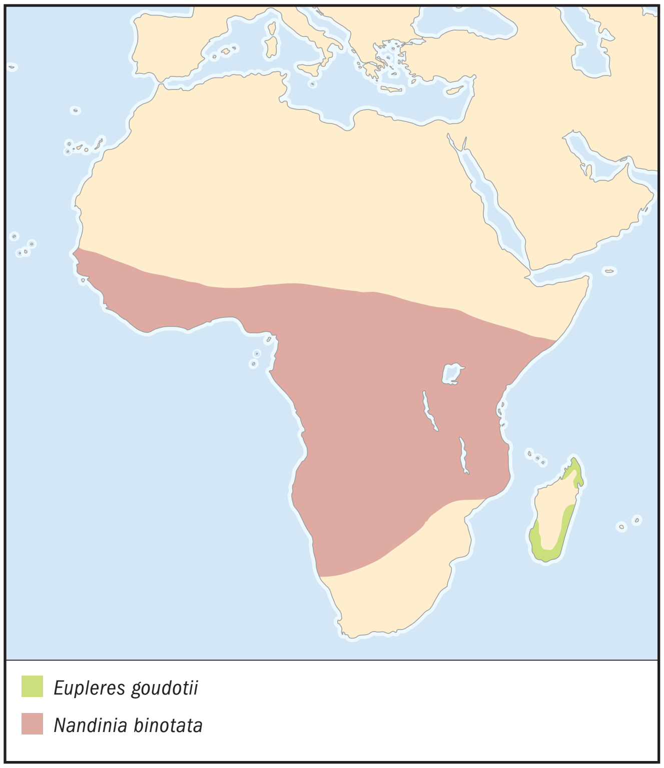
CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Skins used by indigenous people in some areas. ◆

African palm civet
Nandinia binotata

SUBFAMILY
Nandiniinae

TAXONOMY
Viverra binotata (Gray, 1830), Africa, Ashantee (Ghana).



OTHER COMMON NAMES
French: Nandinie d'Afrique; German: Pardel-Roller.

PHYSICAL CHARACTERISTICS
Body length 18–23 in (44–58 cm), tail 19–25 in (46–62 cm), weight 4–11 lb (2–5 kg). The hair is long and very thick, varying in color from yellowish gray-brown to brown. The upper side of the body is darker. The nape of the neck has three dark longitudinal stripes, and there are numerous dark spots on the upper body side. The shoulder has a white blotch. The upper side of the tail is banded. The feet are very short and have naked soles.

DISTRIBUTION
Tropical Africa from Senegal and Angola to southern Sudan and eastern Africa, and south to Zimbabwe.

HABITAT
Tropical forests.

BEHAVIOR
Arboreal and nocturnal. Density of 13 per mi^2 (5 per km^2). Territories marked with scent. African palm civets use their forefeet much more skillfully than other viverrids; they approach the fine movements and dexterity of raccoons (Procyonidae).

FEEDING ECOLOGY AND DIET
Mostly fruits, but also rodents, birds eggs, insects. Animal prey is recognized chiefly by its movement.

REPRODUCTIVE BIOLOGY
Probably polygynous. Births peak in May and October, gestation is 64 days, litter size usually two, but may reach four.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Occasionally tamed and kept as pets. ◆

Binturong
Arctictis binturong

SUBFAMILY
Paradoxurinae

TAXONOMY
Viverra binturong (Raffles, 1821), "Malacca."

OTHER COMMON NAMES
English: Bear cat; French: Binturong; German: Binturong.

PHYSICAL CHARACTERISTICS
Body length 24–38 in (61–97 cm), tail 22–35 in (56–89 cm), weight 20–30 lb (9–14 kg). The body is compact and the feet are short with naked soles. The hair is rough and loose, with a blackish color. The binturong is the only viverrid with a prehensile tail.

DISTRIBUTION
India, Nepal, Thailand, Malaysia, and Indochina.

HABITAT
Dense forests.

BEHAVIOR
Nocturnal and mostly arboreal, the binturong runs like a bear when it is on the ground, putting the entire sole of the foot down. The slinking motion that is normally characteristic of viverrids is not found in the binturong.

FEEDING ECOLOGY AND DIET
Fruits, leaves, birds, carrion, and fish.

REPRODUCTIVE BIOLOGY
Most births occur from January to March, gestation 84–99 days, litter size one to six. Both parents care for the young. Mating system is not known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
May be domesticated and kept as pets. Common as a zoo animal. ◆

Otter civet
Cynogale bennettii

SUBFAMILY
Hemigalinae

TAXONOMY
Cynogale bennettii Gray, 1837, Sumatra.

OTHER COMMON NAMES
English: Water civet; French: Civette-loutre de Sumatra; German: Mampalon; Spanish: Cibeta nutria.

PHYSICAL CHARACTERISTICS
Body length 23–27 in (57–68 cm), tail 5–8 in (13–21 cm), weight 6.5–11 lb (3–5 kg). The body is heavy and compact. The black legs are short and have naked soles and greatly curved claws. All feet are webbed, but the hind legs have less webbing than the forefeet. The broad, flat nose is well supplied with vibrissae. The nasal openings are on top of the nose, and the ears are rounded. The hair is yellowish gray-brown with a black-brown throat and lower lip. The chin and a spot over the eyes are yellowish white.

DISTRIBUTION
North Vietnam, Malaysia, Sumatra, Java, and Borneo.

HABITAT
Streams and swampy areas.

BEHAVIOR
Solitary, good climber, but not strong swimmer. Longevity may reach five years.

FEEDING ECOLOGY AND DIET
Crustacens, mollusks, fish, birds, small mammals, and fruits.

REPRODUCTIVE BIOLOGY
Litter size is two to three. Mating system is not known.

CONSERVATION STATUS
Listed as Endangered by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Falanouc
Eupleres goudotii

SUBFAMILY
Euplerinae

TAXONOMY
Eupleres goudotii Doyère, 1835, Madagascar.

OTHER COMMON NAMES
English: Malagasy mongoose, slender falanouc, small-toothed mongoose; French: Euplère de Goudot; German: Kleinfalanuk; Spanish: Fanaloca, mangosta dentipequeño.

PHYSICAL CHARACTERISTICS
Body length 18–26 in (45–65 cm), tail 9–20 in (22–50 cm), weight 4–9 lb (2–4 kg). The fore limbs are short and weak, with small paws. The hind legs are longer. The claws are very long, curved, and laterally compressed. There are no anal or perineal glands.

DISTRIBUTION
Madagascar.

HABITAT
Humid, lowland forests.

BEHAVIOR
Nocturnal and terrestrial, it sleeps in burrows or crevices during the day. The people of southeastern Madagascar use falanouc tails for ornamental clothing.

FEEDING ECOLOGY AND DIET
Falanoucs dig for food and feed on insects, earthworms, and other invertebrates.

REPRODUCTIVE BIOLOGY
Mating occurs in July or August, litter size is one or two. Mating system is not known.

CONSERVATION STATUS
Listed as Endangered by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Owston's palm civet *Chrotogale owstoni* Spanish: Hemigalo de Owston	Body and base of tail have alternating and sharply contrasting dark and light transverse bands, longitudinal stripes present on neck. Underparts are pale buffy. Head and body length 20–25 in (50.8–63.5 cm), tail length 15–19 in (38.1–48.2 cm).	Species is largely terrestrial, but has been seen in trees. Prefers densely vegetated habitats near water sources in both primary and secondary forests. Mating usually occurs in January and March. Each female has one to two litters, each containing one to three offspring.	Southern Yunan and southwest Guangxi provinces in China; northern Vietnam; and northern Laos.	Heavily consists of earthworms; however, small vertebrates, invertebrates, and some fruit may also be included in their diet.	Vulnerable
Hose's palm civet *Diplogale hosei* Spanish: Hemigalo de Hose	Coloration is dark brown or black , underparts are grayish, yellowish, white, or slightly rufescent. Buffy gray patch from eye to cheek. Tail is not banded, but dark throughout. Head and body length 26 in (66 cm), tail length 11.8 in (30 cm).	Montane forest and is largely terrestrial. Partly arboreal, climbs well. Two young per litter.	Borneo.	Mainly orthopterans, worms, and other invertebrates.	Vulnerable
Banded palm civet *Hemigalus derbyanus* Spanish: Hemigalo franjeado	Narrow, median dark streak on head, two broad stripes from neck to elbow, two imperfect stripes at base of tail. Coloration is whitish to orange buff, usually lighter and more buffy underneath. Head and body length 16.1–20.1 in (41–51 cm), tail length 10–15.1 in (25.5–38.3 cm).	Tall forest. Terrestrial, partly arboreal, climbs well. Two young per litter.	Tenasserim, Malay Peninsula, Sumatra and certain small islands to west, and Borneo.	Mostly orthopterans, worms, and other invertebrates. Also eat fruit.	Not threatened
Small-toothed palm civet *Arctogalidia trivirgata* Spanish: Civeta de los palmares	Coloration of upperparts is tawny, from dusky grayish tawny to bright orange tawny. Head is dark gray and paws are brown. White stripe on muzzle, three brown or black stripes on back. Very long tail. Head and body length 17–20.9 in (43.2–53.2 cm), tail length 20.1–24 in (51–61 cm).	Dense forests, sometimes coconut plantations, but avoids human settlements. Nocturnal and arboreal. Breeding continues throughout year. Two or three young per litter.	Assam to Indochina and the Malay Peninsula, and on Sumatra, Bangka, Java, Borneo, and numerous small nearby islands of the East Indies.	Omnivorous diet, such as squirrels, birds, frogs, insects, and fruit.	Not threatened
Sulawesi palm civet *Macrogalidia musschenbroekii* Spanish: Civeta celebiana	Upperparts are light brown chestnut to dark brown. Underparts range from fulvous to white, with a red breast. Gray patches on face (cheeks and above eyes). Brown spots and bands present on sides and lower back. Short, close fur, whorl in neck. Head and body length 39.4 in (100 cm), tail length 23.6 in (60 cm).	Montane and lowland forests, and in scrubby grassland. Good climber.	Sulawesi.	Rodents and fruit.	Vulnerable
Masked palm civet *Paguma larvata* Spanish: Paguma	White and black mask covers face. General color is gray tinged with buff, orange, or yellowish red. No stripes or spots on body. Head and body length 20–30 in (50.8–76.2 cm), tail length 20–25 in (50.8–63.6 cm).	Forests and brush country. Raises young in tree holes. Arboreal and nocturnal. Solitary. May be two breeding periods per year.	Kashmir to Indochina and the Malay Peninsula, in much of eastern and southern China, on the Andaman Islands, Taiwan, Hainan, Sumatra, and Borneo.	Small vertebrates, insects, and fruit.	Not threatened
Palm civet *Paradoxurus hermaphroditus* Spanish: Musang	Coloration is gray to brown, entirely masked by black tips of guard hairs. Patter of dorsal stripes and lateral spots. Patter consists of white patches and white band across forehead. Backward direction of hairs on neck. Head and body length 17–28 in (43.2–71 cm), tail length 16–26 in (40.6–66 cm).	Tropical forests. Reproduction occurs throughout the year. Litter size is two to four young. Nocturnal and arboreal.	Kashmir in the west to the Philippines in the east; from southern China and the Himalayas in the north to the Greater Sundas and many lesser Sunda Islands in the south.	Primarily frugivorous, feeding on berries and pulpy fruits. Also eats reptiles, eggs, and insects.	Not threatened
Blotched genet *Genetta tigrina* Spanish: Jineta de motas grandes	Coloration is white, gray, or buff. Spots and dark markings cover pelage from shoulders to base of tail. Spots vary from black to rust. Short legs, long body with white-ringed, black-tipped tail. Head and body length 19.3–23.6 in (49–60 cm), tail length 16.5–21.3 in (42–54 cm).	Tropical rainforest, tropical deciduous forest, tropical scrub forest, tropical savanna, and grasslands. Very little known about reproductive patterns. Litter size ranges from one to five offspring. Nocturnal and solitary. Arboreal and nimble. Vocalization important.	South Africa and Lesotho.	Small rodents, birds, reptiles, fruit, and invertebrates.	Not threatened

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Banded linsang *Prionodon linsang* Spanish: Linsang rayado	Coloration varies from whitish gray to brownish gray and becomes creamy on underside. Dark patter of four or five broad, transverse black or dark brown bands across back. One large stripe on each side of neck. Dark spots on sides of body and legs. Head and body length (35–45 cm), tail length (30.4–42 cm).	Forests. Nocturnal and arboreal. Nests made of sticks and leaves. No clear breeding season. Two young per litter.	Western and southern Thailand, Malay Peninsula, Sumatra, Bangka, Java, and Borneo.	Small mammals, birds, eggs, and insects.	Not threatened
Indian civet *Viverra zibetha* English: Large Indian civet; Spanish: Civeta hindú grande	Coloration is gray or brown. Black spots cover body, white stripes on neck. Usually two white stripes and three black stripes. Tail has black rings. Limbs are black. Average body weight 11–24.3 lb (5–11 kg), tail length 13 in (33 cm).	Scrub and densely forested areas. Females are polyestrous, breeding throughout the year. Two litters per year, each producing as many as four offspring. Females raise young alone. Solitary, nocturnal animals. Terrestrial, communicate through glandular secretions.	Nepal and eastern India to southeastern China and Malay Peninsula.	Carnivorous, feeding on birds, frogs, snakes, small mammals, and chickens. They also eat fruit, roots, eggs, and have been recorded eating fish and crabs.	Not threatened
Oriental civet *Viverra megaspila* English: Large-spotted civet; Spanish: Civeta de motas grandes	Long, loose fur elongated in median line of body, forming low crest or mane. Black spots on grayish or tawny ground color. Black and white stripes on sides of neck and throat. Head and body length 23–37.4 in (58.5–95 cm), tail length 11.8–19 in (30–8.2 cm).	Wide variety of habitats in forest, brush, and grassland. Stay in dense cover during day. Nocturnal, mainly terrestrial, good climbers. Generally solitary, one to four offspring per litter.	Peninsular India, Myanmar to Indochina, and Malay Peninsula.	Small mammals, birds, snakes, frogs, insects, eggs, fruit, and some roots.	Not threatened

Resources

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Serge Larivière, PhD

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Mongooses and fossa

(Herpestidae)

Class Mammalia
Order Carnivora
Suborder Feloidea
Family Herpestidae

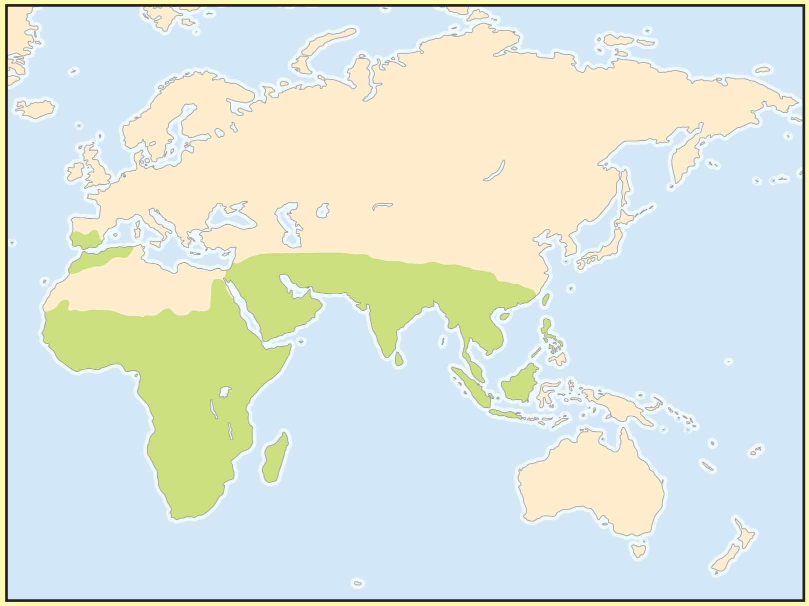
Thumbnail description
Small to medium-sized carnivores with long bodies, short legs, and highly tapered snouts; fur is often grizzled and brown or gray in color

Size
7–31 in (18–80 cm); 7 oz–26.5 lb (200 g–12 kg)

Number of genera, species
20 genera; 41 species

Habitat
Savanna, forest, open woodland, and semi-desert

Conservation status
Endangered: 6 species; Vulnerable: 5 species; Data Deficient: 1 species



Distribution
Africa, Asia, Madagascar, and southern and eastern Mediterranean region

Evolution and systematics

Though once considered in the same family as civets and genets (Viverridae), mongooses are now recognized as a separate family (Herpestidae). This family is comprised of 21 genera, including about 41 species, depending on the authority. Several authors have suggested the division of Herpestidae into three subfamilies and recent molecular evidence supports this division. The subfamilies include: (1) the Herpestinae, primarily solitary or pair-living mongooses (genera: *Atilax*, *Bdeogale*, *Cynictis*, *Herpestes*, *Ichneumia*, and *Rhynchogale*); (2) the Mungotinae, small, highly social mongooses (genera: *Crossarchus*, *Dologale*, *Helogale*, *Liberiictis*, *Mungos*, *Paracynictis*, and *Suricata*); and (3) the Galidiinae, consisting of all endemic Malagasy carnivores (genera: *Cryptoprocta*, *Eupleres*, *Galadictis*, *Galidia*, *Mungotictis*, and *Salanoia*).

Despite the notable variation in physical appearance, the endemic carnivores of Madagascar arose from a single African ancestor 24–18 million years ago (mya). Their common ancestry and close phylogenetic relationship to the mongooses requires placement of the large cat-like fossa (*Cryptoprocta ferox*) within the Herpestidae, even though, superficially, it bears little resemblance to its mongoose kin. In Africa and Asia, herpestid evolution may have been constrained by competition with other carnivore families that dominated several specialized niches. As a result, mongoose radiation in Africa and Asia involved numerous, but rather subtle adaptations and specializations in diet and habitat, most evident in morphology of ears, muzzle, whiskers, jaw, and teeth. However, in Madagascar, the lack of canids, felids, or mustelids allowed a wider radiation of body forms and niches, from small, squirrel-like insectivores (*Mungotictis*) to large, arboreal predators (*Cryptoprocta ferox*).

Physical characteristics

Mongooses are small to medium-sized carnivores. Body lengths vary from 7 to 31 in (18 to 80 cm) and weights range

A meerkat (*Suricata suricatta*) community. (Photo by Harald Schütz. Reproduced by permission.)

Fossa (*Cryptoprocta ferox*) are the largest native predators of Madagascar. (Photo by Harald Schütz. Reproduced by permission.)

An eastern Malagasy ring-tailed mongoose (*Galidia elegans elegans*) feeding on rodent. (Photo by Harald Schütz. Reproduced by permission.)

from 7 oz to 26.5 lb (200 g–12 kg). Most have long, slender bodies and relatively short legs. The ears are small and rounded and the snout is highly tapered. Eyes of most species contain ovular-shaped horizontal pupils. The fur is generally coarse and grizzled and the color often correlates with the local soil, indicating the importance of camouflage. The feet, legs, tail or tail tip are commonly a different hue. A few species have coats bearing stripes (*Mungotictis*, *Galadictis*, *Suricata*, *Mungos*), or ringed tails (*Galidia*), but the majority lack strongly marked coats. Mongooses have four to five toes that do not bear retractile claws, although they are semi-retractile in *Cryptoprocta*. Undersides of the feet tend to be hairless. Unlike the civets and genets, mongooses lack perineal civetone glands; however, a well-developed anal pouch containing at least two glandular openings is present in all species. Scent deposits from the anal pouch function as communication for both solitary and highly social species.

The structure of the auditory bulla is important in characterizing the family. There is a clear demarcation between the entotympanic and ectotympanic parts of the auditory bulla, which is perpendicular to the long axis of the skull (it is oblique in Viverridae). The ectotympanic element is expanded and is as large or larger than the entotympanic element. A median lacerate foramen is present. The teeth, numbering 34–40, are distinctive for each genus. Carnassials are well developed and most species have an internal cusp on the third upper premolar that is variable in size and is vestigial in some species.

Distribution

The family is a widespread successful group but confined to the Old World. Most mongooses are African, occupying the entire continent except for the Sahara. Only one genus (*Herpestes*) exists in Asia, ranging from the Philippines and Borneo to Southeast Asia, south China, Sri Lanka, India and Arabia. It is also present in southern Spain, Portugal, and the

Yellow mongoose (*Cynictis penicillata*) mother and young in Etosha National Park, Namibia. (Photo by Jen and Des Bartlett. Bruce Coleman, Inc. Reproduced by permission.)

A banded mongoose clan (*Mungos mungo*) foraging in the early morning in Botswana. (Photo by Clem Haagner. Bruce Coleman, Inc. Reproduced by permission.)

Near East. The Galidiinae are restricted to the large island of Madagascar. The small Indian mongoose, *Herpestes javanicus*, was introduced by man in the 1800s to Fiji, the Hawaiian Islands, and several islands in the West Indies for biological control of rats in sugarcane plantations. However, they are now considered pests in these areas as their unspecialized diets have rendered them a threat to many native birds and reptiles, as well as to domestic fowl.

Habitat

Mongooses are primarily terrestrial but the marsh mongoose (*Atilax paludinosus*), Bengali water mongoose (*Herpestes palustris*), and ring-tailed mongoose (*Galidia elegans*) are semi-aquatic, spending much time in streams and rivers hunting for aquatic invertebrates. Madagascar's fossa is arboreal and equipped with semi-retractile claws, and a long tail for movement and balance in the trees. The slender mongoose (*Herpestes sanguinus*), though chiefly terrestrial, is also adept at climbing trees in search of food.

Mongooses inhabit a variety of ecotypes including forest, open woodland, savanna, semi-desert, and desert. The Mungotinae are restricted to open habitats with the exception of the cusimanses (*Chrossarchus* sp.) and the Liberian mongoose (*Liberiictis kuhni*), which inhabit the rainforest interior. The Herpestinae occupy a wider range of habitats from rainforest to semi-desert. Madagascar's Galidiinae can be found in rainforest, dry forest, and spiny desert.

Sleeping dens and birth dens often include tree hollows and tree falls in forested regions, and rock crevices, earth holes, and termitaries in open terrain. For many species, presence of denning sites are very important and may be more limiting for a population than food resources.

Behavior

Most mongooses are solitary but some species live in pairs and several form large, stable social groups that forage and den together. The gregarious species of mongooses have social systems that rival only the primates in diversity and complexity. Group living seems to have evolved for reasons unlike the larger social carnivores that primarily benefit from communal hunting. Predation pressure seems more likely to have favored group living in mongooses. Social mongooses tend to be small, diurnal species inhabiting open areas, characteristics that make them extremely vulnerable to predation. Liv-

A dwarf mongoose (*Helogale parvula*) emerging from its burrow. (Photo by Animals Animals ©Michael Dick. Reproduced by permission.)

ing in a group provides some protection and early warning of a predator attack. It has also been proposed that diet is relevant to the development of sociality in these animals. The high abundance and renewability of invertebrate prey reduces the cost of sharing a territory. Mongooses preying upon vertebrate prey tend to be solitary, as the presence of another individual may interfere with a hunt. Diurnal habits and open habitat also facilitate keeping contact, an important part of social living. There are no nocturnal social species; noisy social interactions at night may pose a risk as nocturnal predators often rely on keen sense of hearing. The social cusimanses do not live in open habitat but are able to maintain contact in the dense rainforest understory by giving constant whistling calls while traveling.

A western Malagasy broad striped mongoose (*Galidictis grandidieri*) grooming. (Photo by Harald Schütz. Reproduced by permission.)

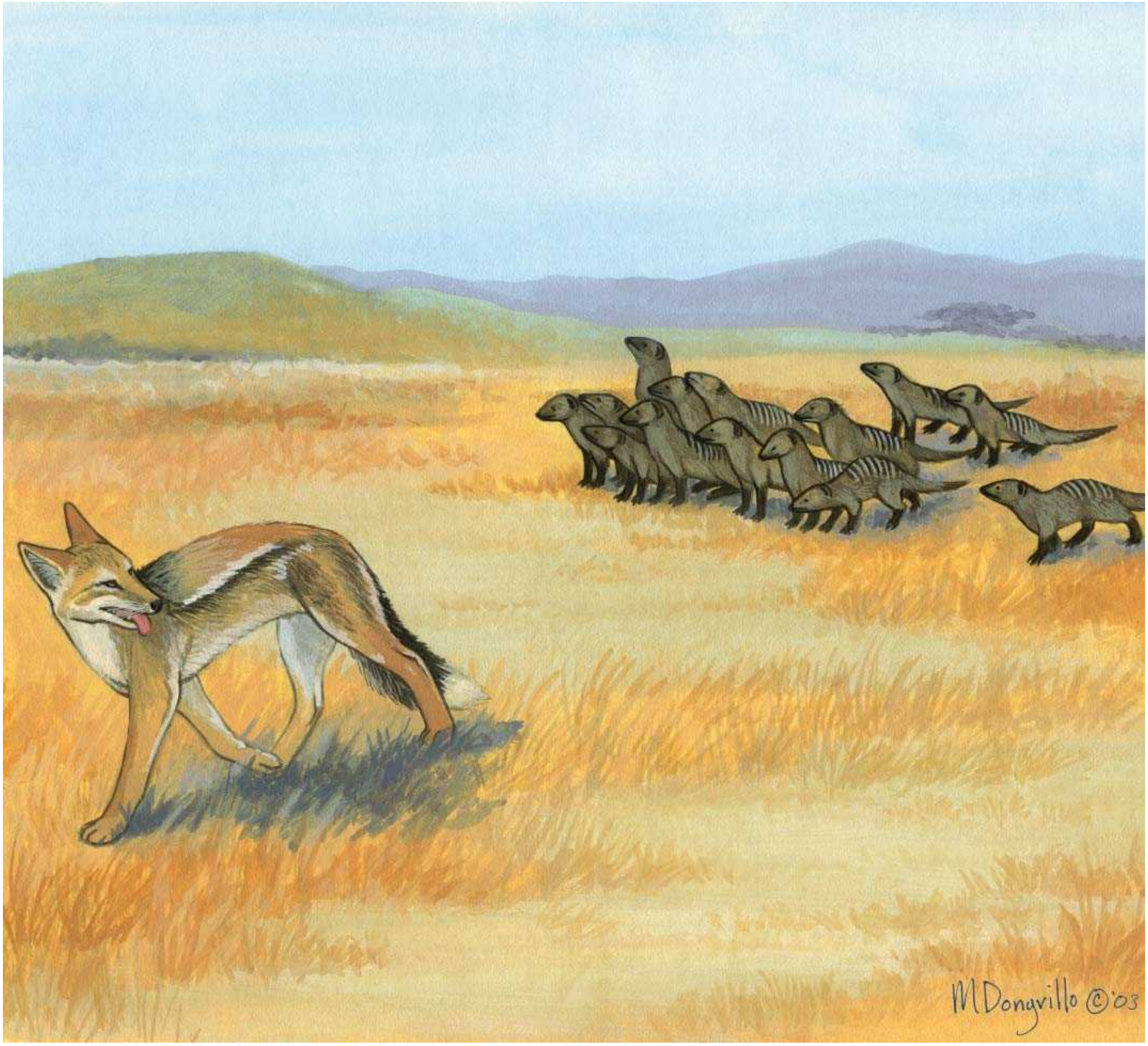
Another advantage to group living in mongooses is increased efficiency in the care of young. In most species, young are born rather helpless and leaving them alone in a den while foraging may be risky. In several species, such as the dwarf mongoose (*Helogale parvula*), the helpless young are guarded by babysitters while the rest of the group forages. Group members also help feed the young by bringing them insects or worms to eat. For species that occupy no permanent den site, such as the cusimanse, young are not able to keep up with the group for several weeks and must be carried to different foraging spots. Individuals in the group take turns carrying the young from place to place and also help feed them.

For many of the highly social species, such as the yellow mongoose (*Cynictis penicillata*) and dwarf mongoose, a strict hierarchy develops with a single dominant breeding pair. Sexual dimorphism is minimal in most genera and dominance is based more on age, size, and assertiveness than on gender. Female dominance is not uncommon.

The size of groups is variable among species. Three to eight individuals have been recorded in Liberian mongoose groups, and up to 40 have been recorded for the banded mongoose (*Mungos mungo*). Pair living is also common. In the ring-tailed mongoose of Madagascar (*Galidia elegans*), strong pair bonds are formed between mates who forage and den together. Even the "solitary" species are occasionally seen foraging in pairs, and some species such as the Cape gray mongoose (*Herpestes pulverulentus*) and the white-tailed mongoose (*Ichneumia albicauda*) may forage individually but den with family members. Communal denning may offer better protection and added warmth and reduces competition for denning sites.

All species communicate through scent marking with the anal glands. Some species also have cheek and chest glands.

An Indian mongoose (*Herpestes nyula*) killing a cobra. (Photo by E. R. Degginger. Bruce Coleman, Inc. Reproduced by permission.)



When a jackal approaches, banded mongooses move towards it in a tightly knit group, creating the appearance of a larger animal from which the jackal will retreat. (Illustration by Marguette Dongvillo)

Chemicals in the anal pouch may constitute individual signatures and indicate reproductive condition, sex, and/or dominance rank. Mongooses commonly mark territory borders, den sites, food resources, and even other group members. Social species have a complex vocal repertoire with several distinct calls.

Feeding ecology and diet

Most herpestids are opportunistic predators, feeding on small vertebrates including rodents, birds, reptiles, and frogs, and various invertebrates such as insects, snails, crabs, and worms. All species are predacious, but a few species also eat plant matter such as fruits and tubers.

Many mongoose species can open bird eggs by hurling the egg towards a hard fixed object with the forepaws, usually between the hind legs. The banded mongoose has been observed hurling stones in the same manner at an ostrich egg that was too large to throw.

Mongooses are most famous for preying on venomous snakes such as cobras, and some species have actually developed resistance to snake venom. The Egyptian mongoose (*Herpestes ichneumon*) and the Indian gray mongoose (*Herpestes*

A Malagasy narrow striped mongoose (*Mungotictis decemlineata*) feeding on excavated lizard eggs. (Photo by Harald Schütz. Reproduced by permission.)

edwardsii) have both been found resistant to hemorrhagic and neurotoxic snake venoms and can withstand up to 13 times the normal lethal dose for mammals.

Although most mongooses are opportunistic feeders on vertebrate and invertebrate prey, a few species have quite specialized diets. The Liberian mongoose has specialized dentition and reduced jaw musculature as an adaptation for eating almost exclusively large, burrowing earthworms. The fossa is specialized with its large canines and cat-like morphology to prey upon large arboreal lemurs.

Reproductive biology

Mating system is variable by species (monogamous or polygamous). Sexual maturity is generally achieved at two years of age. However, the small Indian mongoose may reproduce as early as 10 weeks. Most species are polyestrus, having two or more litters per year. A few are highly seasonal, breeding only when food is most abundant. Copulation is usually preceded by increased frequency of scent marking and some form of chasing or ritualized fighting. During mating, the male clasps the female's back just forward of the pelvic region with his forepaws and grips the back or side of her neck with his mouth without biting. Litter sizes range from one (common in the Galidiinae) to six, with four being most common. All species use a birthing den than may consist of a burrow, termitary, hollow log, or tree. Young are born blind and with little hair in most species, with eyes not opening until week two. In contrast, offspring of the narrow-striped mongoose (*Mungotictis decemlineata*) are born fully furred with eyes open at birth, and walk by day three.

Conservation status

Though generally a successful group, several species are at risk due to loss of habitat. Six species are listed as Endangered and five species are listed as Vulnerable by the World Conservation Union (IUCN). Several more may also be at risk and many are lacking sufficient data to be evaluated. All eight Galidiinae species are threatened (four Vulnerable and four Endangered) because of the high levels of habitat destruction and fragmentation occurring in Madagascar. The Liberian mongoose and Jackson's mongoose of Africa, and the Bengali water mongoose of India have been classified as threatened because of habitat loss. Until recently, mongooses had been largely ignored by the scientific community and as a result, few data exist on population sizes or distributions. Of the mongooses that have not yet been evaluated, those restricted to undisturbed forests or other specialized habitats subject to human disturbance are most likely to be at risk.

Significance to humans

The mongoose has had a long relationship with humans, perhaps starting with the ancient Egyptians. It is found in frescoes and reliefs dating as far back as 2800 B.C. The animal was often embalmed in Egypt and believed to embody a number of gods. It may also have been used for hunting birds. The mongoose's ability to fight snakes gave rise to numerous fables; the oldest and most familiar stories found in the fifth book of the Panchatantra, a group of Sanskrit tales dating from approximately 100 B.C. The mongoose is portrayed as a hero, protecting man from cobra, a story later recounted in Rudyard Kipling's famous tale *Rikki Tikki Tavi*.

Mongooses are easily tamed and frequently kept as pets in both Asia and Africa, as companions and to keep away venomous snakes. They are hunted as food in some parts of Africa.

A marsh mongoose (*Atilax paludinosus*) on guard in Marsai Mara, Kenya. (Photo by Peter Davey. Bruce Coleman, Inc. Reproduced by permission.)

1. Ring-tailed mongoose (*Galidia elegans*); 2. Fossa (*Cryptoprocta ferox*); 3. Liberian mongoose (*Liberiictis kuhni*); 4. Dwarf mongoose (*Helogale parvula*); 5. Small Indian mongoose (*Herpestes javanicus*). (Illustration by Marguette Dongvillo)

Species accounts

Ring-tailed mongoose
Galidia elegans

SUBFAMILY
Galidiinae

TAXONOMY
Galidia elegans Geoffroy, 1837, Madagascar.

OTHER COMMON NAMES
French: Galidie élégante; German: Ringelschwanzmungo; Spanish: Mangosta de cola anillada; Malagasy: Vontsira mena.

PHYSICAL CHARACTERISTICS
Body length 11.8 in (30 cm); tail 8.3 in (21 cm); weight 2 lb (900 g). Fur is soft russet-brown. Tail has five or six black rings.

DISTRIBUTION
Northern, eastern, and west-central Madagascar.

HABITAT
Lives in humid forests.

BEHAVIOR
Diurnal. Living in pairs or small family groups lead by female.

FEEDING ECOLOGY AND DIET
Diet consists of small mammals, birds, frogs, reptiles, aquatic invertebrates, fish, insects, and millipedes.

REPRODUCTIVE BIOLOGY
Monogamous. One young is born, fully furred, with eyes closed. Mature at one year.

CONSERVATION STATUS
Listed as Vulnerable due to habitat loss.

SIGNIFICANCE TO HUMANS
None known. ◆

Fossa
Cryptoprocta ferox

SUBFAMILY
Galidiinae

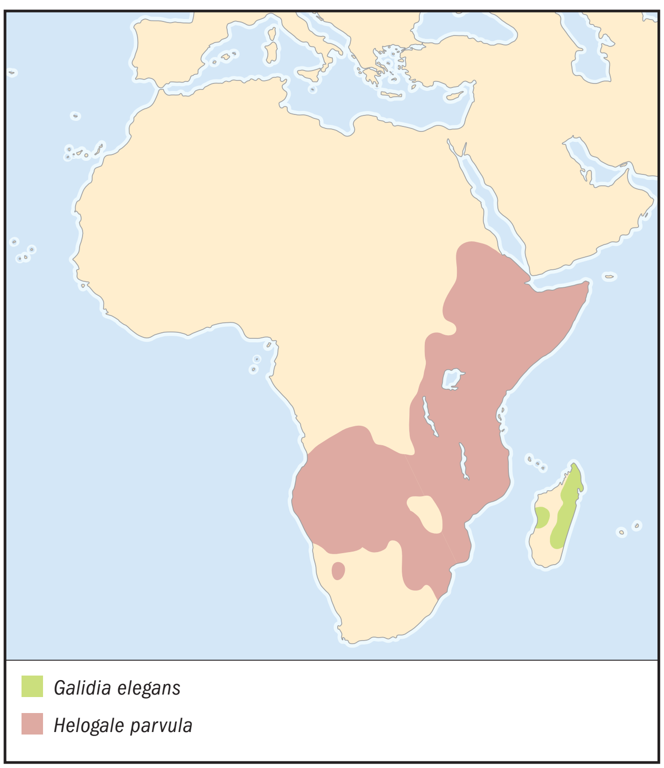
TAXONOMY
Cryptoprocta ferox Bennett, 1833, Madagascar.

OTHER COMMON NAMES
Malagasy: Fosa; French: Fousa; German: Frettkatze; Spanish: Fossa gatuno.

PHYSICAL CHARACTERISTICS
Largest herpestid, 5–6.6 ft (1.5–2 m) with tail. Weight 15.4–26.5 lb (7–12 kg). Coat is reddish brown. Slender body and short legs, square muzzle and round ears. Canines and carnassials are well developed.

DISTRIBUTION
All of Madagascar except High Plateaux.

HABITAT
Lives in forest and woodland.



BEHAVIOR
Crepuscular and nocturnal, solitary. Lives in the trees and on the ground.

FEEDING ECOLOGY AND DIET
Diet includes lemurs, small mammals, birds, reptiles, amphibians, and insects.

REPRODUCTIVE BIOLOGY
Polygamous. Females have one litter per year of two to four young born November to January. Weaning at 4.5 months. Adulthood reached at three years.

CONSERVATION STATUS
Listed as Endangered due to habitat loss and human persecution.

SIGNIFICANCE TO HUMANS
None known. ◆

Small Indian mongoose
Herpestes javanicus

SUBFAMILY
Herpestinae

TAXONOMY
Herpestes javanicus (Geoffroy, 1818), Java.

OTHER COMMON NAMES
English: Javan gold-spotted mongoose; French: Petite mangouste indienne; German: Indien Goldstaub-Manguste; Spanish: Mangosta javanés.

PHYSICAL CHARACTERISTICS
Body length 15.4 in (39 cm); tail 10.2 in (26 cm); weight 1.8 lb (800 g). Coat is brown to reddish brown, speckled with black and gray hair tips.

DISTRIBUTION
Malayan and Indo-Chinese Peninsulas, Sumatra, Java. Introduced to West Indies, Hawaiian Islands, Fiji, Comores, Costa Rica, Japan, and Mauritius.

HABITAT
Habitat generalist. Found in arid plains to wet tropical forests.

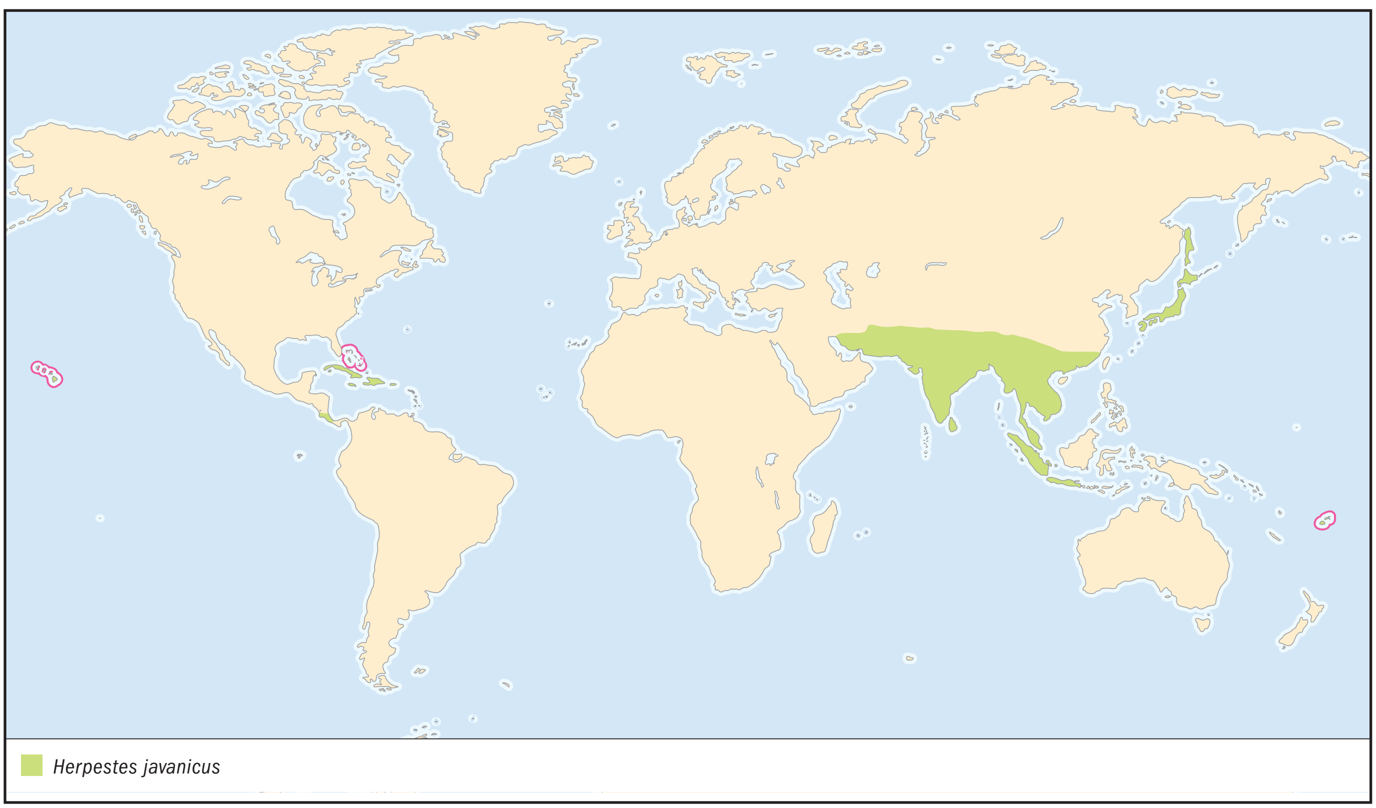
BEHAVIOR
Diurnal and solitary. Home ranges are 0.62 mile (1 km) wide.

FEEDING ECOLOGY AND DIET
Feeds on invertebrates, birds, rodents, and reptiles, including venomous snakes.

REPRODUCTIVE BIOLOGY
Females reproductive as early as 10 weeks. Breed two or three times per year. Litter of two to four young weaned in one month. Mating system is not known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Where introduced, responsible for extinction of several endemic island species, killing of poultry, and the spread of rabies. Estimated to cause $50 million in damage every year in Puerto Rico and the Hawaiian Islands alone. ◆



Dwarf mongoose
Helogale parvula

SUBFAMILY
Mugotinae

TAXONOMY
Helogale parvula (Sundevall, 1846), South Africa.

OTHER COMMON NAMES
Swahili: Kitafe; French: Mangouste nain; German: Zwergichneumon; Spanish: Mangosta enana.

PHYSICAL CHARACTERISTICS
Body length 7–11 in (18–28 cm); tail 5.5–7.5 in (14–19 cm); weight 7–10 oz (200–300 g). Grizzled fur is reddish brown. Adults have juvenile features, including a short muzzle and large head.

DISTRIBUTION
Ethiopia to Angola and eastern South Africa.

HABITAT
Lives in dry savanna and woodland.

BEHAVIOR
Diurnal and highly social. Group is led by matriarch.

FEEDING ECOLOGY AND DIET
Eats mostly insects, and other arthropods, but some small vertebrates are consumed.

REPRODUCTIVE BIOLOGY
Monogamous, only alpha pair breed. Cooperative care of young by group members. Up to three litters per year, each up to six young.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Liberian mongoose
Liberiictis kuhni

SUBFAMILY
Mungotinae

TAXONOMY
Liberiictis kuhni Hayman, 1958, Liberia.

OTHER COMMON NAMES
French: Mangouste de Liberia; German: Liberia-kusimanse; Spanish: Mangosta de Liberia.

PHYSICAL CHARACTERISTICS
Body length 15.7–17.7 in (40–45 cm); tail 7–8.7 in (18–22 cm); weight 4.4–5 lb (2–2.3 kg). Coarse brown coat with grizzled, stiff guard hairs. Black stripe on neck. Tapering tail. Snout is long and mobile, extending beyond lower lip.

DISTRIBUTION
Liberia, western Ivory Coast, and southern Guinea.

HABITAT
Found in riverine and swamp forest.

BEHAVIOR
Diurnal. Living in small family groups of four to eight individuals.

FEEDING ECOLOGY AND DIET
Specialist on large burrowing earthworms and other soft invertebrates.

REPRODUCTIVE BIOLOGY
Breeding thought to occur during the rainy season (May–September) during peak earthworm availability. Mating system is not known.

CONSERVATION STATUS
Listed as Endangered due to habitat degradation and hunting pressures.

SIGNIFICANCE TO HUMANS
Subject to hunting for bushmeat. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Narrow-striped mongoose *Mungotictis decemlineata* English: Ten-lined mongoose; French: Étroit barré mangouste; German: Schmalstreifenmungo; Spanish: Galindo de franjas estrechas	Small mongoose with gray grizzled coat. Narrow reddish brown stripes on back. Bushy tail gives squirrel-like appearance. Large ears and pointed snout. Body 11.8–13.8 in (30–35 cm); tail 8.7–10.6 in (22–27 cm); weight, 15.9–24.7 oz (450–700 g).	Diurnal and group living. Found in dry deciduous forests.	Very restricted. Forested area in Morandava region, Madagascar.	Insects, beetle larvae, and small vertebrates.	Vulnerable
Malagasy brown mongoose *Salanoia concolor* French: Mangouste salanoia; German: Brauner Madagaskar Mungo; Spanish: Salano	Similar to ring-tailed mongoose in form. No tail rings. Brown to reddish brown in color. Body 10.2–11.8 in (26–30 cm); tail 7.9–9.8 in (20–25 cm); weight 24.7–31.8 oz (700–900 g).	Behavior unknown. Found in dense forests.	East coast of Madagascar.	Insects and small vertebrates.	Vulnerable
Slender mongoose *Herpestes sanguinus* French: Mangouste rouge; German: Rote Manguste; Spanish: Mangosta rojo	Long slender body, short legs. Color varies from reddish brown to gray. Tail tip usually black. Body 10.2–13.4 in (26–34 cm); tail 9–12.6 in (23–32 cm); weight 14–28 oz (400–800 g).	Diurnal and solitary. Both sexes hold exclusive territories. Found in forest edge, woodlands, and savanna.	Africa, south of Sahara.	Rodents, reptiles, birds, and insects.	Not listed by IUCN
Banded mongoose *Mungos mungo* English: Water mongoose; French: Mangouste des marais; German: Sumpfmanguste; Spanish: Mangosta acuática	Grizzled gray with black stripes across rump. Feet and tail tip black. Body 11.8–17.7 in (30–45 cm); tail 6–11.8 in (15–30 cm); weight 3.3–4.9 lb (1.5–2.2 kg).	Diurnal, living in large stable groups. Found in savanna, scrub, and woodlands.	Riverine areas of sub-Saharan Africa.	Fish, crabs, bivalves, frogs, insects, birds, reptiles, and small mammals.	Not listed by IUCN
Egyptian mongoose *Herpestes ichneumon* English: Ichnumeon; French: Mangouste ichneumon; German: Ichneumon; Spanish: Mangosta africana	Pale grizzled fur with black tassled tail tip. Slender body and tail. Body 17.7–23.6 in (45–60 cm); tail 13–21.3 in (33–54 cm); weight 4.9–9 lb (2.2–4.1 kg).	Solitary and nocturnal. Found in grasslands, savanna, and forest clearings.	All of Africa except Sahara and forested areas. Also southern Spain, Portugal, and Israel.	Rodents, birds, amphibians, reptiles, and insects.	Not listed by IUCN
Meerkat *Suricata suricatta* English: Suricate; French: Suricate; German: Scharrtier; Spanish: Meerkat	Ochre-gray mongoose with dark stripes on rump and dark eye-rings and ears. Rotund body, long hind legs, and rounded head with tapering snout. Body 11.8–17.1 in (30–45 cm); tail 5.9–11.8 in (15–30 cm); weight 4–5 lb (1.5–2.3 kg).	Diurnal and group living. Occupies grassland, scrub, desert, and rangeland.	South Africa, Namib Desert, Angola, Namibia, and southern Botswana.	Insects associated with large herbivores of grassland. Small mammals and reptiles.	Not listed by IUCN; may be affected by decline of large herbivores, rabies control, and disease
Yellow mongoose *Cynictis pencillata* English: Red meerkat; French: Mangouste de selous; German: Trugmanguste; Spanish: Mangosta amarilla	Yellow to gray coat with white tipped tail. Short muzzle and large ears. Body 9.8–15.7 in (25–40 cm); tail 7–11 in (18–28 cm).	Diurnal. Lives in pairs or social groups led by alpha pair. Founds in grasslands, scrub, and semi-desert scrub	Southern Africa, in Karoo, Botswana, Cape, and Kalahari to southern Angola.	Insects, especially beetles and termites.	Not listed by IUCN
Bushy tailed mongoose *Bdeogale crassicauda* French: Mangouste à queue touffue; German: Buschschwanzichneumon; Spanish: Mangosta canina de cola gruesa	Dark brown mongoose with broad dog-like muzzle and bushy tail. Four toes on each foot. Body 15.7–19.7 in (40–50 cm); tail 7.9–11.8 in (20–30 cm); weight 3.5–5.6 lb (1.3–2.1 kg).	Nocturnal and solitary. Found in coastal thickets and woodlands.	Mozambique, Malawi, Zambia, Tanzania, and Kenya.	Ants, termites, reptiles, and rodents.	Not listed by IUCN
Western cusimanse *Crossarchus obscurus* French: Mangouste brune; German: Dunkelkusimanse	Reddish brown mongoose with long snout and well developed claws on fore feet. Tail tapers to a point. Body 11.8–14.6 in (30–37 cm); tail 5.9–9.8 in (15–25 cm); weight 2.2–3.3 lb (1–1.5 kg).	Diurnal and highly social. Found in dense rainforest, gallery forest, and in the savanna/rainforest transition zone.	Sierra Leone to Ghana.	Leaf litter invertebrates, worms, rodents, frogs, and snakes (including venomous species).	Not listed by IUCN

Resources

Books

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Gittleman, J. *Carnivore Behavior, Ecology and Evolution.* Vols. 1 & 2. Ithaca, NY: Cornell University Press, 1989.

Kingdon, J. *The Kingdon Field Guide to African Mammals.* San Diego: Academic Press, 1997.

Periodicals

Bdolah, A., E. Kochva, M. Ovadia, S. Kinamon, and Z. Wollberg. "Resistance of the Egyptian Mongoose to Sarafotoxins." *Toxicon* 35 (1997): 1251–1261.

Yoder, A., et al. "Single Origin of Malagasy Carnivora from an African Ancestor." *Nature* 421 (2003): 734–737.

Amy E. Dunham

▲

Aardwolf and hyenas

(Hyaenidae)

Class Mammalia

Order Carnivora

Family Hyaenidae

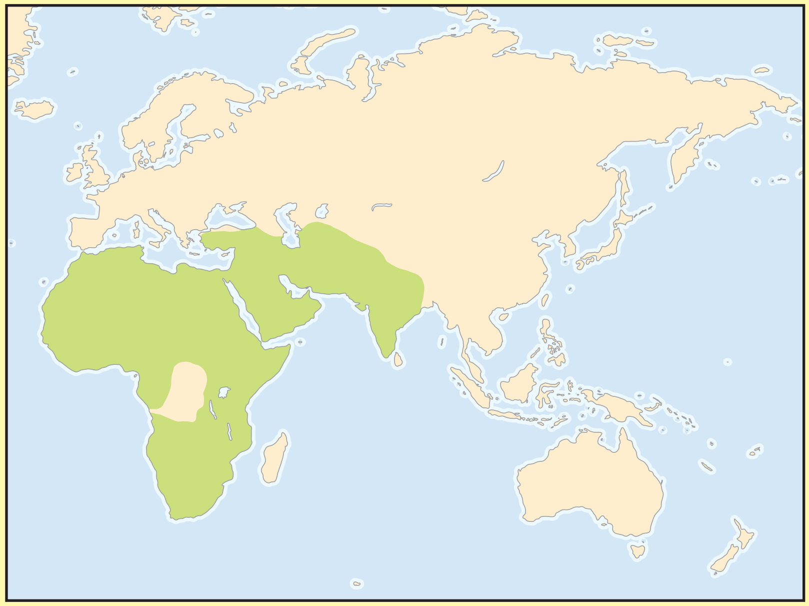
Thumbnail description
Large carnivores with powerful forequarters and less well developed hindquarters, large heads, powerful jaws and robust teeth, with medium length tails and four toes on each limb; the aardwolf is a diminutive form with poorly developed teeth and five toes on the forefeet; well developed anal pouches are present in all species

Size
Shoulder height 18–30 in (45–75 cm); head and body length 38–52 in (95–130 cm); 20–190 lb (9–85 kg)

Number of genera, species
3 genera; 4 species

Habitat
From woodland savanna to desert

Conservation status
Lower Risk/Near Threatened: 2 species; Lower Risk/Least Concern: 1 species



Distribution
Africa, except for the rainforests, and southern Asia as far as the Bay of Bengal

Evolution and systematics

Hyenas are the smallest carnivore family today, and probably arose from civets *Progenetta*. They were the dominant carnivores in the Middle and Upper Miocene of Eurasia. The majority of these forms were generalized, dog-like carnivores rather than the hunter-scavenger and bone-crushing species of today. However, the largest hyena to ever live, *Pachycrocuta*, was a 440 lb (200 kg) mega-scavenger capable of splintering the marrow bones of an elephant. The splits between the lineages leading to the extant forms are old, stretching back to the late Miocene more than nine million years ago. Palaeontological and molecular studies have shown that the aardwolf (*Proteles cristatus*) diverged from other hyenas some 15–32 million years ago (mya). The spotted hyena (*Crocuta crocuta*) split from the brown hyena (*Hyaena brunnea*) and striped hyena (*Hyaena hyaena*) 10 mya, and the brown and the striped, which are each other's closest relatives, split six mya. In the absence of clear-cut data regarding rank among hyenas and because the molecular data unite striped and brown hyenas as sister taxa relative to *Crocuta* and *Proteles*, the two are placed in the genus *Hyaena*. However, recognizing that the split between brown and striped is relatively old, the two have been placed in different subgenera *Hyaena (Parahyaena)* and *Hyaena (Hyaena)* respectively.

Spotted hyena (*Crocuta crocuta*) social greeting behavior. (Photo by Animals Animals ©Joe McDonald. Reproduced by permission.)

Two subspecies of the aardwolf are recognized because of its disjunct distribution, *P. c. cristatus* in southern Africa and *P. c. septentrionalis* in eastern and North Africa. On the basis

An aardwolf (*Proteles cristatus*) in Kenya. (Photo by Animals Animals ©A. Root, OSF. Reproduced by permission.)

A brown hyena (*Hyaena brunnea*) eating eggs at night. (Photo by Animals Animals ©Hamman/Heldring. Reproduced by permission.)

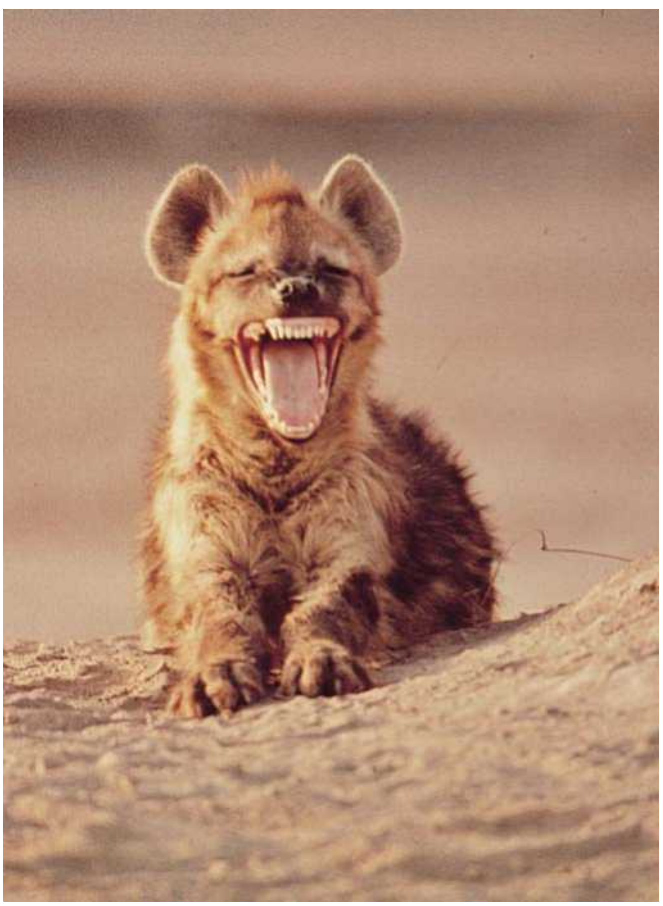
of skull size, the five currently recognized striped hyena subspecies probably form two larger groups, a northeast Africa-Arabian group comprising *H. h. dubbah* and *H. h. sultana*, and a northwest African-Asian group composed of *H. h. barbara*, *H. h. syriaca*, and *H. h. hyaena*. No subspecies of the spotted hyena and brown hyena are recognized.

Physical characteristics

The three large species are dog-like (but they are not closely related to dogs), weighing between 57–187 lb (26–85 kg), with powerful forequarters, large necks and heads and less well developed hind quarters, giving the appearance of a sloping back. In contrast the aardwolf is diminutive, weighing about 24 lb (11 kg). The tail in all is quite short but bushy. The coat of the spotted hyena is short but in the other species it is long and shaggy with an erectile main. There are four toes on each foot, except in the forefeet of the aardwolf which have five. Front feet are far larger than hind feet giving a distinctive track. The premolars are robust and conical, except in the aardwolf where they are reduced to small pegs. The penis is boneless. In all species a large anal pouch secretes scent onto grass stalks in a unique behavior known as pasting.

A spotted hyena (*Crocuta crocuta*) den on the Serengeti Plains, Tanzania. (Photo by Animals Animals ©Breck P. Kent. Reproduced by permission.)

An alert brown hyena (*Hyaena brunnea*) in Kalahari Gemsbok Park, South Africa. (Photo by Animals Animals ©J & B Photographers. Reproduced by permission.)



A hyena “laughing”. (Photo by Pater Davey. Bruce Coleman, Inc. Reproduced by permission.)

The aardwolf (*Proteles cristatus*) is usually seen in Africa. (Photo by © Terry Whittaker/Corbis. Reproduced by pemission.)

A brown hyena (*Hyaena brunnea*) drinking from stream in the Kalahari, South Africa. (Photo by Animals Animals ©Betty K. Bruce. Reproduced by permission.)

Distribution

Mainly a sub-Saharan Africa family, with no species being found in the rainforests of the Congo and only the striped hyena occurring in North Africa, continuing through into southern Asia as far as India.

Habitat

Wide habitat tolerance from heavily wooded savannas to desert.

Behavior

For such a small family, the Hyaenidae show great variability in behavior and social organization, varying from the highly social, clan-living spotted hyena, the monogamous aardwolf, and the blatantly solitary but secretly social brown hyena.

A spotted hyena (*Crocuta crocuta*) feeding on a young elephant killed earlier by a lion. (Photo by Harald Schütz. Reproduced by permission.)

Aardwolf (*Proteles cristatus*) cubs in South Africa. (Photo by Animals Animals ©Helen Thompson. Reproduced by permission.

Feeding ecology and diet

The spotted hyena is a hunter-scavenger and the brown and striped hyenas are predominantly scavengers. The ability of all three to break open bones and extract marrow, and also to digest bone, gives them access to a food source unavailable to other carnivores. The aardwolf is a specialized termite eater.

Reproductive biology

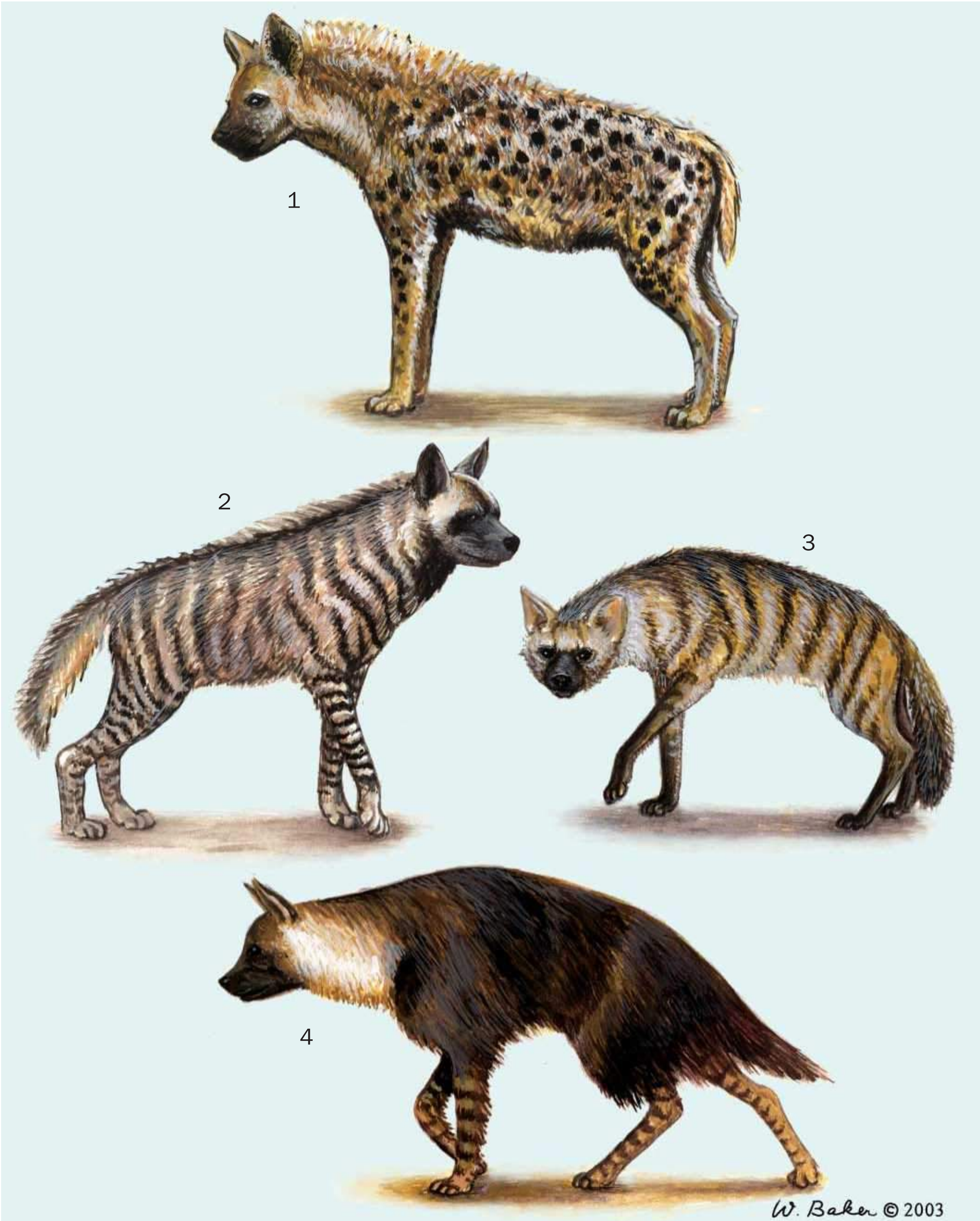
Non-seasonal breeders, except for the aardwolf. Litter size is from one to four, gestation around 90 days. They keep their young in breeding dens which are usually holes in the ground or sometimes caves. Mating systems vary by species (monogamous, polygamous).

Conservation status

Aardwolves are not considered endangered in the wild. The IUCN Red List 2002 classifies spotted hyenas as Lower Risk/Conservation Dependent and the brown and striped hyenas as Lower Risk/Near Threatened.

Significance to humans

Hyenas are often misunderstood and persecuted unnecessarily. Their important role in ecosystems and intricate behavior is often not appreciated. They play a significant role in witchcraft and folklore. They sometimes attack livestock and people, especially the spotted hyena.



1. Spotted hyena (*Crocuta crocuta*); 2. Striped hyena (*Hyaena hyaena*); 3. Aardwolf (*Proteles cristatus*); 4. Brown hyena (*Hyaena brunnea*). (Illustration by Wendy Baker)

Species accounts

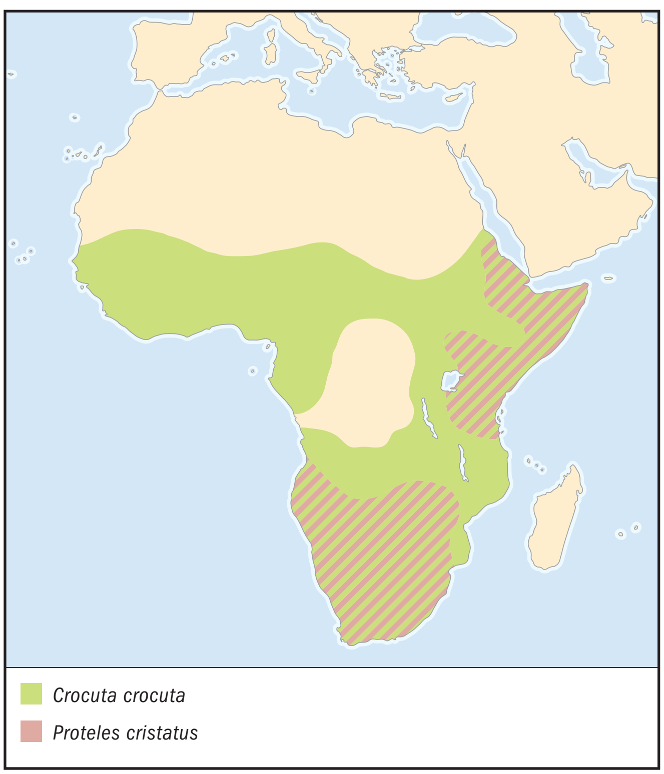
Spotted hyena
Crocuta crocuta

TAXONOMY
Crocuta crocuta (Erxleben, 1777), Guinea, Ethiopia, Cape of Good Hope, designated as Senegambia by Cabrear (1911). No subspecies recognized.

OTHER COMMON NAMES
French: Hyène tachetèe; German: Fleckenhyäne.

PHYSICAL CHARACTERISTICS
The spotted hyena is the largest member of the family. The body color is off-white to brown with dark irregular spots, although some older individuals, particularly females, may lose their spots. The ears are rounded. The tail is black. An adult stands about 34 in (85 cm) at the shoulder. The female is larger than the male; in southern Africa females weigh up to 190 lb (85 kg) and males about 135 lb (60 kg). Southern African spotted hyenas are larger than those in East Africa where the females weigh only about 125 lb (55 kg) and the males 110 lb (49 kg). The female also mimics the male's reproductive organs; she has a pseudo scrotum and the clitoris has become large and penis like. This bizarre organ also contains the opening of the urogenital canal so that a female gives birth through it.

DISTRIBUTION
Mainly confined to the larger protected areas of Africa south of the Sahara, reaching its highest densities in East and southern Africa in parks where large to medium sized prey are abundant. In West Africa its distribution is particularly patchy and it is extinct in southern South Africa.



HABITAT
The spotted hyena has a wide habitat tolerance and until recently was found throughout sub-Saharan Africa except for the tropical rainforests, the top of alpine mountains and extreme desert areas.

BEHAVIOR
Spotted hyenas live in female dominated groups called clans that defend group territories. Females are recruited into their birth clan where they are arranged in a linear hierarchy in which daughters inherit their mother's status. Most males are immigrants, also arranged in a hierarchy, but all are ranked lower than the females. Immigrant males slowly work their way up the social ladder, spending much time developing amicable relations with the adult females so that they can mate with them.

Members of a clan partake in an elaborate meeting ceremony. They stand head to tail, lift the inside hind leg and mutually sniff at each other's erect, male-like, reproductive organs. In essence they are exposing their most vulnerable parts to each other's lethal teeth. This helps to reinforce the close bonds that exist between members of a clan that often cooperate in dangerous activities such as attacking dangerous prey, defending the territory, and mobbing their major competitors—lions.

Clan sizes and the size of their territories vary markedly depending on the amount of food available. In the arid, prey-poor Kalahari in southern Africa five to ten adult spotted hyenas may inhabit a territory of over 400 mi^2 (1,000 km^2). In the productive Ngorongoro Crater, Tanzania clans of up to 80 individuals live in territories as small as 16 mi^2 (40 km^2). Territory clashes are common and fierce and fatal territorial battles take place. In the Serengeti, with its migratory wildebeest and zebra populations, large clans defend small territories, but individuals move through other clan's territories when they commute to the migratory herds far away from their own territory. Non-residents are submissive to and keep away from residents.

All species of hyena mark their territory by scent marking through defecating at latrines and pasting. The spotted hyena has a complex vocal system. Fourteen distinct vocalizations have been identified of which the whoop call is the most often heard and one of the characteristic sounds of the African night. They can recognize each others' whoops which are often used as a rallying call to gather scattered clan members together to help defend the territory, form a hunting party, or attack competitors. Dominant immigrant males whoop often and elaborately as a way of imprinting their presence in the territory. The famous giggle or laugh is a sign of submission, often made when several hyenas are feeding on a carcass.

FEEDING ECOLOGY AND DIET
The spotted hyena is the most successful of the large carnivores in Africa as it is equally adept as a hunter and a scavenger. It is an opportunist and has been recorded to eat almost any mammal, bird, fish or reptile, as well as man-associated organic matter. When scavenging from lion kills spotted hyenas do not always patiently wait for the larger predators to finish. If the relative numbers are right, three to four hyenas per lion

and no large males, the hyenas may cooperate to force the lions off their carcass.

As a hunter it is fast, possesses great stamina and is strong enough to bring down prey as formidable as zebra and even on occasions adult buffalo and the young of rhinoceros, although their usual targets are the young of large antelope. From time to time people sleeping outside in the bush have been attacked by spotted hyenas. They are cursorial hunters that do not stalk their prey. They often run at moderate speeds through herds searching for potential victims. Once one has been selected they chase it at speeds of up to 35 mph (60 kph) for up to 1.9 mi (3 km), until either the prey outruns the hyenas, or more frequently, until the hyenas catch the prey.

Typically the spotted hyena hunts singly or in small groups of two to five. The size of the hyena hunting group depends on the prey being hunted. Largest groups hunt eland and zebra where the average is 11. On the other hand wildebeest are usually hunted in groups of three. In the case of gemsbok calves Kalahari hyenas are just as successful when hunting them singly as they are in hunting them in a group of six. Of 55 encounters seen between spotted hyenas and gemsbok herds with calves 40 (73%) were successful, a hunting success rate surpassed by few other carnivores hunting similar prey.

REPRODUCTIVE BIOLOGY
Polygynous. Females give birth to one or two cubs, very occasionally three. The cubs are born with their eyes open and canine teeth fully erupted. Within minutes of being born they often indulge in a protracted and serious fight that establishes which of the two will be dominant and may even lead to the death of the weaker cub. This is particularly so if both cubs are female. The dominant cub is able to largely control access to the mother's milk and a cub that manages to kill its sibling will grow more quickly than if it was a twin and also have a better chance of surviving to independence at two years.

The focus of activity in a spotted hyena clan is the communal den. The females in a clan keep their cubs together, but do not suckle each other's cubs. For about the first nine months of their lives the cubs stay at the den and their major source of food is their mother's milk. They are only weaned at 14-18 months. In order to provide the nutrition needed to promote cub growth spotted hyena females produce the richest milk of any terrestrial carnivore. Their dominance ensures that they have priority at carcasses so that they can quickly eat, convert the meat into milk and get back to the den to feed the cubs. Dominant females have higher reproductive success than subordinates. They give birth to cubs at shorter intervals and have a better chance of successfully rearing young.

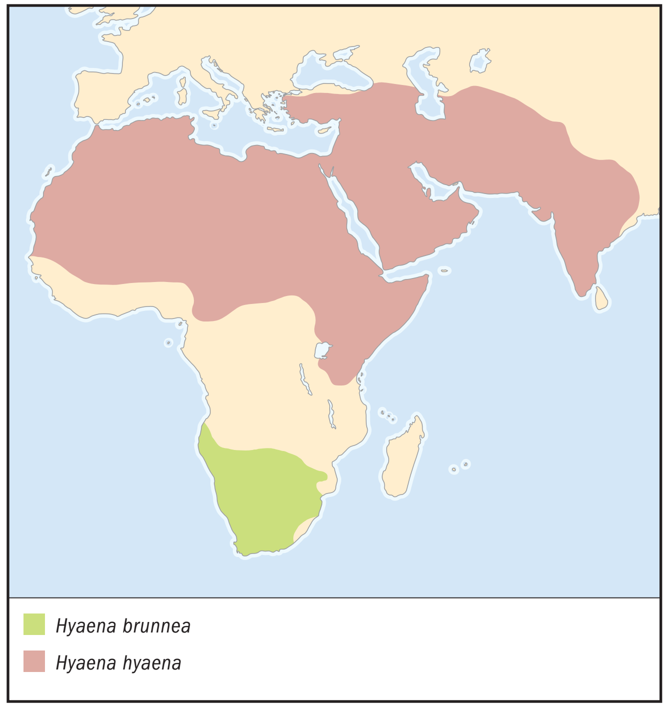
CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Occasionally known to attack humans and livestock. ◆

Striped hyena
Hyaena hyaena

TAXONOMY
Hyaena hyaena (Linnaeus, 1758), Benna Mountains, Laristan, southern Persia. Five subspecies recognized.

OTHER COMMON NAMES
French: Hyène rayèe; German: Streifenhyäne.



PHYSICAL CHARACTERISTICS
The striped hyena has a series of black vertical stripes on a beige to pale grey body, horizontal leg stripes and pointed ears, and a mane along the back which can be held erect. The black throat patch, larger size and more massive head distinguish it from the aardwolf. The size varies from about 60 to 90 lb (26–40 kg) in different parts of its range and it stands about 28 in (70 cm) at the shoulder.

DISTRIBUTION
Patchily distributed in the Sahel region of north Africa as far south as Tanzania in the east, the Arabian Peninsula, the Middle East up to the Mediterranean, across southern Asia into Afghanistan and all of India. Ethiopia, Kenya and Tanzania probably hold the largest continuous population.

HABITAT
Mainly an inhabitant of more arid areas, even found in deserts.

BEHAVIOR
Solitary when looking for food, but little is known about its behavior and social organization. It is probably similar to the brown hyena.

FEEDING ECOLOGY AND DIET
Predominantly a scavenger of vertebrate remains, supplementing the diet on reptiles, insects and birds eggs, as well as the occasional small animal which is killed. In the Serengeti the fruits of *Balinites* trees are highly favored and in Egypt it has been recorded to occasionally cause damage in melon fields and date plantations. In northern Kenya it is very much dependent on the lifestyle of the local Turkana herdsmen, scavenging around their homesteads, and reportedly killing their goats and sheep, although the extent to which they do so has not been properly established.

REPRODUCTIVE BIOLOGY
Two to five cubs are born at any time of the year. In Asia often uses caves as dens, some of which have been used for many years. Mating system is not known.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Brown hyena
Hyaena brunnea

TAXONOMY
Hyaena brunnea Thunberg, 1820, Cape of Good Hope, South Africa. No subspecies recognized.

OTHER COMMON NAMES
French: Hyène brune; German: Braune Hyäne.

PHYSICAL CHARACTERISTICS
Of similar size and shape to the striped hyena, but with a dark brown to black coat except around the neck and shoulders which are white. The ears are pointed. The lower parts of the legs have white stripes. Adults weigh about 90 lb (40 kg) with little variation between the sexes. Exceptionally large brown hyenas of around 160 lb (70 kg) have been recorded from areas as wide apart as the Eastern Cape and Mpumalanga Lowveld in South Africa.

DISTRIBUTION
Endemic to the south west arid and drier savanna regions of southern Africa. Although its range has shrunk this century, particularly in the southern part of its range, it is still widespread and is able to survive close to human habitation.

HABITAT
Like the striped hyena mainly an inhabitant of more arid areas, even found in deserts.

BEHAVIOR
Most sightings are of solitary individuals. A territory, which in the Kalahari is in the region of 120 mi^2 (300 km^2) may consist of a female and her latest litter of cubs, but when food is abundant up to 14 animals will share and defend the territory, although they still forage on their own. Most clan members are relatives, although immigrant males sometimes join a clan.

Communication through visual and vocal means is limited. The most striking display is the raising of the mane along the neck and back which occurs in conflict situations. Territorial fights are usually ritualized neck-biting bouts between two animals of the same sex accompanied by loud yelling and growling by the submissive animal. The brown hyena has no long distance call.

Chemical communication is well developed. Latrines and pastings are distributed throughout the territory. Two distinct substances are pasted, a thin layer of black paste that loses its odor within hours and below that a long-acting white blob. Experiments and chemical analyses have shown that each individual leaves its own smell and that other brown hyenas can identify this. Besides territorial marking, the long-acting paste reinforces an individual's presence in the clan. The short-acting one may inform other clan members where the hyena has been foraging and help to space the hyenas evenly through the territory to lessen the chances of them competing for food.

FEEDING ECOLOGY AND DIET
With the striped hyena the ultimate mammalian scavengers, carrion from a wide range of vertebrate remains forming the bulk of the diet. These are supplemented with wild fruits, insects, bird's eggs (particularly ostrich) and kills. In the southern Kalahari killed prey makes up less than 5% of the brown hyena's diet. Of 128 hunts observed only six were successful. The prey consists of small animals like springhare, springbok lamb, bat-eared fox and korhaan (small bustards). Along the Namib Desert coast it feeds predominantly off Cape fur seal pups, but only about 3% are killed. Here it also scavenges other marine organisms washed up on the shore. Kalahari brown hyenas move an average of 19 mi (31 km) each night and sometimes over 35 mi (50 km).

REPRODUCTIVE BIOLOGY
Brown hyena males have two types of mating systems. In one, mating is done by nomadic males that move around looking for females in heat, mate with them and then move on without investing further in their offspring. The other option is to emigrate to a clan, mate with the females in the clan and then take on parental duties by helping to feed the cubs. The latter strategy seems to be adopted in clans with more than one breeding female. For the first three months of their lives the mother visits the one to four cubs at sunrise and sunset to nurse them. As they grow the milk diet is supplemented by meat carried back to the den by the mother and other clan members. From the age of nine months the cubs begin to go on individual foraging sorties from the den that gradually increase as they become more adept at finding food and the contribution of the adults diminishes. At about 15 months they leave the den.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Aardwolf
Proteles cristatus

TAXONOMY
Proteles cristatus (Sparrman, 1783), near Little Fish River, Somerset East, eastern Cape Province, South Africa. Two subspecies recognized.

OTHER COMMON NAMES
French: Protèle; German: Erdwolf.

PHYSICAL CHARACTERISTICS
Resembles the striped hyena, but is smaller and lacks the robust neck and jaws and large teeth. It has a mane along the back that can be held erect. Its general body color is yellowish-white to rufous with several vertical black stripes along the body and one or two diagonal stripes across the fore- and hindquarters. There are also several stripes on the legs. Males and females weigh about the same, 20 lb (9 kg) in southern Africa, up to 30 lb (14 kg) in East Africa, and they stand about 19 in (47 cm) at the shoulder.

DISTRIBUTION
Occurs in two distinct populations. The southern population occurs over most of southern Africa as far as southern Angola, southern Zambia and southwestern Mozambique. This population is separated by a 930 mi (1,500 km) strip of moist woodland from the northern population in East Africa which ranges as far north as the extreme southeast of Egypt.

HABITAT
Prefers open grassy plains in the 4–24 in (100–600 mm) annual rainfall range.

BEHAVIOR
The aardwolf is monogamous and territorial—a mated pair and its latest offspring occupy a territory of 0.4–1.6 sq mi (1–4 sq km), depending on the density of termites. Territories are marked by pasting. If an intruder is encountered the resident raises the long mane along its back and, particularly if it is of the same sex, it is chased to the border. Intruders usually escape and fights are rare, except between males in the mating season. Although the cheek teeth are reduced to a few small pegs, the canine teeth are well developed and they can inflict injuries to other aardwolves. Fatal fights have been recorded. Deep roars, most uncharacteristic for this delicate looking creature accompany these fights.

FEEDING ECOLOGY AND DIET
The aardwolf feeds almost exclusively on one genus of snouted harvester termite, of the genus *Trinervitermes*. It licks the termites off the ground while they forage at night. Normally a foraging column comprises mainly workers, however, once disturbed the proportion of workers to soldiers changes rapidly, so that the predator starts taking in more and more soldiers, which squirt noxious terpenes when attacked. Eventually the quantity of terpenes taken in becomes too much and the aardwolf terminates the feeding bout.

During the cold winters in South Africa *Trinervitermes* is inactive. At this time the aardwolf switches its diet and activity to feeding in the afternoon on the diurnal, pigmented harvester termite, *Hodotermes mossambicus*. In tropical areas of East Africa the aardwolf has a more varied diet during the rainy season when a number of other termites are also eaten.

REPRODUCTIVE BIOLOGY
Monogamous. The aardwolf is a seasonal breeder. In southern Africa mating takes place in early July. Litter size is one to four. Cubs emerge from the den at about four weeks, begin foraging for termites around the den at nine weeks, and are weaned at four months when the denning period ends and the cubs become independent.

The male aardwolf helps to raise the young by guarding the den against predators. However, males are promiscuous. At the start of the mating season males make scouting trips into neighboring territories, when dominant males frequently mate with the females of less dominant males. The females mate with both males, thereby keeping the cuckolded male interested in the cubs.

CONSERVATION STATUS
Lower Risk/Least Concern.

SIGNIFICANCE TO HUMANS
None known.

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Gus Mills, PhD

▲
Cats
(Felidae)

Class Mammalia
Order Carnivora
Family Felidae

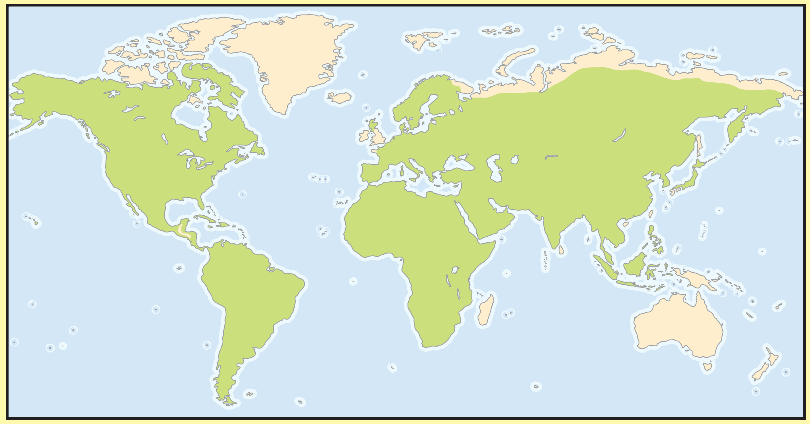
Thumbnail description
Small to large carnivores with lithe, agile bodies and short faces with small, broad skulls. Legs short to long, with large paws. Claws, teeth and strong jaws adapted for grasping and tearing. Tail usually long. Coat soft-furred, with cryptic color, plain or patterned with spots, patches or stripes

Size
Head and body length 14–120 in (35–300 cm); tail 2–40 in (5–100 cm); weight 2.5–670 lb (1–305 kg)

Number of genera, species
18 genera; 36 species

Habitat
All major habitat types except arctic tundra and polar ice

Conservation status
Critically Endangered: 1 species; Endangered: 4 species; Vulnerable: 12 species; Lower Risk/Near Threatened: 8 species



Distribution
Worldwide except Australia, Antarctica and oceanic islands

Evolution and systematics

Felidae are part of the ailurid (cat-like) branch of the order Carnivora, which also includes the hyena, mongoose, and civet families. The earliest cat-like animals can be dated back to the lower Eocene, some 40 million years ago. Today's cat species can be traced to an ancestor named *Pseudailurus*, from which wild cats and saber-toothed tigers evolved in the Oligocene, some 25-30 million years ago. Saber-tooths preyed on primitive, large, slow mammals and died out 10,000-20,000 years ago, but modern cats adapted to hunt large, fast ungulates, and prospered and evolved into the 36 cat species known today.

Cat taxonomy has been subject to considerable confusion and revision. Linnaeus originally classified all cats into a single genus, *Felis*. Later taxonomists subdivided this into as many as 23 genera, then, more recently there was a tendency to "lump" some genera together again. Until recently many authorities recognized only four genera: *Felis* for all small cats, *Panthera* for the "big cats" (defined by their ability to roar), *Neofelis* for the clouded leopard, intermediate between big and small cats, and *Acinonyx* for the cheetah.

In 1996, the Felid Taxonomic Advisory Group (TAG) of the American Zoo and Aquarium Association (AZA) published a revised taxonomy which divided *Panthera* into 4 genera, and *Felis* into 13. There are now four genera (seven species) in the Pantherinae subfamily, one genus (one species: the cheetah) in the Acinonychinae subfamily, and 13 genera (28 species) in the Felinae subfamily. The Iriomote cat (*Prionailurus bengalensis iriomotensis*), once considered a separate species, is now classed as a subspecies of the leopard cat.

The Felid TAG classification is used in this account, with older genus names indicated in parentheses. Molecular research is likely to lead to further revisions to felid taxonomy.

A male African lion (*Panthera leo*) rests in the shade. (Photo by David M. Maylen III. Reproduced by permission.)

A fishing cat (*Felis viverrina*) from Southeast Asia. (Photo by Animals Animals ©John Chellman. Reproduced by permission.)

Physical characteristics

All cat species show considerable resemblance to the domestic cat, being carnivores with long, lithe, muscular bodies, but in a wide range of sizes. Head and body length ranges from 14 in (35.6 cm) for the diminutive black-footed cat (*Felis nigripes*), to more than 10 ft (3 m) for a large male Amur tiger (*Panthera tigris altaica*). The weight range varies more than 300 fold, from as little as 1.7 lb (0.8 kg) for the small cat to in excess of 660 lb (300 kg) for the tiger. Males are larger and more muscular than females, but otherwise there is minimal sexual dimorphism, with the notable exception of lions (*P. leo*). A cat's head is short and rounded with large eyes, long whiskers, powerful jaws, specialized teeth for cutting and gnawing meat, and a rough, rasping tongue covered with horny papillae, to lick bones clean. Ears may be triangular or rounded. Legs are short to long, feet large and padded, with five toes on the front feet, four on the hind feet, and with hooked sickle-shaped claws, which in most species are sharp and retractile. Tails are furred and usually medium to long, up to 40 in (1 m) in large cats, but some species such as bobcats have short, rounded tails.

Coats are cryptically colored, pale gray to brown, with a paler underside and often with black and/or white markings on the face, tail and back of the ears. Many species are spotted, blotched, or striped, for camouflage. Melanistic (black) forms are common among several species, white forms occur rarely. Young often have different markings from the adult coloration—newborn cheetah (*Acinonyx jubatus*) cubs have a long, white-gray mane, absent in the adult, for example. Individual cat species can show considerable variations in color, often linked to geographic location, with animals from warm, humid climates often darker than specimens of the same species living in cooler regions.

Cats have acute, binocular, color vision. The iris, which may be orange, yellow, gray, brown or green, reacts very quickly to darkness and contracts to a small point or slit in bright light. Night vision is very good, helped by a reflecting layer, the tapetum lucidum, outside the retinal receptor layer, which reflects back any light not absorbed by the receptor layer at first pass, and accounts for the eye shine we see in cats at night. Whiskers and long hairs above the eyes are sensitive to touch, which also helps the animals move around at night.

Most felids have acute hearing, especially those species with large ears, which are used like radar dishes to locate prey. The sense of smell is also very important to cats, with a major role in social interaction, maintaining territories, and advertising that females are ready to mate, though not in hunting. Scent glands are often present in foot pads, chin, cheeks and anus.

Distribution

Cats are found the world over, with the exception of Australia, the polar regions, and some oceanic islands where they are usually considered a serious pest. However, domestic cats have been introduced to almost all places settled by humans, including Australia and other islands. Sub-Saharan Africa is home to eight cat species, including the largest populations of lion, cheetah, and leopard (*P. pardus*). These big cats are also found in North Africa and southwest Asia, along with five other species, but their distribution has declined dramatically in this region, and only small, isolated populations remain. Tropical Asia is home to 12 species, including tiger (*P. tigris*), clouded leopard (*Neofelis nebulosa*), leopard, and a range of small cats adapted to jungle habitats. Eurasia has seven species, including snow leopard (*Uncia uncia*), lynx (*Lynx lynx*), and Iberian lynx (*L. pardinus*), but their populations are also

A female African lion (*Panthera leo*) drinks from a water hole. (Photo by David M. Maylen III. Reproduced by permission.)

An adult male lion (*Panthera leo*) eats an elephant's trunk. (Photo by Harald Schütz. Reproduced by permission.)

under severe pressure. Cats are well represented in the Americas, with a dozen species, including jaguar (*P. onca*), puma (*Puma concolor*), and Canada lynx (*L. canadensis*).

Habitat

Cats have colonized almost all major habitat types from desert to equatorial rainforest, swamps, and high mountains. Only treeless tundra and polar ice are felid-free. Although a few species have become highly adapted to a limited range of habitats (the sand cat [*F. margarita*] of stony and sandy deserts, for example) most species are not habitat specialists and can be found in a range of environments.

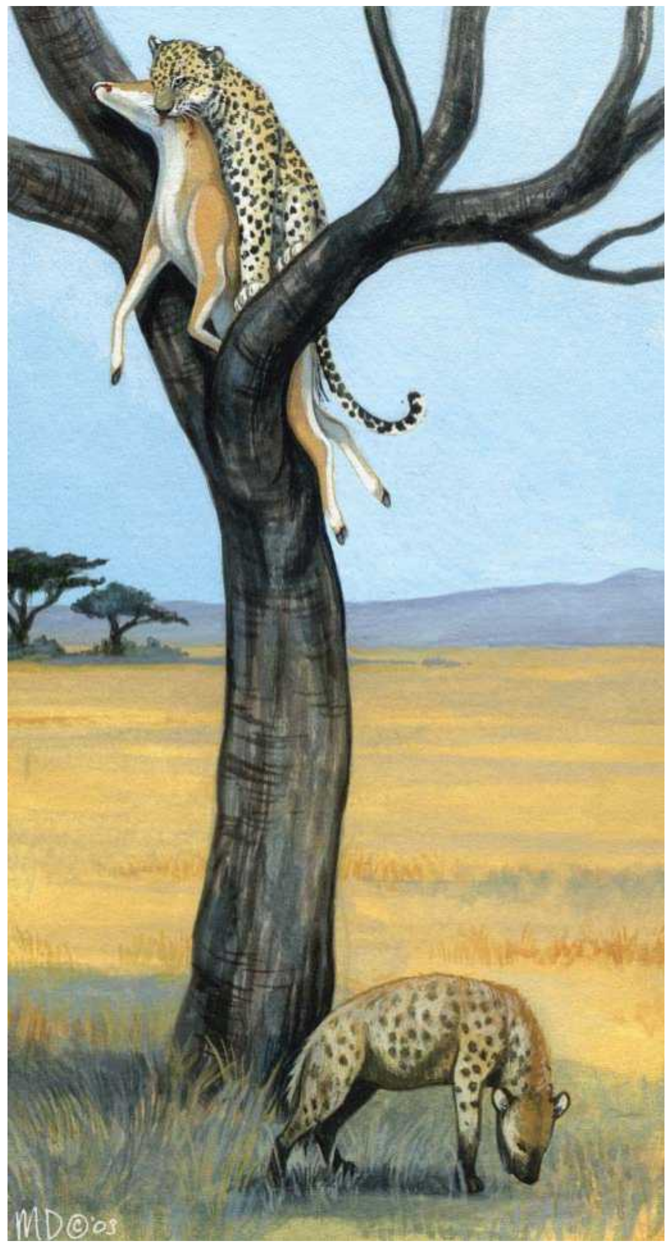
Behavior

The social organization and behavior of cats show remarkable similarity between the majority of species. Most are truly solitary, coming together only to mate. In the closed habitat favored by many species prey is usually dispersed and too small to share, so hunting alone is more efficient. Both males and females have home ranges, with those of males generally larger and often incorporating the range of one or more females. Adult males are usually territorial, defending at least part of their range, while females may or may not be territorial. The notable exception to the typical feline social organization is the lion, which has developed a unique clan-based society, based on close bonds between related females, and involving cooperative hunting, feeding and raising young. Tigers and leopards may also occasionally hunt together. Cheetahs also differ since males may hunt in groups.

Although cats do fight over territory, physical aggression is mostly avoided. Instead cats use scent-marking and calling to advertise their home range and specific whereabouts, enabling even animals with overlapping ranges to avoid running into one another. Cats may sharpen their claws on trees, leaving visual signs of their presence. Big cats also rake their hind feet in the earth as they spray backwards onto above ground objects to leave a scent trail as they patrol. Where fights do occur, usually in contests over an estrous female, they vary in intensity, but may be very serious and even deadly. Territorial fights usually involve a sudden fast attack without preliminary display.

Most cats are primarily nocturnal, but often show activity peaks around dusk and dawn, related to increased prey activity at these times. Their secretive, nocturnal behavior means many species have not been extensively studied in the wild.

Apart from cheetah, tigers, and lions, cats are good climbers, but most climb trees for rest and safety, rather than hunting. Cats have a famous ability to land on their feet, a result of a well-developed sense of equilibrium, important in arboreal species. In treeless environments, cats may den un-



Leopards sometimes take their prey into a tree to keep it safe from scavengers. (Illustration by Marguette Dongvillo)

White tigers are not a separate species, but rather albinos of the same species as the more common orange colored tiger. (Photo by K. Sandved. Bruce Coleman, Inc. Reproduced by permission.)

derground, appropriating the burrows of other animals. Most cats have an aversion to entering water, but some are strong swimmers. Tigers will chase prey into lakes, and some small cats catch fish.

Cats have a wide range of calls, include meowing, purring, panting, gasping, yowling, snorting, growling, and hissing. Small cats lack the roaring distance call of big cats, but some advertise estrous with loud wails. Close range communication involves not just vocalization, but sophisticated visual signals. Cats have a large variety of facial expressions and body language, enabling complex, often ritualized communication, which may avert dangerous physical confrontations between animals armed with sharp claws and teeth. The arched back seen in domestic and other small cats is a defensive threat posture.

Feeding ecology and diet

Cats are generally the purest of carnivores, sitting at the top of the food chain. Small cats prey predominantly on rodents, rabbits and hares, but will also take reptiles, amphibians, fish, crustacea, birds, and insects. Large cats prefer ungulates, but feed opportunistically on any available meat. Many cats will also scavenge carrion. Some species supplement a carnivorous diet with fruit, and desert lions are known to eat tsama melon (*Citrullus lanatus*), though this is for their water content, rather than food. Cats will also swallow grass, which helps rid the body of fur balls formed inside the intestinal tract from hair swallowed when grooming.

Cats mainly hunt at night, though the cheetah is diurnal. Most rely on stealth to approach prey before a final rush or pounce. Even the fastest cats can only outrun their prey over a short distance, as with comparatively small hearts they have very limited stamina and quickly tire.

Small prey animals are pounced on with both front paws, and killed with a specialized bite to the back of the neck, severing the spinal cord, before being eaten, starting with the head. Large, fast-running prey animals are tripped with a foreleg; slower animals grappled over the rump, back, or shoulder. The cat keeps its back legs on the ground for purchase, hooks claws into the quarry's skin, and pulls it off balance. A powerful jawlock on the prey's throat or muzzle then suffocates it.

Cats may gnaw meat from the bone, or pull it off in lumps and swallow it without chewing. Excepting the snow leopard, which eats crouched over food like small cats, all big cats eat lying down and never hold the meat with their fore paws. Whereas small cats use just their molars to pull at meat, big cats (and sometimes the clouded leopard as well) use not only the molars but the incisors and canines as well, grabbing the meat and jerking the head up. Cats have a tooth formation in the upper and lower jaws of three pairs of incisors, one pair of canines, two or three pairs of premolars, and one pair of molars. The molar is modified to a powerful shearing tooth, or "carnassial," so cats bite with the side of the mouth, not with the front. Large kills are often cached by covering with leaves, grass or dirt, or carried into trees. Species that mainly eat small prey such as rodents may feed every day, but for larger cats, feeding often means gorging on large kills for several days, then going hungry for several more days before another successful kill.

Cats are stimulated to stalk and catch prey even when satiated, which explains why even a well-fed domestic cat—or wild lion—cannot resist an easy kill. Given that waiting for suitable prey is the most time-consuming part of predation, this stimulus response ensures cats make the most of every opportunity. It also explains why a caracal or puma in a field of sheep will kill many more animals than it can eat.

Reproductive biology

Female small cats may reach sexual maturity at less than one year old, big cats at around two years, but a female may not produce her first litter until she has established a home range, which might not be until age three or four. Gestation

Bengal cat (*Felis bengalensis euptilura*) female and cub. (Photo by Animals Animals ©Michael Dick. Reproduced by permission.)

A bobcat (*Felis rufus*) with a white-tailed deer fawn carcass. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

ranges from two months in small cats to over three months in lion and tiger. Litters may contain up to eight cubs, but two to four is usual. Small cats may reproduce yearly, larger ones at intervals of at least 18 months, unless they lose a litter, in which case they can come into estrous again within weeks. Many cats are non-seasonal breeders, but in areas with strongly seasonal climatic or prey availability conditions breeding occurs at the most favorable time of year.

Cats are polygamous. Estrus may last from one day to three weeks, depending on the species. Females have multiple estrous cycles until they conceive. They advertise their condition by scent marking, calling, and by becoming hyperactive. Local males may compete for mating rights with displays and sometimes fighting. The successful male may consort with the female for several days, courting with specific calls, by presenting his head, and by rubbing against the female. Females court the male with behavior that is alternatively inviting and defensive, increasingly taking the initiative as they come more into heat. Copulation itself typically lasts less than a minute, but may be repeated several times an hour for up to three days or even longer. Repeated copulation probably serves to induce ovulation in the female. During copulation the female lies prone on her belly, while the male mounts her. In small cats the male bites the female's neck during copulation, but big cats only grab the neck symbolically at ejaculation. Copulation ends with the female twisting to hiss and strike at the male with her paw, before often rolling onto her back. She then resumes affectionate behavior. After several days the male may lose interest and another male may take his place.

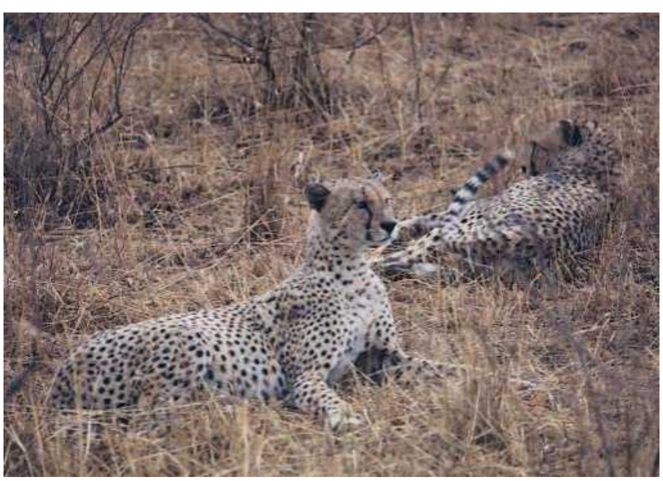
With the exception of lions, males apparently play no further part in raising young. Feline young are born blind, deaf, and barely able to crawl. They remain hidden in a den or nest for several weeks until mobile. In some species, individuals in the litter develop a teat order while nursing, with dominant kittens getting the most milk. The mother will defend her kittens aggressively, even against the odds, and will move the hiding place if disturbed, carrying cubs one-by-one by the head, nape or skin on the back. Mothers start to train cubs to hunt from a very young age, bringing back first dead then live prey for them to practice catching and eating. However, cubs may not be independent for up to 18 months or more in the case of some big cats. When the mother is ready to produce a new litter they depart, but may stay within the mother's home range for another year, or indefinitely in the case of females. Young cats play extensively, mainly developing behaviors of importance in adult predatory behavior. Longevity is commonly approximately 15 years for most species, with some individuals reported to have lived over 30 years.

A female African lion (*Panthera leo*) yawning. (Photo by David M. Maylen III. Reproduced by permission.)

Conservation status

No fewer than 25 of the 36 cat species are listed by the IUCN, and even those which are not are often subject to serious threat at local or subspecies level, or their population status may simply be insufficiently known to classify. The most immediate threat of extinction is faced by the Iberian lynx, found in only small, isolated, populations in Spain and Portugal. But not far behind are such iconic species as the tiger and the snow leopard.

While many species of cat have long been persecuted by farmers on the grounds of their real or imagined threat to livestock, the principal direct human threat to cat species in recent decades has been commercial trapping for fur. A fashion for furs in Western society in the 1960s and 1970s saw large numbers of tiger, leopard, jaguar, and snow leopard pelts appearing in shops, and small cats were also traded extensively, peaking at 600,000 pelts traded in a single year. Species such as the ocelot (*Leopardus pardalis*) and Geoffroy's cat (*Oncifelis geoffroyi*) were hit particularly hard.

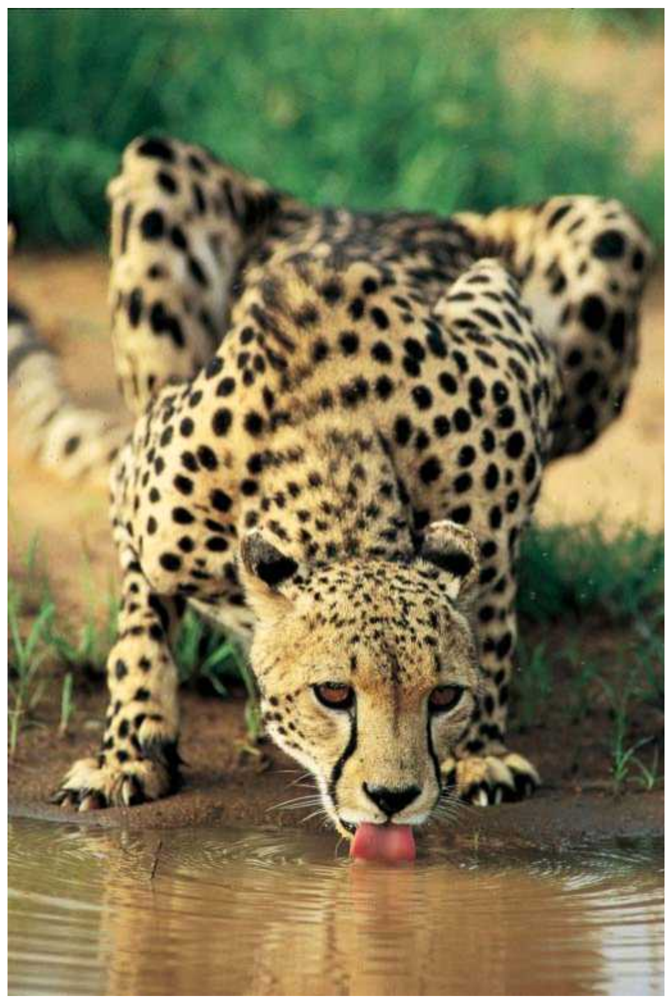


Cheetahs (*Acinonyx jubatus*) rest in the grasslands of Africa. (Photo by David M. Maylen III. Reproduced by permission.)

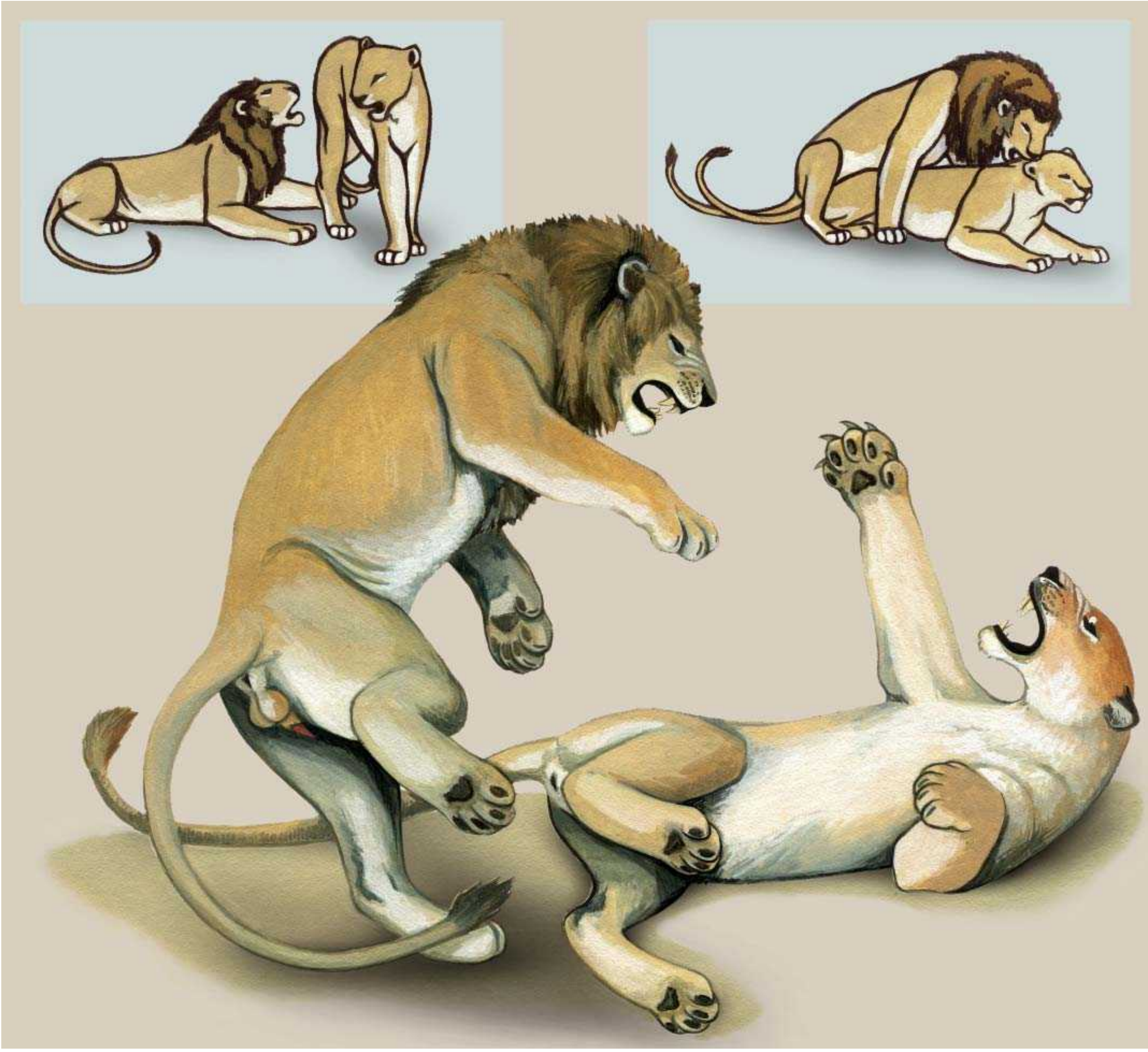
Concern that commercial fur trading at unsustainable levels could drive some cat species to extinction was a major factor behind the 1975 Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Although some countries have been slow to enforce legislation banning trade in endangered species, the international trade in spotted cat pelts has now reduced dramatically, a trend strengthened by public awareness of the impact of fur harvesting on species survival. Today's fur trade relies on three species of lynx and the Chinese leopard cat (*Prionailurus bengalensis*), supplied by the United States, Canada, China, and Russia. Commercial fur trading is not currently considered a significant threat to cat species, with the possible exception of the leopard in some areas.

Illegal poaching driven by a demand for cat body parts for use in traditional Oriental medicine is still a major problem for large Asian cats such as the tiger, which could soon be driven to extinction in the wild.

Habitat loss has mostly affected cats associated with forest habitat. Deforestation, especially in tropical Asia, has made



A cheetah (*Acinonyx jubatus*) drinks water in Kenya. (Photo by Joe McDonald. Bruce Coleman, Inc. Reproduced by permission.)



The lioness entices the male to mate (top left). After mating (top right), the lioness will often aggressively turn on the male, rolling on her back and striking out with her claws (center). (Illustration by Marguette Dongvillo)

several species vulnerable, through the absolute loss of habitat and the fragmentation of populations. Important habitats including tropical rainforest, major wetlands, and tropical montane complexes are declining globally. However, many cat species are adaptable and can survive in modified habitat. The indirect threat of human development posed by the depletion of prey species may be of more immediate concern for the conservation of some cats as well as the incidence of disease in several populations.

Significance to humans

Domestication of the cat can be traced back to the ancient Egyptians, some 7,000–4,000 years ago. The distinctive upright, long-legged posture of sitting cats in Egyptian paintings suggests it was the African version of the wildcat that gave rise to today's domestic tabby. Wildcats were undoubtedly attracted to the granaries and fields of early settlement, where they performed a valuable service preying on rodents and would have grown used to human contact. African, Asian, and old Germanic tribes have also revered the cat. Mohammed called the cat his favorite animal, and the keeping of domestic cats spread across Africa and Asia with the spread of Islam.

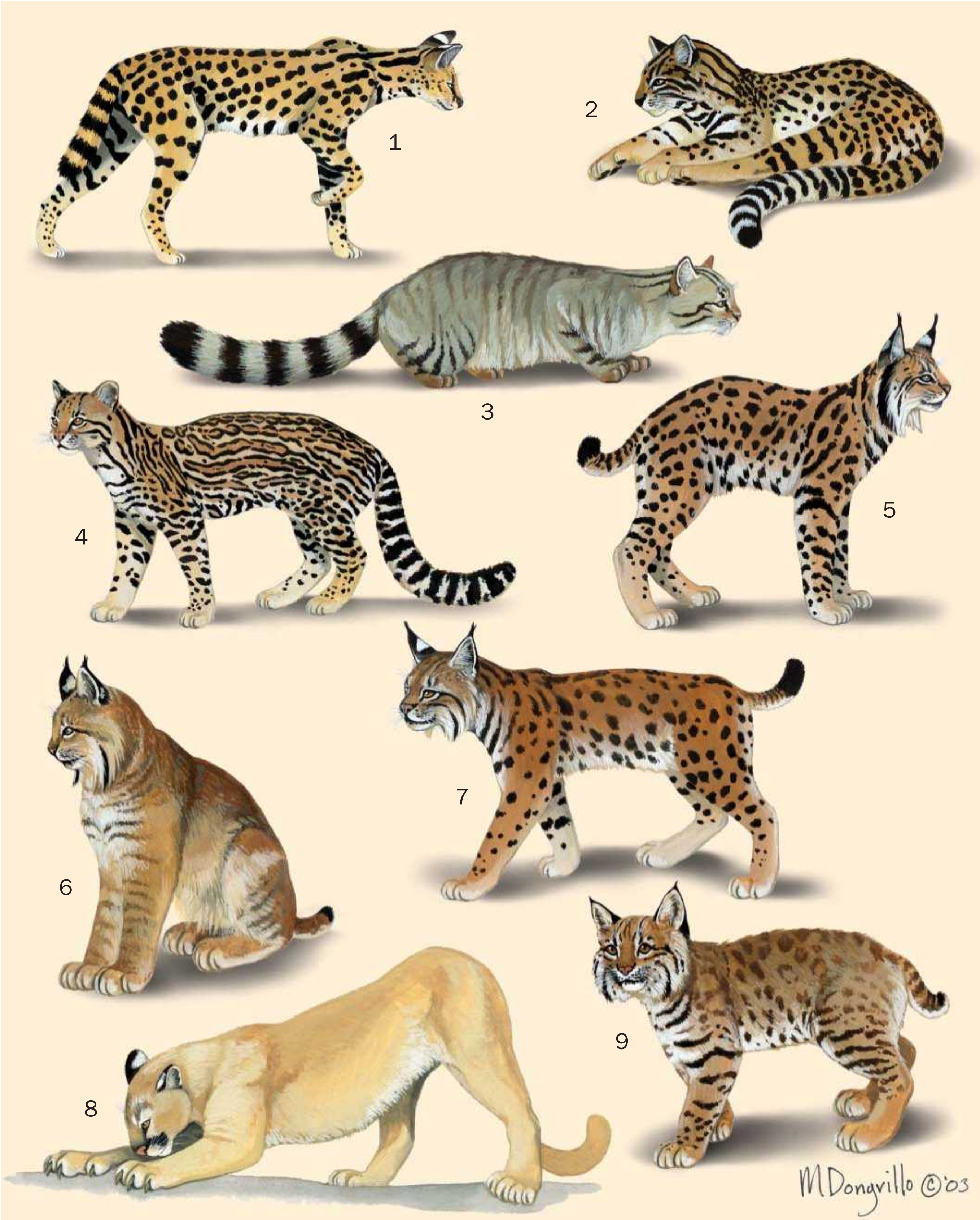
Human fear and persecution of cats no doubt dates back to the prehistoric days of the saber-toothed tiger, which appears in cave paintings dating back tens of thousands of years. Our modern species of big cat still engender fear among communities living close by, with some justification—tigers, lions, and leopards have all been recorded as human-eaters. Human casualties are generally the result of accidental confrontations, or involve injured or sick animals, but in the Sunderbans swamps of India tigers have learned that fishermen and wood gatherers make easy prey, and several dozen people may fall victim in a single year.

A much more widespread cause of conflict with humans is predation on livestock. Although predation rates are usually fairly low, losses may be important to individual owners, especially in developing countries. Conservationists are looking at measures including culling of problem animals, improved anti-predator stock management, and paying compensation for lost livestock, to discourage large scale persecution of cats by farmers.

Cat pelts have been a symbol of status and power in cultures both ancient and modern. While international trade in the fur of endangered species has been reduced to relatively insignificant levels, domestic trade persists in some countries. Unlike animals such as fox or mink, cats killed for fur are entirely caught in the wild, and pelts are of high value compared with other species. Some conservationists have suggested that controlled harvesting, generating relatively high revenues from low level culling, could be one way of encouraging sustainable exploitation of cats.

Larger cat species have an economic value in attracting tourists to national and private reserves in Africa and India. Trophy hunting under quota is carried on in a number of African countries. In Botswana, selective hunting of "trophy" lions, usually by dominant males, is alleged to have caused social imbalance and inbreeding among prides. There has also been controversy in South Africa over "canned lion" hunts, where captive-bred lions habituated to people are "hunted" in enclosures or immediately after release.

1. Leopard (*Panthera pardus*); 2. Lion (*Panthera leo*); 3. Clouded leopard (*Neofelis nebulosa*); 4. Caracal (*Caracal* [*Felis*] *caracal*); 5. Cheetah (*Acinonyx jubatus*); 6. Jaguar (*Panthera onca*); 7. Snow leopard (*Uncia* [*Panthera*] *uncia*); 8. Tiger (*Panthera tigris*). (Illustration by Marguette Dongvillo)



1. Serval (*Leptailurus* [*Felis*] *serval*); 2. Geoffroy's cat (*Oncifelis* [*Felis*] *geoffroyi*); 3. Wild cat (*Felis silvestris*); 4. Ocelot (*Leopardus* [*Felis*] *pardalis*); 5. Iberian lynx (*Lynx* [*Felis*] *pardinus*); 6. Canada lynx (*Lynx* [*Felis*] *canadensis*); 7. Eurasian lynx (*Lynx* [*Felis*] *lynx*); 8. Puma (*Puma* [*Felis*] *concolor*); 9. Bobcat (*Lynx* [*Felis*] *rufus*). (Illustration by Marguette Dongvillo)

Species accounts

Lion
Panthera leo

SUBFAMILY
Pantherinae

TAXONOMY
Felis leo (Linnaeus, 1758), Africa. Asiatic subspecies, *Panthera l. persica*, once widespread in southwest Asia, now only in the Gir Forest, Gujarat, India.

OTHER COMMON NAMES
French: Lion; German: Löwe; Spanish: León.

PHYSICAL CHARACTERISTICS
Length 62–100 in (160–250 cm); tail 24–40 in (60–100 cm); weight 270–570 lb (120-260 kg). Males up to 50% larger than females. Uniform, short tawny coat, white form locally in South Africa. Black on back of ears. Spots on cubs may remain faintly visible on abdomen and legs of adults. Tufted tail. Blond to black mane in adult males, possibly serving as protection during fights, a signal of gender at distance, and an indication of fitness. Asiatic lion has less mane growth on top of head and longitudinal fold of skin running along belly.

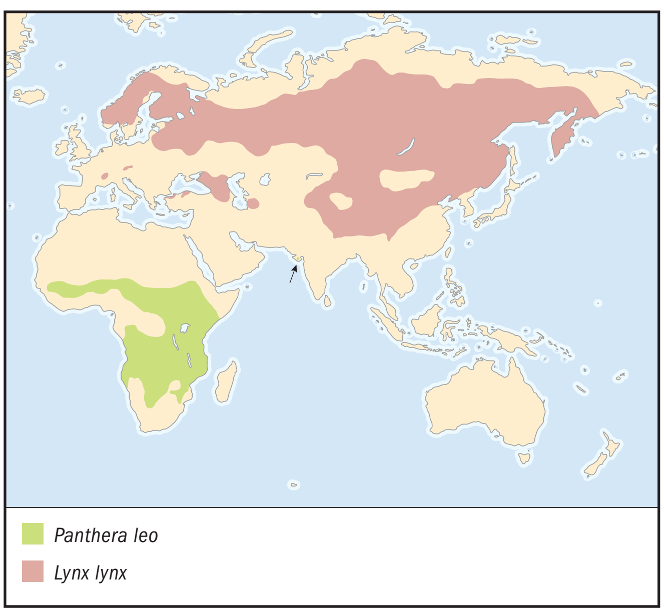
DISTRIBUTION
Sub-Saharan Africa, excluding rainforest. Asiatic lion in Gir Forest, India.

HABITAT
Wide range, except tropical rainforest and interior of Sahara desert. Open woodland, and mixed areas of thick bush, scrub and grass are favored.

BEHAVIOR
The most social of cats. Lion society is based on the pride, a group of related females and cubs. Pride size varies from two to 18 adult females depending on habitat and prey availability, but is typically four to six. A single male or coalition of up to seven males, almost always unrelated to the females, holds tenure over the pride (sometimes several prides), excluding other males from mating. Pride membership is stable, but members often scatter in sub-groups throughout the range, especially when foraging, and individuals spend considerable time alone.

Prides are strongly territorial. Males mark territory by urine-marking and by roaring, usually at night, when the sound can travel 5 mi (8 km). They actively patrol the edges of territory, whereas females tend to stay nearer the center. Males face strong competition for pride tenure, and average tenure is only two to three years (larger coalitions last longer). Males are also highly social, and when not in tenure of a pride will form coalitions to hunt and scavenge together. Large coalitions are invariably related, but pairs and trios of males may be unrelated.

Lion density varies from 0.4 to 15 per 100 mi^2 (250 per km^2), linked to seasonal prey availability. A pride's home range usually varies from 8 to 200 mi^2 (20 to 500 km^2), but can be more than 800 mi^2 (2,000 km^2) in arid zones.



FEEDING ECOLOGY AND DIET
Medium to large ungulates, including buffalo, zebra, wildebeest, and waterbuck make up bulk of diet, but lions will take a wide range of prey from small rodents and birds to young rhinos, hippos and elephant. Asiatic lions prey largely on deer and livestock. Lions also frequently scavenge.

Most hunting nocturnal, but may ambush prey in daytime at waterholes in dry season. Females do most of the hunting, males tackling larger, slower prey such as giraffe or buffalo. Will hunt cooperatively, fanning out to partially surround prey, but more often only one or two lions hunt, while the remainder watch. Lions can only reach 36 mph (58 kph), so rely on stalking to within range of a short dash. They kill prey by suffocation, clamping their strong jaws on an animal's windpipe or muzzle.

Only one in four hunts are successful, with moonless nights best. Lions eat communally, but males take the "lion's share" of the food before lionesses are allowed to eat, then cubs last of all. In lean times, cubs frequently die of starvation. Lions need about up to 15 lb (7 kg) of food per day, but feeding is often irregular and a male may eat 110 lb (50 kg) at one time.

REPRODUCTIVE BIOLOGY
Polygamous. Breeding largely non-seasonal. Females are sexually mature at three to four years. Mating occurs about three times per hour for several days, and a female may mate with more than one pride male. Gestation around 110 days, litter size one to six. Cub mortality can be very high, up to 75% in first year if prey is scarce. Cubs start to eat meat after three months, but nurse until six months. Males leave the pride at two to four years old (earlier if forced out by a pride takeover), most females remain in the pride.

Males that take over a pride will attempt to kill young cubs (though mothers often hide them successfully), to ensure their own chance of fathering offspring during their brief pride tenure. Females show a burst of heightened sexual activity (but are infertile) for three months following a takeover, attracting other males and increasing competition for tenure, to ensure the fittest males breed. Once pride males are established, females often breed synchronously, which increases cub survival rate. Females may also rear young communally, and cubs suckle freely from lactating females.

CONSERVATION STATUS
Classed as Vulnerable by IUCN. *Panthera l. persica* is Critically Endangered, with only around 250 mature animals. Lions are heavily persecuted outside of protected areas and loss of habitat and prey base is contributing to population decline. Total population may be less than 10,000 breeding individuals, with no one population larger than 1,000.

SIGNIFICANCE TO HUMANS
Lions are depicted in the art of many ancient cultures, including European cave paintings from more than 30,000 years ago. Numerous African cultures still believe in the magical and healing properties of lion body parts. The extinct Barbary lion featured in the circuses of ancient Rome.

Where lions conflict with domestic stock, they are vulnerable to poisoned carcasses and trapping and problem animals may be legally shot in some countries. Lions may also pose a threat to human life, turning man-eater if old, injured, or when prey is scarce.

Regulated trophy hunting is allowed in a number of countries, mainly in southern Africa. Preferential shooting of large trophy males is claimed to have adversely affected population dynamics in some locations, with evidence of inbreeding as a result. ◆

Tiger
Panthera tigris

SUBFAMILY
Pantherinae

TAXONOMY
Felis tigris (Linnaeus, 1758), Asia. Five subspecies survive: the Bengal tiger (*Panthera t. tigris*) in India, Bangladesh, Bhutan, China, Myanmar and Nepal; the Amur tiger (*Panthera t. altaica*) in Russia, China, and North Korea; the south China tiger (*Panthera t. amoyensis*) in China; the Sumatran tiger (*Panthera t. sumatrae*) in Sumatra; and the Indo-Chinese tiger (*Panthera t. corbetti*) in China and Southeast Asia. Three other subspecies have become extinct since the 1950s.

OTHER COMMON NAMES
French: Tigre; German: Tiger; Spanish: Tigre.

PHYSICAL CHARACTERISTICS
Length 75–150 in (190–310 cm); tail 28–40 in (70–100 cm); weight 140–670 lb (65–306 kg). The largest cat, with an unmistakable reddish brown to yellow-ochre coat, with black stripes and white belly. Indian and Russian tigers are larger than island races. Males have a prominent ruff. White tigers are very rare in the wild, zoo specimens all descend from just two wild animals.

DISTRIBUTION
Scattered populations in India, from Bangladesh to Myanmar, and in Sumatra, China, and far eastern Russia.

HABITAT
Varied, including tropical evergreen and deciduous forests, mangrove swamps, tall grass jungles, and temperate coniferous and birch woodland. Dense vegetative cover, sufficient large prey species and water are all essential.

BEHAVIOR
Usually solitary but not anti-social, males sometimes associate with females when feeding or resting, as well as to breed. Territorial, both males and females defending territory against intruders of the same sex. Scent-mark to advertise territorial ownership.

Ranges vary with prey density, and are larger for males which need access to females to mate with. In prey-rich parks such as Kanha, India, a female's range may be only 4 mi^2 (10 km^2) and a male's only 12 mi^2 (30 km^2), whereas in far eastern Russia females may need 160 mi^2 (400 km^2), and males up to 400 mi^2 (1,000 km^2).

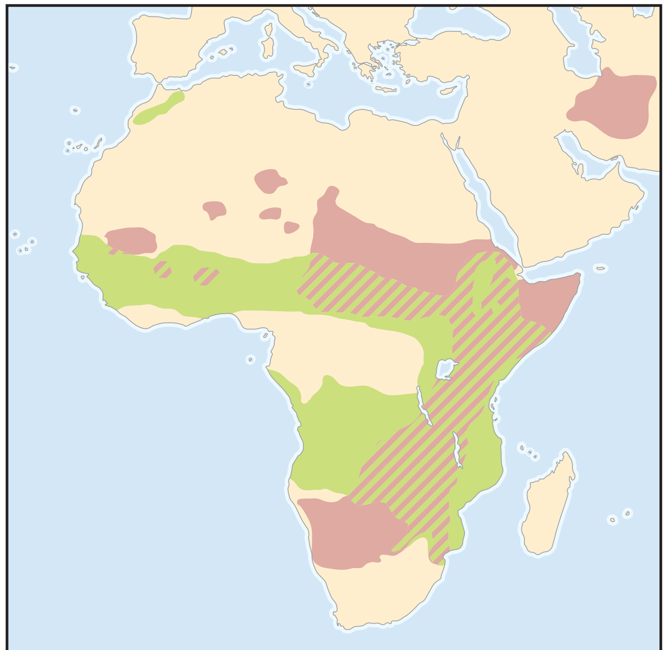
FEEDING ECOLOGY AND DIET
Hunts mainly between dusk and dawn, usually alone. Prey includes deer species, wild pigs, and gaur, occasionally young elephants and rhino, and small species such as monkeys, birds, reptiles, and fish. Also carrion. Large prey are stalked from the rear, then attacked in a rush and killed with a throat hold or bite to the back of the neck. Tigers are strong and willing swimmers and will chase deer into water. Prey is dragged to cover after being killed. Hunts are often unsuccessful but large prey is taken about once a week. A tiger may eat up to 90 lb (40 kg) of meat at a time, returning to the kill for up to six days.

REPRODUCTIVE BIOLOGY
Polygamous. Females reach sexual maturity at three to four years, males at four to five. An estrous female advertises by roaring and increased scent-marking. The territorial male retains exclusive breeding rights with females in his territory, so long as he can guard it. A male which takes over territory may kill cubs fathered by another male, bringing the mother into estrus.

Mating may happen 40 times over four days. Tigers are not seasonal breeders, but mating peaks in November–April. Gestation 103 days, litter one to seven, usually two or three. Cubs are born blind and helpless and are kept in hiding for at least a month. Mortality is high, around one third of cubs not surviving their first year, mainly due to infanticide. Cubs are taken to kills at six months but are not independent until at least 18 months.

CONSERVATION STATUS
Classified as Endangered by the IUCN. An estimated population of 100,000 a century ago has shrunk to perhaps fewer than 2,500, and the south China subspecies verges on extinction. Habitat loss, poaching for trophy skins and traditional medicines, and prey depletion due to unsustainable human hunting are the main threats. Conservation measures include preserving habitat "corridors," allowing tigers to move between increasingly fragmented populations, and habitat restoration schemes involving giving incentives to local people to protect land.

SIGNIFICANCE TO HUMANS
International legislation partially banning trade in tiger products has been only partly successful, and there is still huge demand for tiger parts for use in traditional medicine and for skins as trophies in countries such as Japan, Hong Kong, and South Korea. Greatly reduced tiger numbers mean human deaths from attacks are now rarer, but dozens of people are still killed in some areas, especially India's Sunderbans reserve, where fishermen and wood collectors are vulnerable to human-eaters. Tigers also kill livestock, earning retaliation in the form of poisoned carcasses. ◆



Cheetah
Acinonyx jubatus

SUBFAMILY
Acinonychinae

TAXONOMY
Felis jubata (Schreber, 1775), South Africa. Two subspecies, African cheetah (*Acinonyx j. jubatus*) and Asiatic cheetah (*Acinonyx j. venaticus*). The king Cheetah, a mutant form with spots along the spine joined together into stripes, was formerly incorrectly described as a separate species, *Acinonyx rex*. Cheetahs show a very low level of genetic variation, suggesting they all descend from a very small population bottleneck 10,000 years ago.

OTHER COMMON NAMES
French: Guépard; German: Gepard; Spanish: Guepardo, chita.

PHYSICAL CHARACTERISTICS
Length 44–53 in (112–135 cm); tail 26–33 in (66–84 cm); weight 86-143 lb (39–65 kg). Slight physique, long legs, small head and deep, narrow chest built for speed. Flexible spine increases stride length, non-retractile claws give traction, and long tail helps balance the animal when running. Most claws are blunt, but prominent dew claws used to trip running prey are sharp. Coat is tawny, with small, round black spots. "Tear stripes" on face.

DISTRIBUTION
Sub-Saharan Africa, North Africa, and Iran.

HABITAT
Savanna, dry forest. Ideal habitat includes some cover, or broken ground.

BEHAVIOR
Adult females solitary except when with cubs, males solitary or in small coalitions (usually related). Females are nomadic, ranging over areas up to 560 mi^2 (1,500 km^2). Some males territorial, urine marking and defending a territory of around 5–60 mi^2 (12–150 km^2). Other males nomadic, roaming over areas of up to 300 mi^2 (780 km^2). Nomads may gain territories, especially if they form a coalition, or may remain nomadic all their life. Population density ranges from 1 per 80 mi^2 (200 km^2) to 1 per 2.5 mi^2 (6 km^2) linked to prey availability and competition from other predators.

Scent marking is the most important form of communication for male and female cheetahs. Mothers and cubs communicate with chirping or yelping calls. Cheetahs also snarl, growl and hiss in anger or fear, and purr in contentment.

FEEDING ECOLOGY AND DIET
Diet mainly medium-sized antelope, also hares and small mammals. Hunt in daytime, stalking to within 100 ft (30 m) before sprinting at prey. Capable of speeds of at least 60 mph (95 kph), but cheetahs have little stamina and after 550 yd (500 m) are exhausted. Most chases last only 20–60 seconds and rarely exceed 200 yd (190 m). About half are successful. Prey killed by suffocating throat-hold. Cheetahs are often driven off kills by larger predators.

REPRODUCTIVE BIOLOGY
Polygamous. Breed year round, but mating peaks after rains. Females advertise estrous by scent marking. Gestation 90–98 days, litter size one to six (usually three or four). Cubs are kept hidden until eight weeks old, then accompany the mother and start on solid food. Weaned after 3–4 months, but dependent on mother until 14–18 months. Cubs mortality is very high—two thirds do not reach independence, more where other large predators, the main cause of infant mortality, are numerous. After independence cubs stay together for six months, then females leave to live a solitary life, while brothers stay together for life.

CONSERVATION STATUS
Classed as Vulnerable by the IUCN. African population estimated at below 10,000 breeding adults. Habitat loss, prey depletion and human persecution are the main threats. The Iranian and North African populations are Critically Endangered, with as few as 250 remaining. Cheetahs formerly ranged through the Near East into India, where they became extinct in 1950s.

SIGNIFICANCE TO HUMANS
Cheetahs are not dangerous to man, but do take livestock, especially where natural prey levels are reduced, and they are persecuted by farmers. However, in Namibia, cheetahs have benefited from the removal of lions and hyena from cattle ranches. Cheetahs do not flourish where lions are numerous, as lions prey on cubs and steal kills, so formal reserves are often not ideal for cheetah conservation. Controlled trophy hunting has been allowed to encourage farmers to conserve cheetah. Other conservation efforts include using guard dogs to protect stock. ◆

Puma
Puma (Felis) concolor

SUBFAMILY
Felinae

TAXONOMY
Felis concolor (Linnaeus, 1771), Brazil. Subspecies include eastern cougar (*Puma c. cougar*) and Florida cougar (*Puma c. coryi*).

OTHER COMMON NAMES
English: Cougar, mountain lion, catamount, panther; French: Puma; German: Puma, Silberlöwe; Spanish: Léon, léon colorado, léon de montaña.

PHYSICAL CHARACTERISTICS
Length 41–77 in (105–196 cm); tail 26–31 in (67–78 cm); weight 75–264 lb (34–120 kg). Slender body, large feet, and long hind legs. Silvery gray to tawny to reddish coat, unpatterned. Faint horizontal lines sometimes on forelegs. Melanistic (black) forms common.

DISTRIBUTION
Southern Canada to Patagonia. Pumas have a very broad latitudinal range encompassing a diverse array of habitats from arid desert to tropical rainforest to cold coniferous forest.

HABITAT
Very diverse, from arid desert to tropical forest to cold coniferous forest, from sea level to 19,000 ft (5,800 m) in the Andes.

BEHAVIOR
Primarily nocturnal with activity peaks at dawn and dusk. Home range 13–410 mi^2 (32–1,031 km^2), with male range at least 100 mi^2 (260 km^2) and encompassing several slightly overlapping female ranges. Males make scrapes in prominent locations and along boundaries of home ranges. Population density varies from one to 17 per 100 mi^2 (260 km^2). Mountain-living pumas may follow ungulate prey to lower altitudes in summer. Pumas cannot roar, but have a distinctive call like a woman's scream, probably associated with courtship.

FEEDING ECOLOGY AND DIET
Diet very varied, from insects, birds and small rodents to capybara, porcupine, pronghorn, bighorn sheep, and moose. Deer and other large ungulates are main prey in North America. Large kills often covered with soil and vegetation, and returned to later.

REPRODUCTIVE BIOLOGY
Polygamous. Breed year round, but in north of range most births in warmer months. In the Torres del Paine National Park in southern Chile, all known births took place between February and June. Gestation 90 to 96 days, litter one to six (usually two or three). Sexually mature at 24 months, but females do not breed until they have established a territory.

CONSERVATION STATUS
Classified as Lower Risk/Near Threatened by IUCN. Remaining eastern populations, including the Florida panther, are considered Critically Endangered. The Florida panther is down to a few dozen individuals and subject to inbreeding and severe genetic abnormality and pumas from Texas are being translocated to this state to increase the population's viability. Pumas have been eliminated from most of their former range in eastern North America by prey reduction, forest clearance and persecution. The spread of deer has led to pumas colonizing new areas such as the Great Basin Desert.

SIGNIFICANCE TO HUMANS
Pumas take calves and sheep and are persecuted by ranchers. Attacks on people, although infrequent, have increased as pumas now occur very close to settled areas in western North America. ◆

Ocelot
Leopardus (Felis) pardalis

SUBFAMILY
Felinae

TAXONOMY
Felis pardalis (Linnaeus, 1758), Mexico.

OTHER COMMON NAMES
French: Ocelot; German: Ozelot; Spanish: Tigrillo, ocelote, gato onza.

PHYSICAL CHARACTERISTICS
Length 26–38 in (65–97 cm); tail 11–16 in (27–40 cm); weight 18–35 lb (8.5–16 kg). Ocher to orange yellow coat in forest animals, grayer in arid scrub, striped and spotted black, white underside. Ringed tail.

DISTRIBUTION
Southeast Texas to north Argentina.

HABITAT
Varied, including tropical forest, savanna, marshes, mangroves. Needs dense cover. Tolerates disturbed habitat and human settlement.

BEHAVIOR
Territorial and strongly nocturnal. An excellent climber and swimmer. Homes range of 0.8 to 12 mi^2 (2 to 31 km^2), depending on habitat. Population also includes significant numbers of nonbreeding transients.

FEEDING ECOLOGY AND DIET
Small mammals, birds, reptiles. Prey varies seasonally, may take spawning fish and land crabs in wet season. May follow prey odor trails.

REPRODUCTIVE BIOLOGY
Polygamous. Gestation 79–85 days, litter one to three. Young independent at one year, but may be tolerated in adult's range for another year.

CONSERVATION STATUS
Not listed by IUCN. Hunting and trapping severely reduced populations in some parts of range, but populations may now be recovering and recolonizing.

SIGNIFICANCE TO HUMANS
Heavily exploited for fur trade from early 1960s to mid-1970s, when up to 200,000 a year were trapped. International trade fell from mid-70s and ceased in late 1980s. ◆

Wild cat
Felis silvestris

SUBFAMILY
Felinae

TAXONOMY
Felis (Catus) silvestris Schreber, 1775, Germany. Up to 26 subspecies have been claimed. Four groups are commonly recognized, including the domestic cat (*Felis s. catus*), the African wild cat group (*Felis s. lybica*), the forest cats of Europe (*silvestris* group), and the steppe cats (*ornata* group) of south and central Asia. European form is oldest, descended from Martelli's cat (*Felis [silvestris] lunensis*) 250,000 years ago. African wildcat diverged only 20,000 years ago. Domestic cat derived from African form 4,000 to 7,000 years ago.

OTHER COMMON NAMES
French: Chat silvestre, chat sauvage; German: Wildkatze; Spanish: Gato montés, gato silvestre.

PHYSICAL CHARACTERISTICS
Length 20–31 in (50–80 cm); tail 11–14 in (28–35 cm); weight 6.5–13 lb (3–6 kg). Medium brown, striped black or brown. African wild cat appears lighter built than European wild cat, because fur is thinner, and has less distinct markings and thin, tapering tail. African wild cat difficult to distinguish from domestic cat. Asiatic wild cat more grayish yellow or reddish, with small black or red-brown spots, sometimes fused into stripes.

DISTRIBUTION
Western Europe to India, Africa. Domestic cat introduced worldwide.

HABITAT
Very varied, including open forest, savanna, steppe, deserts. Absent from tropical rainforest. Mainly forest in Europe, scrub desert in Asia.

BEHAVIOR
Solitary, territorial, primarily nocturnal, especially in hot environments or near human settlement. Also active in early morning and late afternoon. Home ranges from 0.8 to 3.3 mi^2 (2.1 to 8.3 km^2) for males, and from 0.5 to 1.5 mi^2 (1.3 to 2.3 km^2) for females, with males overlapping several female ranges.

FEEDING ECOLOGY AND DIET
Small mammals, birds, reptiles, insects. Rabbits or rodents are main prey items where they occur. Will cache its kills.

REPRODUCTIVE BIOLOGY
Polygamous. Gestation 63–68 days, litter one to eight (usually three to six). Kittens independent at ten months.

CONSERVATION STATUS
Not listed by IUCN. Hybridization with domestic cats is leading to increased rarity of pure wild cats, surviving only in remote, protected areas. European wild cats eradicated from much of Europe in eighteenth century, but have re-colonized some countries. There is controversy over whether pure wild cats still exist in Europe, and over whether this really matters, given the small difference between domestic and wild cats. European reintroduction projects have had mixed results. Russian population decreasing. Other threats include habitat and population fragmentation, road kills, disease transmitted by feral cats.

SIGNIFICANCE TO HUMANS
See family account for history of domestication. Asiatic wildcats were trapped in large numbers in past, but at present there is little international trade in their pelts. Introduced feral cats have had disastrous consequences for the indigenous small mammals and ground birds of Australia and other islands. ◆

Serval
Leptailurus (Felis) serval

SUBFAMILY
Felinae

TAXONOMY
Felis serval (Schreber, 1776), South Africa.

OTHER COMMON NAMES
French: Serval, chat-tigre, lynx tacheté; German: Serval Katze; Spanish: Serval.

PHYSICAL CHARACTERISTICS
Length 26–39 in (67–100 cm); tail 14–16 in (35–40 cm); weight 20–40 lb (9–18 kg). Slim, long legged, tall cat, adapted to hunting in long grass. Elongated neck, small head, tall ears with very acute hearing. Pale yellow coat marked with solid black spots along sides and bars on neck and shoulders. Black servals widely recorded.

DISTRIBUTION
Sub-Saharan Africa. Isolated relict populations may remain in North Africa.

HABITAT
Well-watered long grass savanna, reed beds and riparian vegetation. Found in alpine grasslands up to 12,795 ft (3,900 m) in Kenya.

BEHAVIOR
Largely crepuscular or nocturnal, but may hunt in daytime, especially in cool conditions. Home range 3.7 to 7.7 mi^2 (9.5 to 20 km^2) for females, 4.4 to 12.4 mi^2 (11.5 to 32 km^2) for males, ranges may overlap. Both sexes urine mark, and rub saliva on grass or ground. Males territorial.

FEEDING ECOLOGY AND DIET
Small mammals, especially rodents. Also birds, reptiles, frogs, fish and insects. Locates prey in tall grass or reeds by hearing. Stalks then pounces with characteristic high leap. May leap to bat birds and insects from the air.

REPRODUCTIVE BIOLOGY
Polygamous. Non-seasonal breeders, but births peak in wet season. Gestation 70–79 days, litter one to five (usually two or three). Kittens independent by 6–8 months but females may stay in mother's home range for over a year. Males are driven away.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Servals adapt well to agricultural development where predation on rodents benefits farmers. Occasionally kill domestic poultry, but not a significant problem. Serval pelts are traded, but more for ritual use or tourist trade than international commerce. ◆

Geoffroy's cat
Oncifelis (Felis) geoffroyi

SUBFAMILY
Felinae

TAXONOMY
Felis geoffroyi (d'Orbigny and Gervais, 1844), Patagonia.

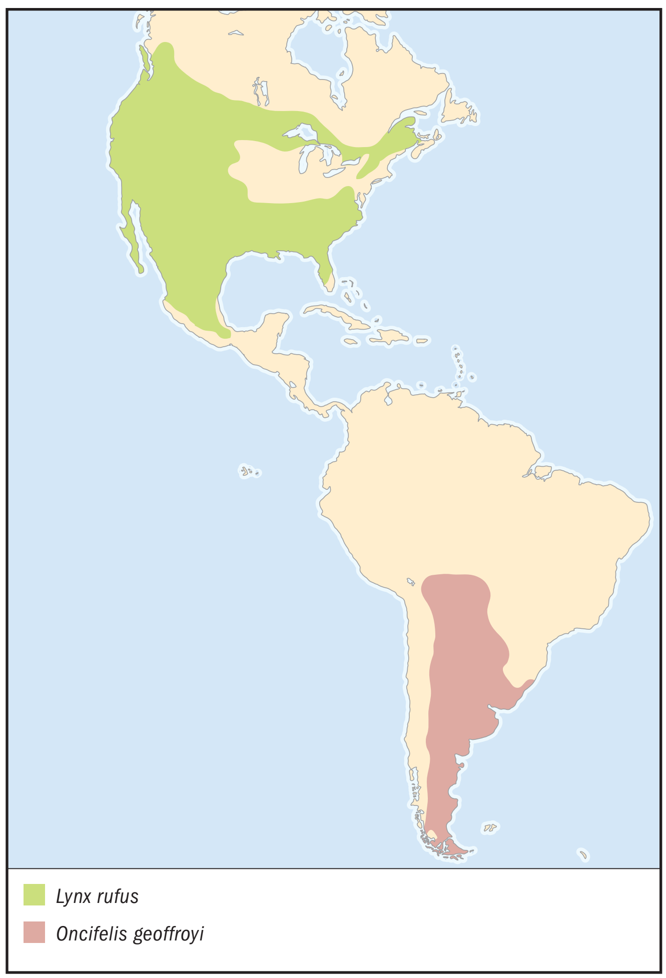
OTHER COMMON NAMES
English: Geoffroy's ocelot; French: Chat de Geoffroy; German: Geoffroykatze, Kleinfleckkatze, Salzkatze; Spanish: Gato de mato, gato montés, gato de las salinas.

PHYSICAL CHARACTERISTICS
Length 18–28 in (45–70 cm); tail 10–14 in (26–35 cm); weight 4.5–10.5 lb (2–4.8 kg). Coat silver-gray to brownish yellow with uniform small black spots. Melanistic form fairly common.

DISTRIBUTION
Bolivia to Patagonia.

HABITAT
Varied. Upland forest and scrub, pampas grassland, alpine saline desert. Prefers dense, scrubby vegetation.

BEHAVIOR
Strong climber and swimmer, primarily nocturnal. Home range around 4 mi^2 (10 km^2) for males, 1.5 mi^2 (4 km^2) for females. Female ranges overlap, males do not.



FEEDING ECOLOGY AND DIET
Birds, small mammals, and fish. May cache kills in trees.

REPRODUCTIVE BIOLOGY
Polygamous. Gestation 72–78 days, litter two or three. Sexually mature at 18 months (female), two years (male).

CONSERVATION STATUS
Classified as Lower Risk/Near Threatened by IUCN. Previously described as most common of the small cats throughout its range, but fur trade in the late 1960s and early 1970s may have severely reduced the population—350,000 skins were exported from Argentina in four years.

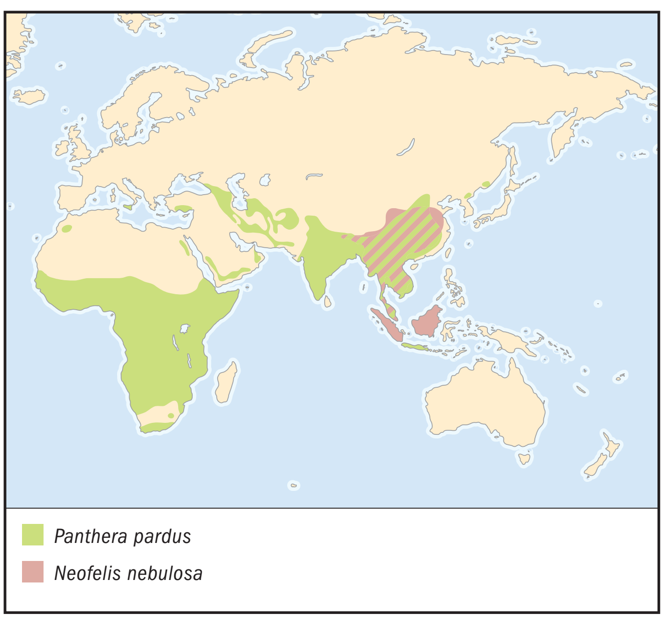
SIGNIFICANCE TO HUMANS
International fur trade has declined, but domestic markets in some South American countries remain important. Commercial hunting largely superceded by pelts from cats killed as pests. Geoffroy's cat will take small livestock. ◆

Leopard
Panthera pardus

SUBFAMILY
Pantherinae

TAXONOMY
Felis pardus (Linnaeus, 1758), Egypt. The African subspecies (*Panthera p. pardus*) occurs over most of the leopard's range. Six other subspecies are in small or isolated populations, most now critically at risk: the Amur leopard (*Panthera p. orientalis*); Anatolian leopard (*Panthera p. tulliana*); Barbary Leopard (*Panthera p. panthera*) of North Africa; south Arabian leopard (*Panthera p. nimr*); Zanzibar leopard (*Panthera p. adersi*); and Sinai leopard (*Panthera p. jarvisi*).

OTHER COMMON NAMES
English: Panther; French: Léopard, panthére; German: Leopard, panther; Spanish: Leopardo, pantera.



PHYSICAL CHARACTERISTICS
Length 40–75 in (100–190 cm); tail 28–37 in (70–95 cm); weight 66–155 lb (30–70 kg). Massive skull, powerful jaws, short, powerful limbs. Coat varies from pale yellow to deep gold or tawny, patterned with black rosettes. Head, lower limbs and belly spotted with solid black. Black leopards are a melanistic variation.

DISTRIBUTION
The most widely distributed of wild cats, found in most of sub-Saharan Africa and in south Asia, with scattered populations in North Africa, and the Middle and Far East.

HABITAT
Any habitat with some cover, prey, and annual rainfall above 0.3 in (50 mm), from tropical rainforest to desert, at altitudes up to 18,700 ft (5,700 m).

BEHAVIOR
Highly adaptable but secretive. Males almost entirely solitary, females solitary or with cubs. Males defend territories which they declare by scent marking and roaring. The leopard's roar is a rough rasp, like a handsaw cutting wood, also used by females to attract mates or call cubs. A male's range may be anywhere from 7 to 440 mi^2 (18–1,150 km^2), depending on prey availability. Females have smaller ranges, 4–190 mi^2 (10–480 km^2), which often overlap.

FEEDING ECOLOGY AND DIET
Diet exceptionally broad, from dung beetles to eland. Medium-sized ungulates are the main target of hunts, but rodents, birds, hares, primates, and arthropods are taken opportunistically and leopards also scavenge. Leopards hunt alone, mainly at night, relying on stealth to stalk and ambush prey, rarely chasing, despite being capable of speeds up to 36 mph (60 kph). Large kills are sometimes cached in trees—the leopard is a powerful climber.

REPRODUCTIVE BIOLOGY
Polygamous. Breeds year round, but birth peaks may coincide with the birth season of main prey animals. Gestation 90–105 days, litter size one to six cubs (usually one to two). First year mortality rate up to 50%. Cubs are hidden at first, follow their mother at 6–8 weeks, and are weaned from three months, but are not independent until 18–22 months. They then disperse, but females may settle in a range overlapping the mother's. There are strong maternal bonds, and offspring often have reunions with mothers.

CONSERVATION STATUS
African leopard is not listed by the IUCN. Four subspecies (south Arabian, Anatolian, Amur, and Barbary leopards) are Critically Endangered, the Zanzibar leopard is possibly extinct. Inbreeding, loss of prey base, and human persecution are the main threats.

SIGNIFICANCE TO HUMANS
Trade in leopard skins during the 1970s and '80s raised fears about survival of the species, but changing public opinion about fur and trade controls imposed by CITES led to a market collapse. Hunting for skin and loss of prey to the bushmeat trade continues to affect numbers in West Africa, but elsewhere in sub-Saharan Africa the leopard population seems generally buoyant despite pressure from habitat degradation and persecution by farmers. Leopards take livestock where natural prey is depleted and occasionally kill humans. Trophy hunting by quota is allowed in some countries. ◆

Jaguar

Panthera onca

SUBFAMILY
Pantherinae

TAXONOMY
Felis onca (Linnaeus, 1758), Central America.

OTHER COMMON NAMES
French: Jaguar; German: Jaguar; Spanish: Tigre, tigre real, yaguar.

PHYSICAL CHARACTERISTICS
Length 44–73 in (112–185 cm); tail 18–30 in (45–75 cm); weight 125–250 lb (57–113 kg). Similar in appearance to leopard. Massive head and strong canines. Yellowish brown coat, marked with dark rosettes around small black spots. Black spots on belly, pale chest. Melanistic (black) forms common. Tail ringed black near to tip.

DISTRIBUTION
Patagonia to southwest United States.

HABITAT
Dense forest, swamps, open grassland, deciduous forest. Strongly associated with water.

BEHAVIOR
Solitary, mainly nocturnal, but often active in daytime. Can roar, but more commonly heard grunting or coughing when hunting, snarling or growling when threatened. Excellent swimmer. Territory 10–60 mi^2 (25–150 km^2), linked to prey availability.

FEEDING ECOLOGY AND DIET
Deer, peccaries, tapirs, monkeys, birds, rodents, fish, frogs. Mainly hunts large prey, but takes smaller items opportunistically. The only big cat which regularly kills prey by piercing skull with canines. Massive head and strong canines enable jaguars to crack open tortoises and turtles.

REPRODUCTIVE BIOLOGY
Polygamous. Gestation 95–110 days, litter one to four. Cubs independent after 18–24 months. Females sexually mature at two to three years, males at three to four.

CONSERVATION STATUS
Classified as Lower Risk/Near Threatened by IUCN. Now virtually eliminated from much of drier northern range in the United States, and pampas scrub of Agrentina and Uruguay. Deforestation and fragmentation of forest habitats pose a threat in central America.

SIGNIFICANCE TO HUMANS
Jaguars takes cattle as a significant portion of their diet in some parts, and are heavily persecuted by cattle ranchers. Commercial trade in skins has become insignificant since CITES trade ban of 1975. ◆

Snow leopard

Uncia (Panthera) uncia

SUBFAMILY
Pantherinae

TAXONOMY
Felis uncial (Schreber, 1775), Persia.

OTHER COMMON NAMES
English: Ounce; French: Panthére des nieges, léopard des nieges, once; German: Schneeleopard, Irbis; Spanish: Leopardo nival, pantera de las nieves.

PHYSICAL CHARACTERISTICS
Length up to 51 in (130 cm); tail 31–39 in (80–100 cm); weight 77–120 lb (350–55 kg). Highly adapted to extreme conditions. Well-developed chest muscles, short forelimbs, thick tail to keep balance. Enlarged nasal cavity warms air passing into body. Thick coat up to 5 in (12 cm) long, with dense, woolly underfur. Coat color smoky gray, tinged yellow, with dark gray rosettes and black spots. Molts twice a year.

DISTRIBUTION
Central Asia, from Himalayas to Mongolia and south Russia.

HABITAT
Alpine steppe, grassland, scrub, open conifer forest, from 3,000 to 18,000 ft (900–5,500 m). Steep, broken terrain preferred. Can endure temperatures of −40°F (−40°C) to 104°F (40°C).

BEHAVIOR
Solitary. Home ranges 12–25 mi^2 (20–40 km^2) in good habitat, up to 400 mi^2 (1,000 km^2) in Mongolia. Male and female ranges

overlap, but animals avoid one another except when female in estrous. Paths marked with scrapes, feces and scent-sprays.

FEEDING ECOLOGY AND DIET
Ibex and blue sheep are main prey. Also goats, deer, livestock, including young yak, sheep and horses. Marmots and hares in summer. Stalks to within 40 yd (36 m) before rushing.

REPRODUCTIVE BIOLOGY
Polygamous. Mating season January–March. Females scent mark and make long wailing calls to advertise estrous. Gestation 98–104 days. Litter one to five (usually two to three), born in spring or early summer in a rocky den. Cubs dependent until 18–22 months.

CONSERVATION STATUS
Classified as Endangered by the IUCN. Population estimated at below 2,500 breeding adults. Extremely rare in much of range and many reserves have unviably small populations. Prey population hunted out in many areas.

SIGNIFICANCE TO HUMANS
Hunted for fur and for bones and body parts, used as substitutes for tiger bones in traditional medicine. International trade in pelts now virtually ceased, but domestic trade may still be a problem. Predation on livestock locally significant. ◆

Clouded leopard
Neofelis nebulosa

SUBFAMILY
Pantherinae

TAXONOMY
Felis nebulosa (Griffith, 1821), China.

OTHER COMMON NAMES
French: Panthére longibande, panthére nébuleuse; German: Nebelparder; Spanish: Pantera longibanda, pantera nebulosa.

PHYSICAL CHARACTERISTICS
Length 24–43 in (60–110 cm); weight 24–44 lb (11–20 kg). Silvery gray to tawny coat, marked with distinctive cloud-shaped ellipses of darker color, edged in black, sometimes with black spots. Large black ovals on limbs and underbelly, two black bars on back of neck. Tail black-ringed, long and large, up to 24–35 in (60–90 cm). Short legs. Very long, sharp canine teeth.

DISTRIBUTION
South China, India, Nepal, Myanmar, Indochina, Sumatra, and Borneo.

HABITAT
Tropical rainforest, dry tropical forest, mangrove swamps, and tall grassland.

BEHAVIOR
Very secretive, mainly nocturnal. Excellent climber, uses trees mainly for resting, not hunting. Swims well. Density one per 2.5–9 mi^2 (4–14 km^2).

FEEDING ECOLOGY AND DIET
Birds, primates, small mammals, porcupines, deer, and wild boar.

REPRODUCTIVE BIOLOGY
Polygamous. Gestation 90–100 days, litter size one to five (usually three). Cubs probably independent by nine months. Both sexes sexually mature at two years.

CONSERVATION STATUS
Classified as Vulnerable by IUCN. Population estimated at less than 10,000 breeding adults. Deforestation is most serious threat. Status unclear in many range countries.

SIGNIFICANCE TO HUMANS
Widely hunted illegally for pelt, teeth and bones for decorative use and in traditional medicine. ◆

Caracal
Caracal (Felis) caracal

SUBFAMILY
Felinae

TAXONOMY
Felis caracal (Schreber, 1776), South Africa

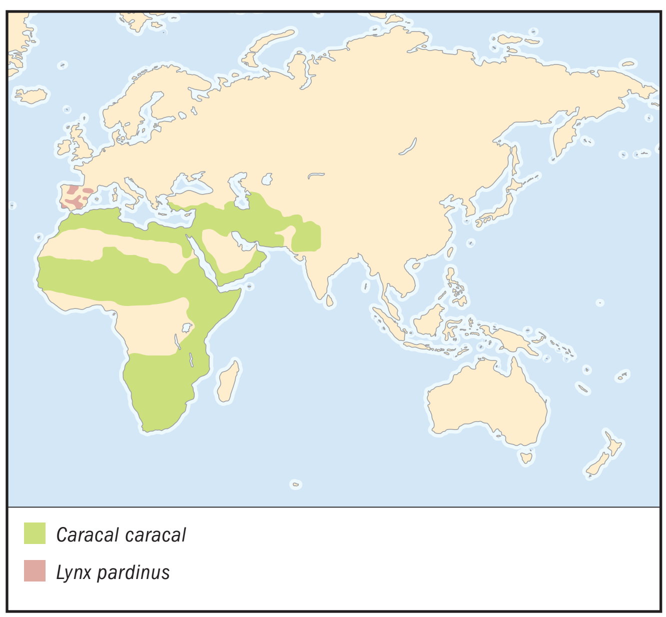
OTHER COMMON NAMES
English: Desert lynx; French: Caracal: German: Caracal, Wüstenluchs; Spanish: Caracal, lince africano.

PHYSICAL CHARACTERISTICS
Length 22–35 in (55–90 cm); tail 9–13 in (22–34 cm); weight 35–48 lb (16–22 kg). Uniform tawny brown to brick-red coat. Short face, large ears with black backs and 2 in (5 cm) black tufts. Dark facial markings on cheeks and above eyes, edged with white. Very long legs, with high hindquarters and big feet.

DISTRIBUTION
Sub-Saharan Africa, Asia from Arabia to northern India, and Russia.

HABITAT
Dry savanna and woodland, especially scrubby, arid habitat. Rarely in evergreen and montane forest.

BEHAVIOR
Solitary, territorial. Predominantly nocturnal, but also seen in daytime. Agile climber. Home ranges of males 12–26 mi^2 (31–65 km^2), females 1.5–12 mi^2 (4–31 km^2).



FEEDING ECOLOGY AND DIET
Rodents, hares, hyraxes, small antelope and deer, and birds. Can take antelope up to size of young kudu, suffocating them with a throat bite. May (rarely) cache kill in tree. Can leap high to knock birds out of the air.

REPRODUCTIVE BIOLOGY
Polygamous. Breeds year round, gestation 62–81 days, litter one to four. Kittens begin eating meat after 4–6 weeks, weaned at 4–6 months.

CONSERVATION STATUS
Not listed by the IUCN. Population stable or expanding (in South Africa and Namibia local removal of jackals by farmers may benefit caracal).

SIGNIFICANCE TO HUMANS
Once trained in India and Persia to catch game birds and deer. Thousands are killed because of predation on small livestock, especially in southern Africa. However, caracals quickly recolonize farmland. Hunting for skin and bushmeat may be a threat in west and central Africa. ◆

Eurasian lynx
Lynx (Felis) lynx

SUBFAMILY
Felinae

TAXONOMY
Felis lynx (Linnaeus, 1758), Sweden.

OTHER COMMON NAMES
French: Lynx; German: Luchs; Spanish: Lince.

PHYSICAL CHARACTERISTICS
Length 32–51 in (80–130 cm); tail 2–7 in (5–19 cm); weight 17–68 lb (8–31 kg). Light grayish brown coat with dark spots, striped or unpatterned. Black-tipped tail, long, black ear tufts, two tassels on throat. Paws large are padded with thick fur, acting as "snowshoes."

DISTRIBUTION
Western Europe to Siberia, central Asia to Himalayas.

HABITAT
Cold coniferous forest and thick scrub in Europe and Siberia. Rocky hills and mountains of Central Asian deserts.

BEHAVIOR
Most active at dawn and dusk. Population density varies considerably with prey availability but may reach 46 per 100 mi^2 (250 km^2) in optimal conditions. Male home range typically 100 mi^2 (260 km^2), female range 66 mi^2 (168 km^2). Males visit borders of territory regularly, females spend most time in core areas. Males may share range with just one female and offspring.

FEEDING ECOLOGY AND DIET
Rodents, hares, blue sheep, deer. Take prey up to four times their own size, including red deer and reindeer. Larger ungulates most often killed in winter, when snow restricts their movement. Forage over wide areas.

REPRODUCTIVE BIOLOGY
Polygamous. Gestation 60–74 days. Litter one to five.

CONSERVATION STATUS
Considered Lower Risk/Near Threatened by IUCN. Very widely distributed but locally rare in many places. In Europe almost eradicated from all but the north and east, but populations have been reintroduced in several parts of Western Europe. Main threats are destruction of ungulate prey base, hunting pressure, and deforestation.

SIGNIFICANCE TO HUMANS
More than 5,000 may be trapped for fur in Russia in some years. Russia and China have set export quotas. Impact of fur-trapping difficult to quantify. Stock losses have been a problem with lynx reintroductions to Western Europe, but are compensated by government or environmental groups. ◆

Canada lynx
Lynx (Felis) canadensis

SUBFAMILY
Felinae

TAXONOMY
Felis Lynx canadensis Kerr, 1792, Canada. Probably descended from Eurasian lynx, which migrated into North America during glacial period.

OTHER COMMON NAMES
French: Lynx du Canada; German: Kanadaluchs; Spanish: Lince del Canada.

PHYSICAL CHARACTERISTICS
27–43 in (70–110 cm); tail 2–6 in (5–16 cm); 11–37 lb (5–17 kg). Reddish-brown to gray coat, with "frosted" appearance. Flared facial ruff, black ear tufts, long hind legs. Large, spreading feet act like snowshoes.

DISTRIBUTION
North America, especially Canada and Alaska.

HABITAT
Boreal forest.

BEHAVIOR
Male home range 1.6–90 mi^2 (4–225 km^2), female range 1.6–43 mi^2 (4–107 km^2). Population densities fluctuate dramatically with prey cycle. In good quality habitat varies from 7–93 per 100 mi^2 (250 km^2). Male ranges usually include female range and may overlap with other males. Males are unusually tolerant of independent offspring.

FEEDING ECOLOGY AND DIET
Very close predator-prey relationship with snowshoe hare. Lynx population peaks one to two years after the cyclic 10-year peak in hare numbers. Lynx density can differ by 15-fold between highs and lows of cycle. Breeding rate and success dips as hare numbers decline, but reproduction increases as hare population recovers. Also preys on small rodents, birds and deer. May travel up to 750 mi (1,200 km) in search of patches of hare abundance.

REPRODUCTIVE BIOLOGY
Polygamous. Births mainly in May–June. Gestation 63–70 days, litter one to eight, largest when prey is abundant. Kittens independent at 10 months. Females may breed from ten months old if prey is abundant, usually in second year.

CONSERVATION STATUS
Not listed by the IUCN. Locally endangered, but generally populations are healthy. Displaced in some areas by bobcat.

SIGNIFICANCE TO HUMANS
Easily trapped, but trapping for fur is now controlled to avoid seriously depleting populations during vulnerable parts of the hare cycle. Demand for pelts is declining. ◆

Iberian lynx
Lynx (Felis) pardinus

SUBFAMILY
Felinae

TAXONOMY
Felis pardina (Temminck, 1827), Portugal.

OTHER COMMON NAMES
English: Pardel lynx; French: Lynx d'Espagne; German: Pardelluchs; Spanish: Lince Iberico.

PHYSICAL CHARACTERISTICS
Length 25–39 in (65–100 cm); tail 2–8 in (5–19 cm); weight 11–28 lb (5–13 kg). Light brown coat marked with black spots on body, tail and limbs.

DISTRIBUTION
Spain and Portugal.

HABITAT
Woodland and scrub with areas of open pasture.

BEHAVIOR
Primarily nocturnal, activity peak at dusk. Active in daytime more in winter. Male home range averages 7 mi^2 (18 km^2), female 4 mi^2 (10 km^2) in Coto Doñana National Park. No overlap between ranges of same sex animals, but male's range encompasses females' ranges.

FEEDING ECOLOGY AND DIET
Mainly rabbits, some birds, and deer.

REPRODUCTIVE BIOLOGY
Polygamous. Gestation 60 days, litter two to three. Births peak in March–April. Kittens independent at 7–10 months, but may remain in natal territory until two years. Females may breed at one year, but only if territory has been acquired.

CONSERVATION STATUS
Critically Endangered. Population estimated at 1,200 adults and subadults, with only 200 breeding females. Populations small, isolated and majority considered unviable. Illegally trapped and shot, habitat lost to cultivation, and rabbit prey decimated by myxomatosis.

SIGNIFICANCE TO HUMANS
Persecuted for skin and meat for thousands of years. Spanish government placed bounty on species in early twentieth century. Now protected but illegally killed as livestock predator. ◆

Bobcat
Lynx (Felis) rufus

SUBFAMILY
Felinae

TAXONOMY
Felis rufa (Schreber, 1776), New York State.

OTHER COMMON NAMES
French: Lynx rous; German: Rotluchs, Luchskatz; Spanish: Lince, lince rojo, gato montés.

PHYSICAL CHARACTERISTICS
Length 24–42 in (62–106 cm); tail 5–8 in (13–20 cm); weight 13–37 lb (6–17 kg). Heavily built with short tail. Light gray to reddish brown coat barred and spotted with black, white belly, black tip to tail. Ruff around face. Ears with short tufts.

DISTRIBUTION
Southern Canada to northern Mexico, mainly United States.

HABITAT
Varied. Rocky scree, broken terrain, conifer and mixed forest, thickets, swamps, and desert scrub.

BEHAVIOR
Active day and night, but peak activity at dusk and dawn. Males home range 0.25–130 mi^2 (0.6–326 km^2), typically overlapping smaller ranges of several females. Density 1–38 adults per 10 mi^2 (25 km^2).

FEEDING ECOLOGY AND DIET
Rabbits and hares, rodents, deer, and large birds.

REPRODUCTIVE BIOLOGY
Polygamous. Gestation 50–70 days, litter one to eight (usually two to three). Birth peaks in April–May. Females generally breed from second year, males from 18 months. Kittens independent from one year.

CONSERVATION STATUS
Not listed by the IUCN. Populations generally healthy, but some concern over sustainability of heavy trapping.

SIGNIFICANCE TO HUMANS
In recent years the most heavily trapped and traded of cat species. Demand for fur rose in the 1960s and 1970s, especially after CITES restricted trade in other cat furs. Over 90,000 cats were killed annually at the peak, but trade is now declining due to lower demand and a European Community ban on import of furs caught by leghold traps. Bobcats occasionally raid poultry, but are not generally treated as pests, except in Mexico, where they kill sheep. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Bay cat *Catopuma badia* English: Bornean bay cat; Spanish: Gato de Borneo	May occur in two different colors: chestnut red or gray. Dark, rounded ears, whitish stripe running down ventral side of body. Head and body length 20.9–27.6 in (53–70 cm), weight 6.6–11 lb (3–5 kg).	Dense primary forests and areas of rocky limestone. Also seen in highland areas and near rivers. Nocturnal.	Borneo.	Includes small rodents and birds, carrion, and even monkeys.	Endangered
Asiatic golden cat *Catopuma temminckii* Spanish: Gato dorado asiático	Coloration is dense, coarse, from golden brown, to red, to grayish brown. Underparts are white. Patter of black and white streaks marking face. Head and body length 28.7–41.3 in (73–105 cm), tail length 16.9–22 lb (43–56 cm).	Dry deciduous forests, tropical rainforests, and occasionally open habitats with rocky areas. Predominantly nocturnal, usually terrestrial, but capable of climbing trees. Litters of one to two offspring.	Southeast Asia, from as far north as southern China, west to Nepal, east of Fukien in China, and south to Sumatra.	Carnivorous. Diet consists of wild hares, small deer, birds, lizards, and other small animals. They have been known to kill sheep, goats, and buffalo calves.	Not threatened
Chinese desert cat *Felis bieti* Spanish: Gato del desierto chino	Coloration is yellowish gray in summer and darker brown in winter. Horizontal stripes on sides of body and legs, brown streaks across each cheek. Tail striped with 5–6 gray bands, black tip. Yellowish brown ears, tips specked with long hairs. Head and body length 26.8–33.1 in (68–84 cm), tail length 11.4–13.8 in (29–35 cm).	Datong and Daban mountains around Xining, at elevations ranging from 9,190 to 13,450 ft (2,800–4,100 m). Preferred habitat is mountainous areas where cover is available, usually in the form of sparse trees and shrubs. Typically occupy alpine meadows and scrub, although they may occur marginally in deserts. Primarily nocturnal, not social, travel in packs. Males and females live separately.	Southern Mongolia, central China.	Rodents, such as mole-rats, pikas, and white-tailed voles. They also have been known to catch birds, including pheasants.	Vulnerable
Jungle cat *Felis chaus* English: Swamp lynx; Spanish: Gato selvático	Coloration is sandy gray to tawny brown, no distinctive markings. Tail has several dark rings, tipped in black. Head and body length 19.7–29.5 in (50–75 cm), tail length 9.8–11.4 in (25–29 cm).	Wide variety of habitats, typically wet grasslands and reed thickets near stagnant or slowly flowing water. Solitary animals, active day and night. Competitors include leopards, wolves, red dogs, and hyenas.	Volga River Delta and Egypt to Sinkiang and Indochina, Sri Lanka.	Hares and other small mammals, ground birds, snakes, lizards, and frogs.	Not threatened
Sand cat *Felis margarita* Spanish: Gato del desierto	Coloration is pale sandy to gray straw in color. Back is darker, belly is white. Two reddish streaks on face. Tail has two or three rings and black tip. Head and body length 17.7–22.5 in (45–57.2 cm), tail length 11–13.7 in (28–34.8 cm).	Desert biome, which include extremely arid conditions, especially involving loose soil (sand dunes). Two to four young per litter, no more than two litters annually. Solitary and nocturnal.	Desert zones from Morocco and northern Niger to Soviet central Asia and Pakistan.	Prey on rodents, hares, birds, and reptiles.	Lower Risk/Near Threatened
Black-footed cat *Felis nigripes* Spanish: Gato de patas negras	Coloration from dark ochre to pale ochre, covered with bold pattern of round dark brown to black spots, two stripes on each cheek, stripes on forelegs. Closely resembles house cat in shape. Average male length 16.7–19.7 in (42.5–50 cm), female 13.3–14.5 in (33.7–36.8 cm), average weight 2.2–4.4 lb (1–2 kg).	Dry country of South Africa. Solitary, nocturnal, strong territorial system. One to three kittens born per litter.	Namibia, Botswana, and South Africa.	Mainly small prey, including various rodents, spiders, insects, and birds.	Vulnerable
Jaguarundi *Herpailurus yaguarondi* Spanish: Yaguarundí	Two color morphologies; 1. Coloration is gray, except for two white spots beside nose on upper life, and possibly some white on belly; 2. Coloration is reddish brown, except for white on throat and lips. Short legs, long body, long tail. Head and body length 23.6–27.6 in (60–70 cm), tail length 11.8–23.6 in (30–60 cm), weight 8.8–19.8 lb (4–9 kg).	Lives near water, sleeps in natural dens under banks, in tall grasses, or in caves. Reproduce year round, producing typically two to three offspring per litter. Solitary, except when mating or raising young. Usually nocturnal, but can be diurnal.	Southern Arizona and southern Texas, United States, to northern Argentina.	Prey on many different animals, including frogs, rabbits, small deer, insects, reptiles, and fish; birds are its prey of choice. Willing to enter water to catch fish.	Not threatened

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Little spotted cat *Leopardus tigrinus* English: Tiger ocelot; Spanish: Tigrillo	Coloration of upperparts is light to rich ochre with rows of large, dark spots. Underparts paler and less spotted. Tail has 10 to 11 rings and black tip. Head and body length 15.7–21.7 in (40–55 cm), tail length 9.8–15.7 in (25–40 cm).	Forests. Habits in wild are not known. One or two young per litter.	Costa Rica to northern Argentina.	Usually consumes small rodents, frogs, rabbits, and birds of choice.	Lower Risk/Near Threatened
Margay *Leopardus wiedii* Spanish: Gato tigre	Coloration tan, from grayish to cinnamon. Underparts are white. Dark brown spots for longitudinal rows. Petite, small, and slender. Head and body length 18.2–31.1 in (46.3–79 cm), tail length 13–20.1 in (33.1–51 cm), weight 5.7–8.6 lb (2.6–3.9 kg).	Tropical and subtropical forests. Active during day and night. Asocial, with temporary pair bonds formed during the breeding season. Home range size 5.8–16.6 mi^2 (15–43 km^2).	Northern Mexico and possibly southern Texas, United States, to northern Argentina and Uruguay.	Terrestrial and arboreal mammals, birds and their eggs, amphibians, reptiles, arthropods, and fruit.	Not threatened
Pampas cat *Oncifelis colocolo*	Coloration ranges from yellowish white and grayish yellow to brown, gray brown, silvery gray, and light gray. Bands of yellow or brown run from back to flanks. Two bars run from eyes to cheeks. Coat is long, tail is bushy, face is broad, ears are pointed. Head and body length 22.3–27.6 in (56.7–70 cm), tail length 11.6–12.7 in (29.5–32.2 cm).	Open grassland in some areas, but also humid forests and mountainous regions. Nocturnal. Litters contain one to three young.	Ecuador and Mato Grosso region of Brazil to central Chile and Patagonia.	Mainly small mammals, especially guinea pigs and ground birds.	Lower Risk/Near Threatened
Andean cat *Oreailurus jacobita* Spanish: Colocolo	Coat is soft, fine, silvery gray with irregular brown or orange yellow spots and transverse stripes. Underparts are white and have black spots. Bushy tail, ringed with black to brown, lightly tipped. Head and body length 23.6 in (60 cm), tail length 13.8 in (35 cm).	Arid and semiarid zone of Andes at elevations up to 16,400 ft (5,000 m). Nothing is known about the reproductive or social behavior of this species. They are most likely solitary.	The Andes of southern Peru, southwestern Bolivia, northeastern Chile, and northwestern Argentina.	Small mammals, such as chinchillas and viscachas.	Endangered
Pallas's cat *Otocolobus manul* Spanish: Gato de Pallas	Coloration is from light gray to yellowish buff and russet, frosted appearance. Two dark streaks across each side of head, four rings on dark-tipped tail. Long, dense coat. Massive body, short legs, short, broad head. Head and body length 19.7–25.6 in (50–65 cm), tail length 8.3–12.2 in (21–31 cm), weight 5.5–7.7 lb (2.5–3.5 kg).	Steppes, deserts, and rocky country up to elevations over 13,120 ft (4,000 m). Usually nocturnal, but can be diurnal. Dens in caves, crevices, or burrows dug by other animals. Five to six young per litter.	Caspian Sea and Iran to southeastern Siberia and Tibet.	Pikas and other small mammals.	Lower Risk/Near Threatened
Leopard cat *Prionailurus bengalensis* Spanish: Gato de bengala	Upperparts pale tawny, underparts white. Body and tail covered with dark spots, tail is ringed toward tip, head is small, muzzle is short, ears are long and rounded. Head and body length 17.5–42.1 in (44.5–107 cm), tail length 9.1–17.3 in (23–44 cm), weight 6.6–15.4 lb (3–7 kg).	Many kinds of forested habitat at both high and low elevations. Mainly nocturnal, but often seen during the day. One to four offspring per litter.	Ussuri region of southeastern Siberia, Manchuria, Korea, Quelpart and Tsushima Islands (between Korea and Japan), eastern China, Taiwan, Hainan, Pakistan to Indochina and Malay Peninsula, Sumatra, Java, Bali, Borneo, and several islands in the western and central Philippines.	Hares, rodents, young deer, birds, reptiles, and fish.	Not threatened
African golden cat *Profelis aurata* Spanish: Gato dorado africano	Coloration ranges form chestnut to fox red, fawn gray brown, silver gray, and blue gray to dark slaty. Underparts are white. Body covered with dark brown or dark gray dots, may vary. Long legs, small head, large paws. Head and body length 24.3–40 in (61.6–101.6 cm), tail length 6.3–18.1 in (16–46 cm), weight 2.1–6.3 lb (5.3–16 kg).	Deciduous forests, tropical rainforests, and more open habitats at times. Usually terrestrial, no confirmed breeding season, one or two offspring per litter.	Senegal to Kenya and northern Angola.	Hares, small deer, birds, lizards, and domestic livestock.	Vulnerable

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Organizations

Cheetah Conservation Foundation. P.O. Box 1380, Ojai, CA 93024 United States. Phone: (805) 640-0390. Fax: (805) 640-0230. E-mail: info@cheetah.org Web site: <http://www.cheetah.org>

Florida Panther Society. Rt. 1, Box 1895, White Springs, FL 32096 United States. Phone: (386) 397-2945. E-mail: old_florida@earthlink.net Web site: <http://members.atlantic.net/oldfla/panther/panther.html>

International Snow Leopard Trust. 4649 Sunnyside Ave N, Seattle, WA 98103 United States. Phone: (206) 632-2421. E-mail: info@snowleopard.org Web site: <http://www.snowleopard.org>

IUCN Cat Specialist Group. Thunstrasse 31, Muri b, Bern, 3074 Switzerland. Phone: 41 (31) 951 9020. Fax: 41 (31) 951 9040. E-mail: urs.breitenmoser@ivv.unibe.ch Web site: <http://lynx.uio.no/catfolk>

Mountain Lion Foundation. P.O. Box 1896, Sacramento, CA 95812 United States. Phone: (916) 442-2666. Fax: (916) 442-2871. E-mail: mlf@mountainlion.org Web site: <http://www.mountainlion.org>

Other

African Lion Working Group (IUCN). <http://www.african-lion.org>

Asiatic Lion Information Centre. <http://www.asiatic-lion.org>

Big Cats Online. <http://dspace.dial.pipex.com/agarman/bco/ver4.htm>

Carnivore Conservation. <http://www.carnivoreconservation.org>

Tiger Information Center. <http://www.5tigers.org>

WorldLYNX. <http://lynx.uio.no/jon/lynx/lynxhome.htm>

Ann and Stephen B. Toon

Eared seals, fur seals, and sea lions

(Otariidae)

Class Mammalia
Order Carnivora
Suborder Pinnipedia
Family Otariidae

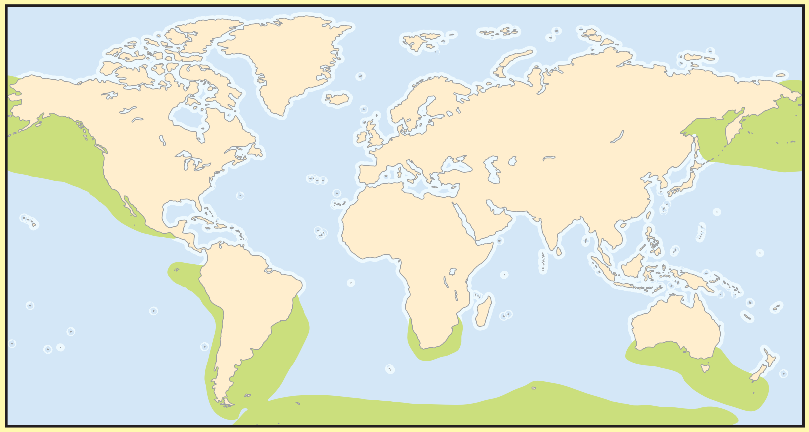
Thumbnail description
Medium- to large-sized pinnipeds that have large front flippers for underwater propulsion, a dog-like head, and the ability to walk or run on all fours on land

Size
Males range from 154 lb (70 kg) (Galápagos fur seal) to 2,469 lb (1,120 kg) (Steller sea lion); females range from 77 lb (35 kg) (Galápagos fur seal) to 772 lb (350 kg) (Steller sea lion); neonates range from 11 to 51 lb (5–23 kg)

Number of genera, species
7 genera; 15 species

Habitat
Feed in coastal or deep ocean areas, and they breed on sandy and rocky substrate, mostly on islands

Conservation status
Endangered: 1 species; Vulnerable: 5 species



Distribution
Bering Sea, north and south Pacific Oceans, south Atlantic Ocean, southern Indian Ocean, Southern Ocean; they occupy subpolar, temperate, and equatorial waters

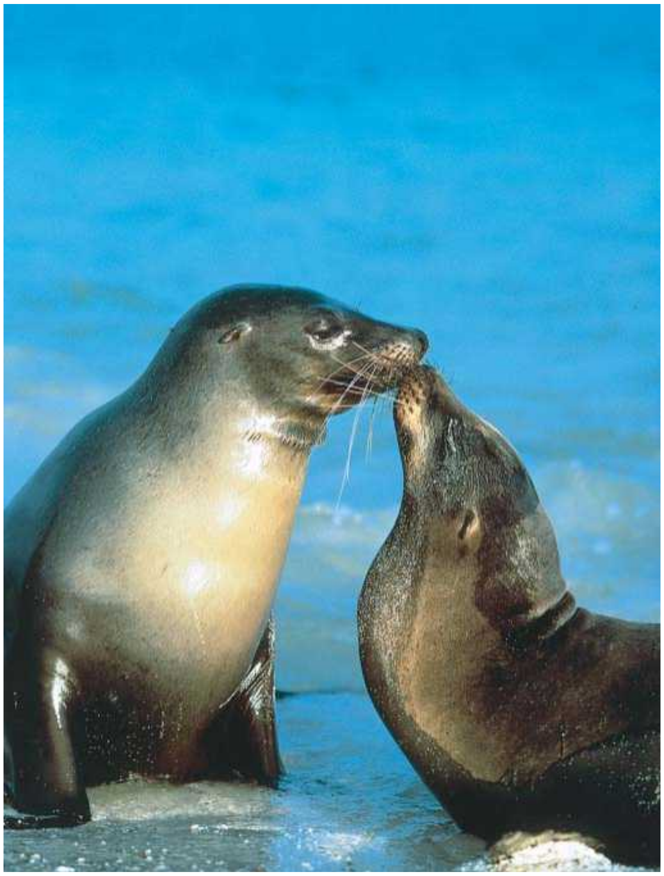
Evolution and systematics

The most recent view is that all pinnipeds (walruses, true seals, and eared seals) had a single evolutionary origin. However, this should be considered a provisional view because the evolutionary sequences for these three groups are still incompletely known. Pinnipeds are most closely related to the arctoid carnivores, especially bear-like and racoon-like mammals. The current debate is whether walruses are more closely related to the true seals or the eared seals. The eared seals arose in the late early Miocene (20–15 million years ago) in the North Pacific. From there they moved south and diversified in the Southern Hemisphere where most species now live. Fur seals are considered to be older than sea lions. *Callorhinus* (northern fur seal) is the genus having the oldest lineage. Otariids are not perfectly separable into sea lions and fur seals; the Afro-Australian fur seal is intermediate between the two in behavior and anatomy.

Physical characteristics

All eared seals are sexually dimorphic. Males are two to four times larger, have proportionately larger heads, necks, and chests (related to fighting), and may have a wider range of colors than females. Otariids as a group are somewhat smaller than true seals as a group. The head is dog-like, and both sexes have sharp, dog-like canine teeth. The eyes are large, irises are brown, and the pupils usually close to a pinhole in bright light. The postcanine teeth, a series of inter-

An Antarctic fur seal (*Arctocephalus gazella*) pup. (Photo by © Paul A. Souders/Corbis. Reproduced by permission.)

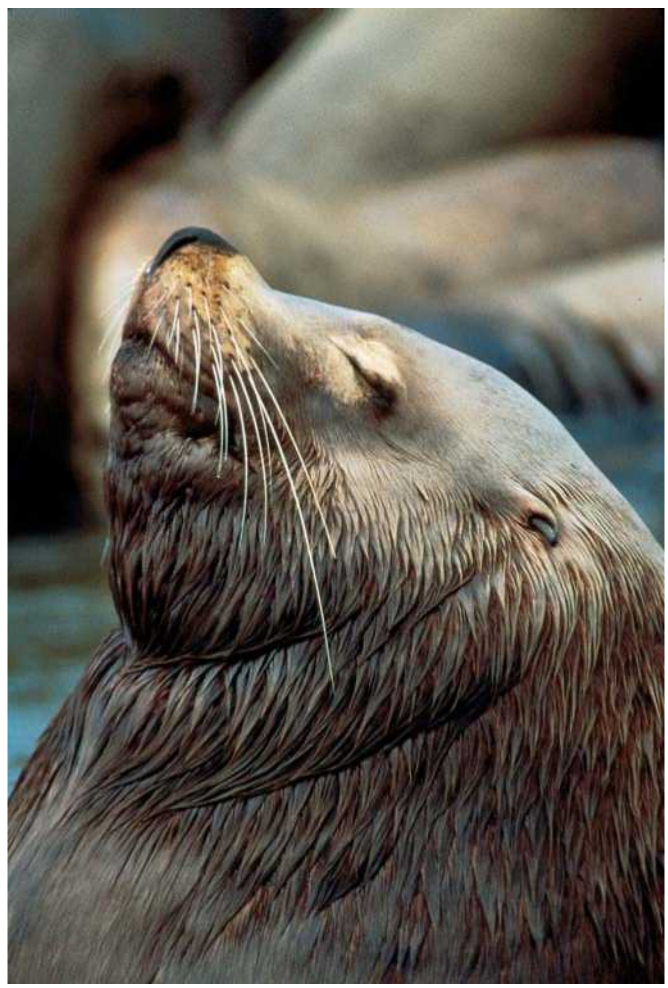


Galápagos sea lion (*Zalophus wollebaeki*) cow and yearling pup nuzzle in greeting. (Photo by Tui De Roy. Bruce Coleman, Inc. Reproduced by permission.)

meshing points, are adapted for seizing prey, not for shearing or chewing. All species have small, cone-like external ears (hence the scientific name), unlike the true seals and walrus which have only an external auditory meatus (passageway). The vibrissae are well developed, white in adults, and 3–18 in (8–45 cm) long. The flippers are black and either hairless or have sparse hair. The pectoral muscles are well developed in both sexes and provide fore-flipper propulsion. Sea lions (Otariinae five genera, six species) have a pelage composed only of coarse guard hairs. The females are usually brown to light tan, whereas the males may vary from almost white to black. Fur seals (Arctocephalinae, two genera, nine species, two subspecies) have a pelage composed of guard hairs emerging from a dense, fine, brown, usually unseen underfur. Fur seal females are usually grizzled gray (black when wet) with light bellies, and males vary from white to reddish to black, depending on the species. Pups are usually black. Females make loud, prolonged calls related to finding their young. Males make a variety of calls, including repeated pulses (like barks), and prolonged calls.

Distribution

Four genera of otariids still inhabit the ancestral home of this family, the north Pacific Ocean (northern fur seal, *Callorhinus ursinus*; Steller sea lion, *Eumetopias jubatus*; California sea lion, *Zalophus californianus*; Guadalupe fur seal, *Arctocephalus townsendi*). All four co-occur only at San Miguel Island, California. Two species (Galápagos fur seal, *A. galapagoensis*, and sea lion, *Z. wollebaeki*) live at the equator, and two (South American sea lion, *Otaria byronia*, and fur seal, *A. australis*) are found along the Pacific and Atlantic coasts of South America and associated islands. One species (Juan Fernández fur seal, *A. philipii*) is confined to the Juan Fernández Islands off Chile. One species (Cape fur seal, *A. pusillus pusillus*) occurs around the tip of southern Africa, and a subspecies (Australian fur seal, *A. p. doriferus*) occurs only in Australia. New Zealand and Australia have one species of sea lion each (Hooker's [*Phocarctos hookeri*] and Australian sea lion, respectively), and the New Zealand fur seal (*A. forsteri*) is found in both places. The subantarctic fur seal (*A. tropicalis*) breeds on a series of islands from the latitude of New Zealand to the Antarctic Convergence. Finally, the Antarctic fur seal (*A. gazella*) breeds south of the convergence in the Atlantic and Indian Ocean sectors of the Southern Ocean, and extends as far south as the Antarctic Peninsula. The extent to which the distributions of modern otariids reflect the depredations of



A Steller sea lion (*Eumetopias jubatus*) napping. (Photo by Tom & Pat Leeson/Photo Researchers, Inc. Reproduced by permission.)

The Australian sea lion (*Neophoca cinerea*) spends much of its time on land. (Photo ©Tony Wu/www.silent-symphony.com. Reproduced by permission.)

nineteenth-century sealing, which nearly exterminated some species, is not known.

The at-sea distributions of otariids are poorly known because the main source of data has been satellite transmitters attached to foraging mothers. The two Galápagos species are believed to forage locally. But species like the subantarctic, Juan Fernández, and Guadalupe fur seals are known to forage over moderately large 580 mi^2 (1,500 km^2) areas. The northern fur seal makes an annual migratory loop from breeding colonies as far north as the Bering Sea, south over the open ocean to about 35°N latitude, then north to the breeding islands again along the continental shelf break. The Antarctic fur seal may also migrate, but its pathway is less well known because it was never hunted at sea as the northern fur seal was.

Habitat

All otariids bear young and suckle on land. All mate on land, but at least four species also mate to a small degree in the water. They prefer islands, possibly because these sites afford more freedom from land predators, winds and spray that provide better cooling, and a shorter transit time to offshore feeding areas (or a combination of these benefits) than mainland sites do. Nevertheless, large mainland breeding sites now exist in Africa, Argentina, and Peru, and historically existed along the Pacific Coast of North America. Animals prefer breeding on sand or rock, and tend to avoid mud. Most species breed on beaches or headlands, but when the northern fur seal is numerous its colonies extend several hundred yards (meters) up hillsides. Hooker's sea lion breeds under trees on at least two islands, and often suckles its young under dense brush. The Antarctic and northern fur seals can tolerate snow, but do not habitually breed on ice. Where cold water is available, several species live in very hot climates. Otariids can climb nearly vertical surfaces, an ability that gives them access to land areas that true seals cannot use.

Otariids tend to use very few of the many land sites available to them. All species have a long (more than four month) period of neonate dependency, which forces mothers to alternate between feeding themselves and suckling. Land sites must be located where the feeding/nursing pattern is energetically feasible, and this may reduce the number of sites they can use. True seals wean young at a few days to weeks of age, and suspend feeding while nursing. Thus, they are not constrained to breed on sites that permit commuting to feeding areas, and, as a group, tend to breed in smaller groups at more sites than eared seals.

An Australian sea lion (*Neophoca cinerea*) nursing a pup. (Photo ©Tony Wu/www.silent-symphony.com. Reproduced by permission.)

Fur seals tend to feed in the open ocean; sea lions tend to forage on the continental shelf.

Behavior

In most species, males arrive at breeding sites first and establish territories in habitat that females will later use (usually land but also water areas in hot climates). They maintain territories by fighting and by vocal and visual threat displays. The frequency and intensity of aggression depends largely on the turnover rate of adult males. It is most intense when males first come together as neighbors, and when they are not separated by rocks or ledges. In almost all species, males defend space, not females. In established colonies, territory holders are the largest, most mature males. But in colonization situations, subadult males may defend territories and do all the mating. No evidence has been found for hierarchies, but a lek system has been suggested for the California sea lion. All male otariids fast while defending territories. Northern fur seal males have been recorded fasting for 80 successive days with no food at all.

Reproductive females arrive on shore a day or so before giving birth and settle on a parturition (birthing) site, sometimes the same one used in previous years. Females of all species are gregarious but do not form social bonds or hierarchies that denote permanent status. Sea lion females tend to lie in body contact with each other, but fur seal females usually do not. Females regulate space by making low-level threats. As parturition nears, females of some species may become more aggressive, separate from the group, and appear to hold a territory (Steller sea lion) until estrus approaches. Fostering has been seen in four of the otariid species; the others suckle only their own young.

The attempt by males to herd or control females varies by species. Northern fur seal and South American sea lion males may bite and injure females while herding them, but Steller and Hooker's sea lion males rarely touch or interfere with females. The term "harem" is an inappropriate term to describe social organization in most otariids because it implies an exclusivity in mating access that usually does not exist. Males interact with females frequently as estrus approaches, but may simply approach and mount when the female is fully recep-

California sea lions (*Zalophus californianus*) swimming near Guadalupe Island, Mexico. (Photo by Phillip Colla. Bruce Coleman, Inc. Reproduced by permssion.)

tive. Females mate usually once per estrus, and usually depart on their first foraging trip soon after. When they return the lack of a formal social structure allows them to rejoin the group without aggression. Females interact with their young intensely after birth and after foraging absences, but play with them very little, and protect them only moderately from other females.

The young are precocial. They can swim on the day of birth if forced, and they spontaneously show components of adult behavior, such as copulation and fighting, in the first weeks of life. They gather in groups during the mothers' absence.

Juvenile males gather on the fringes of breeding groups, but juvenile females may join those groups, before or after the peak of mating.

Feeding ecology and diet

As stated previously, fur seals tend to forage on the high seas, and sea lions tend to forage near the coast. Fur seals are

Galápagos sea lion (*Zalophus wollebaeki*) subadults, sparring. (Photo by Tui De Roy. Bruce Coleman, Inc. Reproduced by permission.)

fairly small (females average less than 110 lb [50 kg]), and can thrive on large numbers of small fish (like myctophids) and squid that rise to the surface at night in association with the deep scattering layer. The Antarctic fur seal exploits euphausids (krill) that undergo similar vertical migrations. Fur seal females can dive to 656 ft (200 m) or so, which enables the largest of them to feed on the bottom where the continental shelf is broad and productive.

Sea lion females may dive to 1,312 ft (400 m) or so, and generally take small numbers of larger fish and squid that are

The New Zealand fur seal (*Arctocephalus forsteri*) on land. (Photo ©Tony Wu/www.silent-symphony.com. Reproduced by permission.)

A Callifornia sea lion (*Zalophus californianus*) congregation in Monterey Bay, California, USA. (Photo by Jeff Foott. Bruce Coleman, Inc. Reproduced by permission.)

part of the continental shelf fauna. Unlike fur seals, which suspend feeding in the middle of the day when their prey are at maximum depth, sea lions may forage night and day without stopping. Their greater energy needs may preclude them from exploiting the smaller organisms of the deep scattering layer. Both groups are capable of exploiting silvery schooling fish, such as herring, anchovy, or sardines, wherever they are encountered.

The length of the mothers' feeding absence depends on the foraging environment they use, and therefore tends to be longer for fur seals than for sea lions. The shortest trips are made by the equatorial species that feed locally (a few hours to one day). The longest trips are made by the temperate fur seals (Guadalupe, Juan Fernández, subantarctic, and some populations of the New Zealand fur seal) that feed on organisms of the deep scattering layer. Pup fasting ability varies accordingly.

Most sea lion species (males only) have been observed preying on other species of seals, but fur seals have not. Both groups occasionally eat birds. Otariids are visual feeders; echolocation has not been demonstrated for any species, although researchers have looked for this ability in the laboratory.

Reproductive biology

Otariids are strict annual breeders except for the Australian sea lion which, for reasons yet unknown, follows an unusual 17.5 month cycle. Females of all species bear a single, large pup per season. Twins are rare (1 in 10,000 births) in some species. The uterus is bicornuate (has two sections), which allows females to undergo a postpartum estrus. All otariids, including the Australian sea lion, undergo an embryonic diapause (delayed implantation) for about four months before the embryo implants and begins active growth. Diapause seems to function as a timing mechanism, insuring that births occur near particular dates. The timing can be quite precise; in northern and Antarctic fur seals, individual females give birth within three to four days of the same date (specific to each female) in successive years.

All otariids are polygynous; adult sex ratios of 60 females per adult male have been observed in populations subjected to sealing, but undisturbed sex ratios are typically between 2:1 and 10:1. Polygyny is an apparent result of several factors, including breeding at a few large colonies instead of many small ones, gathering at a predictable time and place, higher age-specific mortality in males than in females, length of the

Australian sea lions (*Neophoca cinerea*) breeding. (Photo by Charles G. Summers, Jr. Bruce Coleman, Inc. Reproduced by permission.)

breeding season, male competition rate, and a postpartum estrus. Males may mate 100 or more times during a breeding season, depending on their location relative to females.

Females have a single estrus that occurs less than 10 days postpartum (except in the California sea lion where it is 30 days). Most females mate only once per estrus, rarely twice. If they fail to mate, estrus may last less than two days (36 hours in the northern fur seal). If they mate, estrus may be terminated by coitus (the Whitten effect). Females of most species mate indiscriminately with whichever male is nearest when they enter estrus. Females usually do not mate with juvenile or peripheral males because adult males exclude them from the breeding sites. However, in colonization situations, when males intercept females on their way to feeding (South American and Hooker's sea lions), or in captivity, females of some species readily mate with juvenile or peripheral males. Pregnancy rates may exceed 90% in some age classes of females.

The duration of the breeding season varies with latitude. The interval in which 90% of the females enter estrus varies from 21 days in the Antarctic fur seal to 70 days in the Galápagos fur seal. Many aspects of the social system change when the breeding season is long lasting.

Conservation status

Most otariids were exploited by nineteenth-century sealers to some extent. Fur seals were exploited most heavily because their pelts, with guard hairs removed, were prized for clothing. Sea lions were taken mostly for oil, hides, vibrissae, and organs. After a very long lag time (50–60 years) fur seals are showing better recovery from sealing than sea lions, and at present seem to be thriving somewhat better. The most spectacular recovery was made by the Antarctic fur seal, which was once believed to be extinct and now numbers 3–4 million animals. All fur seals are presently increasing except the northern fur seal. This species recovered from nineteenth-century sealing and reached a peak in 1956, but has been declining ever since. Because the reason for this decline is unknown, there is as much concern for this species as there is for those that have smaller total numbers (Guadalupe, Juan Fernández, South American, subantarctic fur seals) but a good growth rate. The Galápagos fur seal recovered from sealing, but its total numbers appear to be limited now by periodic El Niño events that depress adult survival. The Galápagos, Juan Fernández, Guadalupe, and northern fur seal are all listed as Vulnerable by the IUCN.

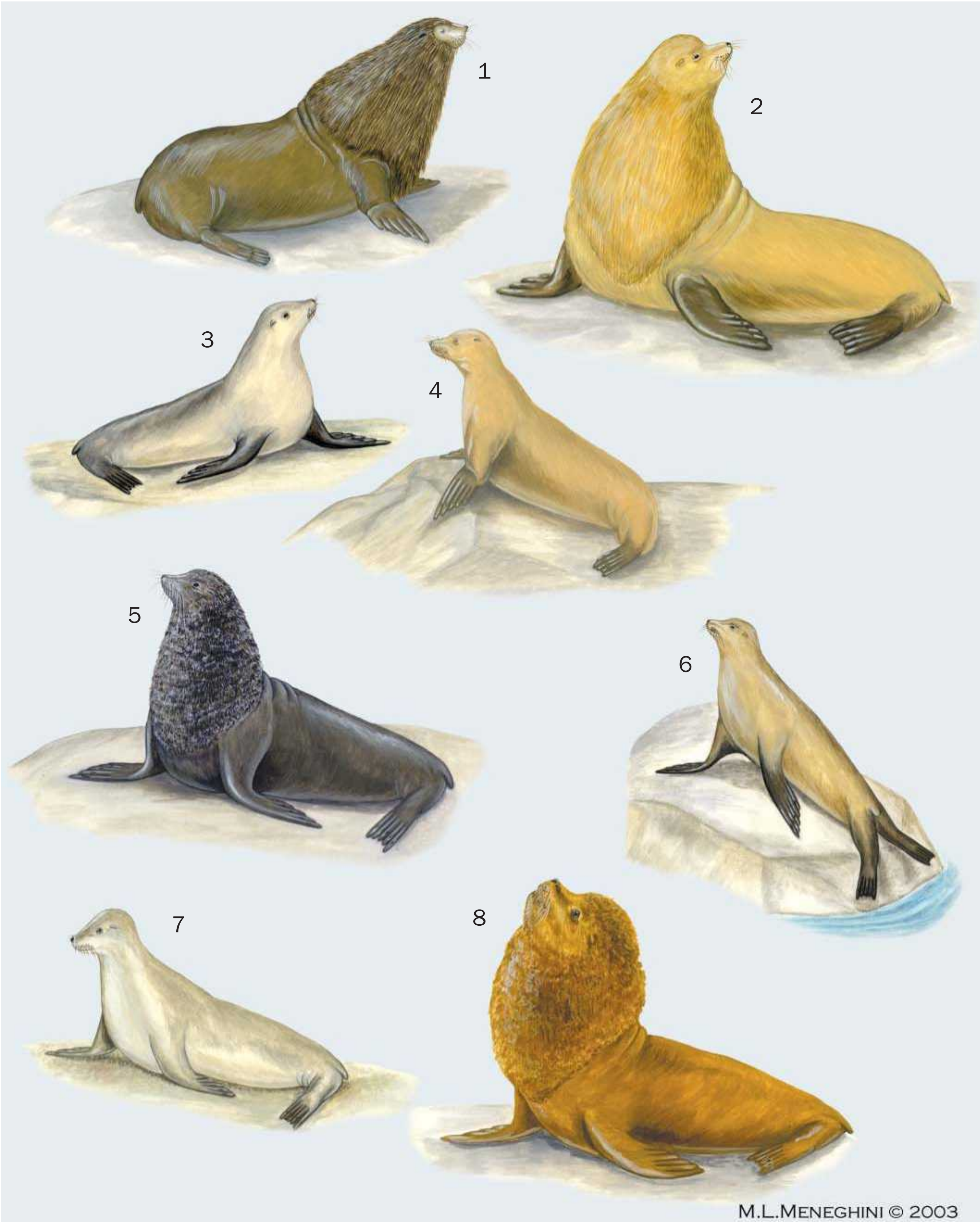
Sea lions are harder to summarize. California and South American sea lions are increasing. The Galápagos sea lion

Galápagos fur seal (*Arctocephalus galapagoensis*) mother and pup. (Photo by Tui De Roy. Bruce Coleman, Inc. Reproduced by permission.)

seems to be limited by El Niño events like Galápagos fur seals. Hooker's sea lions are of concern because, while never present in large numbers, they have been stable for 20 years and are facing competition with a squid fishery. The Steller sea lion has declined by more than 90% in the last 20 years and may be impacted by a commercial fishery. The Stellar sea lion is listed as Endangered, and Hooker's sea lion is Vulnerable.

Significance to humans

Fur seals were formerly a source of pelts from which clothing was made. From 1760 to about 1900, they were the subjects of intense international trade, treaties, and even small wars. A more controlled form of trade continued until 1985 when the last commercial sealing ended. Since the 1970s otariids have been increasingly seen as competitors of commercial fishing operations, or a problem in fisheries bycatch. All pinnipeds are used as scapegoats to explain declining fisheries catches.



1. Male northern fur seal (*Callorhinus ursinus*); 2. Male Steller sea lion (*Eumetopias jubatus*); 3. Female Hooker's sea lion (*Phocarctos hookeri*); 4. Female California sea lion (*Zalophus californianus*); 5. Male Antarctic fur seal (*Arctocephalus gazella*); 6. Female Galápagos sea lion (*Zalophus wollebaeki*); 7. Female Australian sea lion (*Neophoca cinerea*); 8. Male South American sea lion (*Otaria byronia*). (Illustration by Michelle Meneghini)

Species accounts

Northern fur seal
Callorhinus ursinus

SUBFAMILY
Arctocephalinae

TAXONOMY
Callorhinus ursinus (Linnaeus, 1758), "Bering Island."

OTHER COMMON NAMES
English: Sea bear; French: Otarie des Pribilofs; German: Nördliche Pelzrobbe; Spanish: Lobo fino del norte.

PHYSICAL CHARACTERISTICS
Males to 606 lb (275 kg), gray to black or reddish. Females to 110 lb (50 kg), gray. Rear flippers long and slender; hair on front flippers stops abruptly at the wrist joint. In all other otariids hair extends beyond the wrist joint.

DISTRIBUTION
The species breeds from southern California to the Kuril Islands with the main populations at the Pribilof and Commander Island groups. Females and juveniles forage south to 35°N latitude, then migrate back to breeding sites in spring.

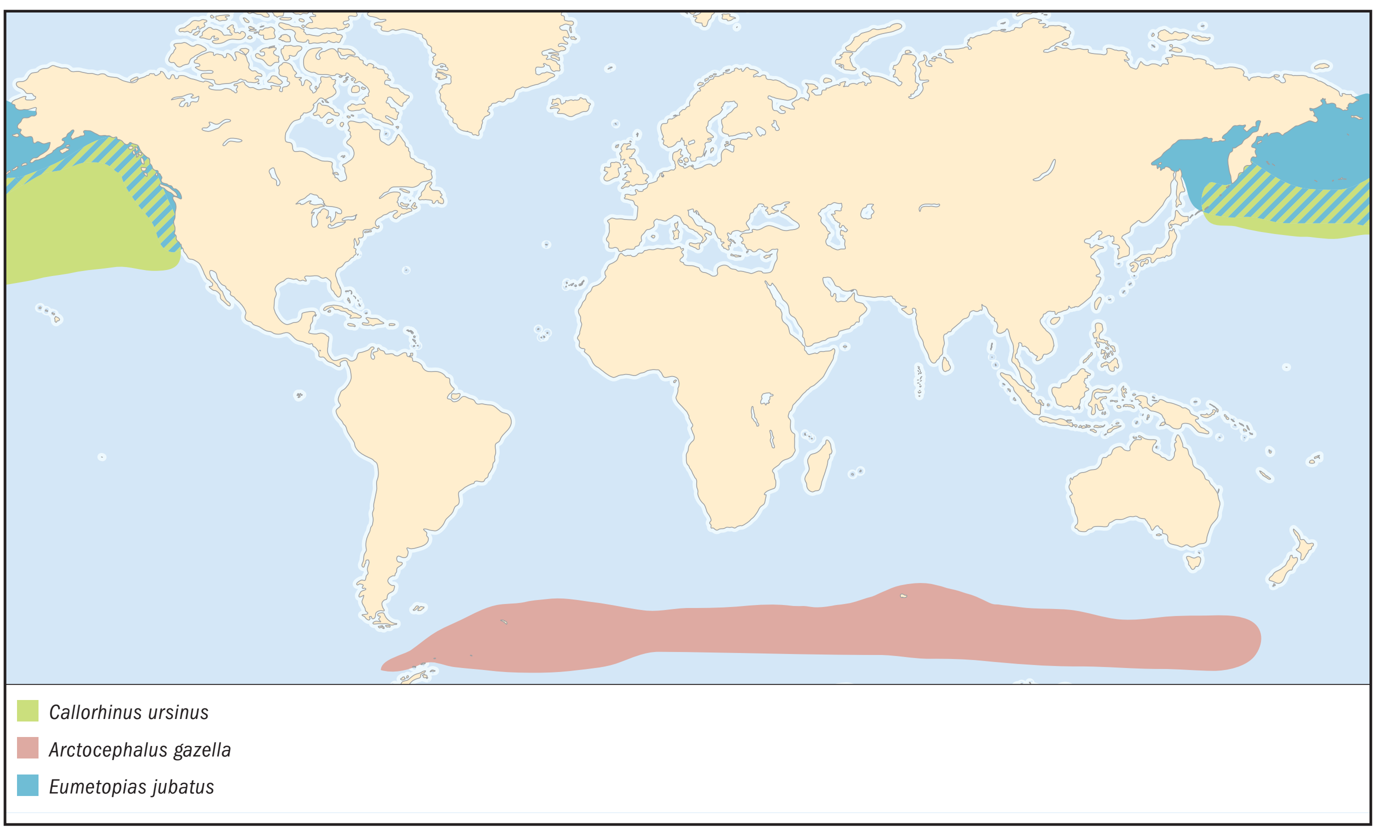
HABITAT
This species now breeds exclusively on islands (formerly on the mainland). One of the breeding sites is known to have been used for over 250 years. It is one of the most pelagic otariids, spending all but 35–45 days per year at sea.

BEHAVIOR
It follows the basic otariid behavior, described above. It forms only a few large breeding colonies where males fast while defending terrestrial territories. Females arrive on predictable dates, form amorphous social groups, give birth, mate, then alternate foraging with nursing until weaning at four months. Females and males are highly site specific.

FEEDING ECOLOGY AND DIET
The species takes over 75 species of fish and cephalopods, many of them associated with the deep scattering layer. The diet was determined by extensive collections at sea.

REPRODUCTIVE BIOLOGY
Polygymous. The notion of seal harems may have developed with this species. The species does not deviate from the basic otariid pattern, except that females wean young at four months of age. More is known of its reproductive biology than other species because an international treaty (1911 to 1985) mandated certain kinds of research.

CONSERVATION STATUS
The species is listed as Vulnerable, and numbered only a few hundred thousand in 1911, increased to 2.5 million in the mid 1950s, then declined to approximately 1 million in 2002. The



reasons for the decline are unknown, but it is proceeding in parallel with decreases in the Steller sea lion, harbor seal, and sea otter in Alaska.

SIGNIFICANCE TO HUMANS
The species was of great significance to society from the 1860s to 1985 because of pelts. It was the first marine mammal to which a management regime was applied, and it was the subject of an international treaty in 1911. Presently Alaska natives use the species for subsistence. ◆

Antarctic fur seal
Arctocephalus gazella

SUBFAMILY
Arctocephalinae

TAXONOMY
Arctocephalus gazella (Peters, 1875), "Anse Betsy" 49°09'S, 70°11'E.

OTHER COMMON NAMES
English: Kerguelen Island fur seal; French: Otarie antarctique; German: Kerguelen-Seebär, Antarktischer Seebär; Spanish: Lobo fino antarctico.

PHYSICAL CHARACTERISTICS
Males to 114 lb (200 kg); 1–2% of them are white but not albino. Females are gray, to 110 lb (50 kg).

DISTRIBUTION
Occurs mostly on subantarctic islands. Large populations are found south of or close to the Antarctic polar front, with 95% of the population breeding on South Georgia.

HABITAT
The species breeds on islands in the south Atlantic and south Indian Ocean sectors of the Southern Ocean. It abandons land areas in winter, but its pelagic distribution is unknown. It is fully as pelagic as the northern fur seal. Most breeding sites are south of the Antarctic Convergence. Like the northern fur seal, it tolerates snow but does not breed on ice.

BEHAVIOR
This species follows the description of otariid behavior given above. Males fast and are territorial, females form dense aggregations, and lack a specific form of social organization.

FEEDING ECOLOGY AND DIET
This is the only otariid that frequently feeds on euphausids (krill). It also takes fish, crustaceans, and some birds. It feeds at night at shallow depths over deep water in association with the deep scattering layer.

REPRODUCTIVE BIOLOGY
Polygynous. It deviates from the usual otariid reproductive biology only in that females wean their young at the age of four months. Their breeding seasons are short, as expected for the length of summer at their breeding sites. Antarctic fur seals sometimes hybridize with subantarctic fur seals at Marion Island.

CONSERVATION STATUS
Not threatened. The species appeared to be extinct in the late 1800s. Its recovery may have been aided by commercial whaling in the 1940s and 1950s, which removed the fur seal's major competitor for krill. The population has been increasing at 9% or more annually, and now exceeds 3 million animals.

SIGNIFICANCE TO HUMANS
It was formerly the subject of intense international competition for pelts. At present it is of no particular significance to humans. ◆

Hooker's sea lion
Phocarctos hookeri

SUBFAMILY
Otariinae

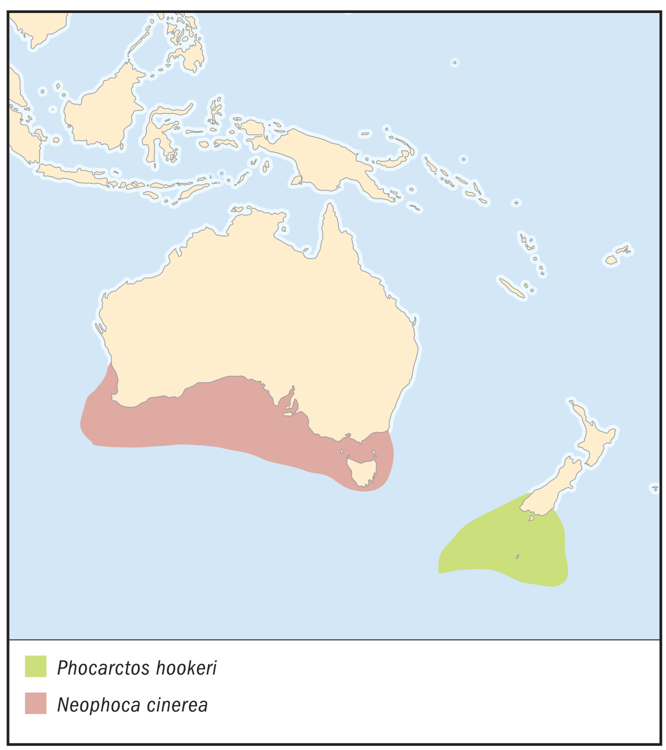
TAXONOMY
Phocarctos hookeri (Gray, 1844), "Falkland Islands and Cape Horn" (in error, actually "Auckland Islands").

OTHER COMMON NAMES
English: Auckland sea lion, New Zealand sea lion; French: Lion de mer de Nouvelle-Zélande; German: Neuseeland-Seelöwe; Spanish: Léon marine de Nuevo Zelandia.

PHYSICAL CHARACTERISTICS
Males to 992 lb (450 kg), nearly black; females to 364 lb (165 kg), light tan in color. Pups of various colors with a light stripe down the nose.

DISTRIBUTION
Ocean near Auckland Islands, Campbell Island, and other islands near New Zealand.

HABITAT
The species breeds on protected beaches on three islands of the Auckland Island group, Campbell Island. It hauls out on many other islands in the New Zealand area. Animals may breed on sand or under shoreline trees.



BEHAVIOR
The species forms relatively small colonies. Males are territorial, and females form a dense aggregation. At Enderby Island the female aggregation moves along the beach parallel to the water line during breeding. Juvenile males intercept females departing for foraging, and may mate. After the breeding season females move inland to suckle their young in the forest.

FEEDING ECOLOGY AND DIET
The species is reported to take 33 species of prey (fish 59% of diet, cephalopods 22%, crustaceans 15%). Females are largely bottom feeders, dive night and day continuously while at sea, and reach maximum depths of 1,312 ft (400 m). Males occasional take penguins, and cannibalism has been reported. Females often regurgitate rocks and octopus beaks.

REPRODUCTIVE BIOLOGY
Polygynous. The females wean their young by one year of age. No major deviations from typical reproductive biology are known.

CONSERVATION STATUS
Listed as Vulnerable. Hooker's sea lions were formerly more abundant and widespread before being reduced by commercial and subsistence (Maori) sealing. The present population is estimated at 13,000. Its numbers have been stable for 20 years.

SIGNIFICANCE TO HUMANS
Bycatch in a squid fishery on the Auckland shelf may threaten this species. ◆

Australian sea lion
Neophoca cinerea

SUBFAMILY
Otariinae

TAXONOMY
Neophoca cinerea (Péron, 1816), Kangaroo Island, Australia.

OTHER COMMON NAMES
English: White-capped sea lion; French: Lion de mer d'Australie; German: Australischer Seelöwe; Spanish: Lobo marino de Australia.

PHYSICAL CHARACTERISTICS
Males are dark brown to nearly black with a white patch on the head and nape of the neck. They weigh more than 441 lb (200 kg). Females weigh up to 231 lb (105 kg), and have a white belly and tan back.

DISTRIBUTION
Ocean off the southern coast of Australia.

HABITAT
This species breeds in protected locations at many sites along the southern coast of Australia. Females seek holes in rock or under brush to bear and suckle young. More than 50 breeding colonies are known, only five of which produce more than 100 young per year.

BEHAVIOR
Australian sea lions are territorial like other otariids, and females form groups. They will not flee when approached by humans. Many aspects of their behavior are altered by the long breeding season.

FEEDING ECOLOGY AND DIET
The species takes a combination of cephalopods, crustaceans, and fish. It often feeds on the bottom, and has been known to take lobsters from inside fishing pots.

REPRODUCTIVE BIOLOGY
Polygynous. This species has the most unusual reproductive biology of any otariid. Females have a 17.5-month breeding cycle; colonies breed out of synchrony with each other. The breeding season lasts five months. Individuals have strong site fidelity.

CONSERVATION STATUS
Not threatened. The species was once hunted for skins and oil but was probably never as numerous as the local fur seals. Their numbers are now estimated at 9,300–11,700. Their potential for further increases is limited by the low productivity of their limited feeding habitat.

SIGNIFICANCE TO HUMANS
Tourist attraction on Kangaroo Island. Here and elsewhere the species shows little fear of humans. ◆

South American sea lion
Otaria byronia

SUBFAMILY
Otariinae

TAXONOMY
Otaria byronia (Blainville, 1820), "Island of Tinian (in error, probably strait of Magellan).

OTHER COMMON NAMES
French: Lion de mer d'Amérique du Sud; German: Mähnenrobbe, Südamerikanischer Seelöwe; Spanish: Lobo común.

PHYSICAL CHARACTERISTICS
Males to 772 lb (350 kg), brownish in color with a rough mane and unusually large neck and head. Females to 331 lb (150 kg), tawny.

DISTRIBUTION
Ocean near the Falkland Islands and eastern coast of South America.

HABITAT
Breeds on sand, cobble, or rock. Found on the Falkland Islands, from southern Brazil to Cape Horn (more than 53 breeding sites in central to southern Patagonia), and north to Peru.

BEHAVIOR
Animals do not make prolonged foraging absences, nor do they migrate. Some colonies are occupied all year. Mating is seasonal. Males display a variety of mating strategies in addition to territoriality. Males vigorously herd females, sometimes injuring them.

FEEDING ECOLOGY AND DIET
The species takes fish, crustaceans, and cephalopods. Males occasionally take young fur seals and penguins. Females make short (three day) foraging trips, typical for sea lions.

REPRODUCTIVE BIOLOGY
Polygynous. The operational sex ratio is 1.2 females per male. As with other otariids, females bear a single pup per year, and have a postpartum estrus.

CONSERVATION STATUS
Not threatened. The species was commercially exploited for oil, and is still killed by fishermen. The population is presently estimated at more than 110,000, which may be 20% of its original numbers. Numbers may be increasing. Populations in the Pacific decline in response to El Niño events.

SIGNIFICANCE TO HUMANS
The species is being taken as bait for king crab pots, and is considered to be a nuisance by other fishermen. ◆

California sea lion
Zalophus californianus

SUBFAMILY
Otariinae

TAXONOMY
Zalophus californianus (Lesson, 1828), San Francisco Bay, California, United States.

OTHER COMMON NAMES
English: Black sea lion; French: Lion de mer de Californie; German: Kalifornischer Seelöwe; Spanish: Lobo marino de California.

PHYSICAL CHARACTERISTICS
Males black/brown with a prominent saggital crest topped by white hair. The call is a loud, sharp bark. Males to 772 lb (350 kg), females to 220 lb (100 kg), tawny.

DISTRIBUTION
Ocean from central Mexico to southern California, including Guadalupe Island and the Sea of Cortez. Males migrate north as far as Canada, but females do not.

HABITAT
Breeds on sand or rock from central Mexico to southern California (plus Guadalupe Island and the Sea of Cortez). No mainland breeding sites now exist.

BEHAVIOR
The most successful males defend territories that afford females access to water. Female aggregations move across the beach depending on daily temperatures. This species may perform more aquatic copulations than other otariids.

FEEDING ECOLOGY AND DIET
These are opportunistic feeders, primarily depending on anchovy, whiting, rockfish, cephalopods, mackerel, myctophids, sardines, etc., depending on location, season, and El Niño events. Animals feed at all hours. Feed in groups, and may feed with Steller sea lions where the ranges overlap (San Miguel and Año Nuevo Island, California).

REPRODUCTIVE BIOLOGY
Polygynous. Male biology is typical for otariids. Female California sea lions enter estrus 30 days postpartum, instead of less than 10 days like other otariids. Breed on islands with northern fur seals, but hybrids are not known.

CONSERVATION STATUS
Not threatened. California sea lions were exploited in the nineteenth century, and reached a low of 1,500 in the 1920s. They then increased, displacing the Steller sea lion as the most numerous sea lion in California. Their numbers are now between 211,000 and 241,000 and are growing at 5% per year.

SIGNIFICANCE TO HUMANS
This species is known as the common "circus seal," and has served to introduce generations of humans to the family Otariidae. As a laboratory animal, the species has contributed significantly to what we know about vision, hearing, learning, and cognition in marine mammals. Some consider it a nuisance because it is noisy, increasing, and likely to foul the many human structures (buoys, piers, etc.) it uses as resting sites. ◆

Galápagos sea lion
Zalophus wollebaeki

SUBFAMILY
Otariinae

TAXONOMY
Zalophus wollebaeki Sivertsen, 1953.

OTHER COMMON NAMES
German: Galapagos Seelöwe.

PHYSICAL CHARACTERISTICS
Males are gray/brown to black; no weights reported. Their call is a sharp, intense bark. Females are tawny, and weigh up to 176 lb (80 kg).

DISTRIBUTION
Galápagos Islands. It is restricted to feeding in upwelling plumes around the islands and cannot emigrate during El Niño events.

HABITAT
The Galápagos sea lion breeds on all the major islands of the Galápagos. It prefers gently sloping beaches of sand and rock, and therefore shares no breeding sites with the Galápagos fur seal.

BEHAVIOR
Their behavior has not been well studied, but appears to resemble that of California sea lions in general. It defends shoreline territories. Most animals are on shore at night.

FEEDING ECOLOGY AND DIET
These animals forage usually in the daytime on sardines (70% of diet). They may switch to green eyes and myctophids during El Niño events.

REPRODUCTIVE BIOLOGY
Polygynous. The species maintains an annual cycle of breeding, and has a long (6–8 month) breeding season. Females suckle young for two years on average (range 1–3 years), and may simultaneously suckle a pup born that year.

CONSERVATION STATUS
The species was not commercially exploited. It numbered to 50,000 in 1963, but declined to 14,000 after the 1997–98 El Niño event. It may now be below historic numbers.

SIGNIFICANCE TO HUMANS
An ecotourism attraction as part of the native fauna of the Galápagos Islands. ◆

Steller sea lion
Eumetopias jubatus

SUBFAMILY
Otariinae

TAXONOMY
Eumetopias jubatus (Schreber, 1776), Commander and Bering Islands, Russia.

OTHER COMMON NAMES
English: Northern sea lion; French: Lion de mer de Steller; German: Stellers Seelöwe; Spanish: Lobo marine de Steller; Aleut: qawax; Russian: Sivuch.

PHYSICAL CHARACTERISTICS
This is the largest of the otariids. Males are reddish or dark brown to nearly white, average 1,248 lb (566 kg), and reach a maximum of 2,469 lb (1,120 kg). Females are tan, average 580 lb (263 kg), and reach a maximum of 772 lb (350 kg). Pups are chocolate, wooly, and weigh approximately 44 lb (20 kg) at birth.

DISTRIBUTION
Ocean from central California to the Kuril Islands.

HABITAT
They breed on rock, sand, or cobble beaches from central California to the Kuril Islands with the population peak in the Aleutian chain. They breed on islands except at one site, a cave in Oregon. Where the ranges overlap, Steller sea lions have extensive contact with California sea lions and northern elephant seals. No hybrids are known.

BEHAVIOR
Males are territorial, and females form aggregations, often very dense because of their tendency to rest in full body contact with others. Females move to the water's edge in hot weather.

FEEDING ECOLOGY AND DIET
The species takes a wide variety of fish and cephalopods, including walleye pollock, cod, mackerel, flatfish, small schooling fish, salmon, and occasionally birds or other seals. Feeds at all hours of the day, often in groups.

REPRODUCTIVE BIOLOGY
Polygynous. They have a predictable annual breeding season. Most females wean young by one year of age, but a few return to breeding sites still suckling two to three year-old young.

CONSERVATION STATUS
Listed as Endangered. The species has been declining in California since the 1920s. Their overall numbers have declined by 90% since the 1980s, especially in the central Aleutian Islands. In 1994 a census revealed 100,000 animals, but the number may now be as low as 75,000.

SIGNIFICANCE TO HUMANS
The population decline may be linked to commercial fishing for walleye pollock, the largest single-species fishery in the United States. The legal, financial, and research implications of this possible impact are having significant effects on many aspects of human society at present. The species is declining in parallel with northern fur seals, harbor seals, and sea otters in Alaska. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Subantarctic fur seal *Arctocephalus tropicalis* English: Amsterdam Island fur seal; French: Otarie subantarctique; German: Kerguelen-Seebär; Spanish: Oso marino de subantarctico	Only seal with white or yellowish hair on the face, neck, and chest. Dorsally, it is gray, like other fur seals. Males to 287 lb (130 kg); females to 79 lb (36 kg).	Males spend most of the year at sea, females stay relatively close to the rookeries. Breeding occurs on temperate coastal areas. Females have the longest known feeding absences of any otariid, which means their pups have very prolonged fasts.	Temperate islands north of the Antarctic Convergence, including the islands of Amsterdam, Crozet, Grough, Marion, Prince Edward, St. Paul, Tristan, and Macquarie.	Females take myctophids and squid associated with the deep scattering layer, as well as some krill and penguins. They forage up to 310 mi (500 km) from land on a trip to sea.	Not threatened
New Zealand fur seal *Arctocephalus forsteri* English: Antipodean fur seal, Western Australian fur seal; French: Otarie de Nouvelle-Zélande; German: Australischer Seebär, Neuseeland-Seebär; Spanish: Oso marino de Nueva Zelandia	Both sexes gray in color.	Gathers in fairly small colonies at a large number of sites. Males are small and have fairly brief territorial tenure, resulting in a high turnover rate among males, and fairly frequent aggression. Females gather in groups, and may move to the water on hot days (Australia). Females make moderately long trips to sea.	Islands around New Zealand and the southern coast of Australia.	Squid, octopus, and fish, and occasionally birds.	Not threatened
Afro-Australian fur seal *Arctocephalus pusillus* French: Otarie d'Australie; German: Südafrikanischer Seebär, Australischer Seebär; Spanish: Oso marino de Australia.	Both sexes gray/brown. Largest species of fur seal. Males reach more than 551 lb (280 kg), females 176 lb (80 kg).	*A. p. pusillus* breeds from Namibia to the Indian Ocean coast of southern Africa at several island sites, and at several mainland sites. The species feeds only on the continental shelf. *A. p. doriferus* breeds only in the Bass Strait region of southern Australia on a small number of sites near limited foraging grounds. Males are territorial, and females form dense groups that move to water and back, depending on solar radiation.	*A. p. pusillus:* coast of Namibia and the south and west coasts of South Africa; *A. p. doriferus:* islands in Victoria and Tasmania, all in the Bass Strait near Australia.	50% fish (surface, mid-water, and bottom species), 37% cephalopods, 13% crustaceans, plus six species of birds.	Not threatened
Juan Fernández fur seal *Arctocephalus philipii* French: Arctocéphale de Juan Fernandez; German: Juan-Fernandez Seebär; Spanish: Oso marino de Chile	Mostly gray. Males to 309 lb (140 kg); females to 106 lb (48 kg).	Females forage on the deep scattering layer, and may travel as far as 310 mi (500 km) from shore per trip; their prey is patchily distributed. Some males defend shoreline territories and perform free floating copulations. Female foraging trips are very long (average 12 days, maximum 21 days), which affects many aspects of the social system.	Robinson Crusoe Island as well as Alejandro Selkirk and Santa Clara Islands in the Juan Fernández group of islands off the Chilean coast.	80% myctophids, and about 20% squid associated with the deep scattering layer.	Vulnerable
South American fur seal *Arctocephalus australis* French: Otarie d'Amérique du Sud; German: Südliche Pelzrobbe; Spanish: Oso marino austral.	Gray. Males to 441 lb (200 kg), females to 132 lb (60 kg). Considered to be the most primitive member of the genus.	Some colonies are occupied all year long. Males are territorial; some are landlocked, some are along the waterline, and some are mostly aquatic. Females move low or high on the beach depending on solar radiation, and males attempt unsuccessfully to control them.	Neotropical ocean coasts from the Península Pacaranas in southern Peru, south around the cape and north to Rio Grande do Sul in southern Brazil.	Weakfish, cutlassfish, anchoveta, anchovy, and cephalopods. In Peru the species takes mostly anchoveta.	Not threatened

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Galápagos fur seal *Arctocephalus galapagoensis* French: Arctocéphale des Galapagos; German: Galapagos Seebär; Spanish: Oso marino de las Galápagos	Both sexes are brownish. Smallest of the otiids. Males 154 lb (70 kg), females 77 lb (35 kg).	The largest colonies are on Isabella and Fernandina Islands. Animals are present in their colonies all year. They forage in upwelling plumes around the islands, and do not emigrate during periodic El Niño events. The species has a very prolonged breeding season. Females forage at night and are on land in day-time, seeking the water's edge during high temperatures.	Limited to the Galápagos Islands.	Mostly myctophid and bathylagid fish associated with the deep scattering layer, and switches to sardine and *Selene declivifrons* during El Niño events. Feeding is depressed during the full moon because prey do not ascend to the surface at night under those conditions.	Vulnerable
Guadalupe fur seal *Arctocephalus townsendi* English: Lower Californian fur seal; French: Arctocéphale de Guadalupe, otarie à fourrure d'amérique; German: Guadeloupe Seebär; Spanish: Oso marino de Guadalupe	Both sexes are gray/brown. Males average 414 lb (188 kg), females average 110 lb (50 kg).	Breeds on the east coast of Guadalupe Island, Mexico. Lone animals are occasionally seen as far north as northern California. Some animals breed inside lava tubes that extend to the shore. This habit of breeding in caves may have protected the species from being exterminated by sealers in the nineteenth century.	The Pacific Coast, from the northern Channel Islands of California, United States, south to Cedros Island, Baja California, Mexico.	Females feed on fish and cephalopods of the deep scattering layer, and may cover 1,240 mi (2,000 km) on a trip to sea, resulting in long foraging trips.	Vulnerable

Resources

Books

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Perrin, W. F., B. Würsig, and J. G. M. Thewissen. *Encyclopedia of Marine Mammals.* San Diego: Academic Press, 2002.

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Roger Gentry, PhD

Walruses

(Odobenidae)

Class Mammalia
Order Carnivora
Suborder Pinnipedia
Family Odobenidae

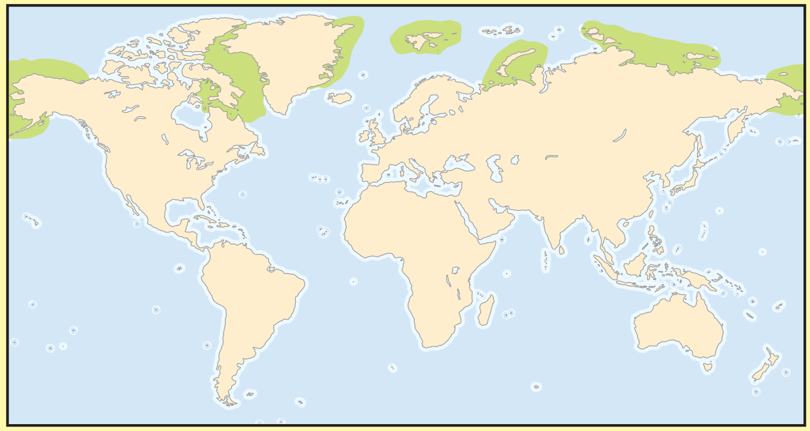
Thumbnail description
Large marine mammal that waddles on fore and rear flippers on land and propels itself with rear flippers in water; brown in color with short hairs over pinkish skin beneath and more visible around the neck; canines have evolved into long tusks in both males and females

Size
44–126 in (112–320 cm); 139–2662 lb (63–1210 kg)

Number of genera, species
1 genus; 1 species

Habitat
Shallow marine areas, polynyas (open water within large ice masses), drifting ice floes, island beaches (sand, cobble and rock)

Conservation status
Data Deficient for both the Atlantic and Pacific subspecies



Distribution
Circumpolar waters, including the Bering and Chukchi Seas (around Alaska and Russia), the western and eastern Atlantic Ocean (around Canada, Greenland, Scandinavia and Russia), and the Laptev Sea (around Russia)

Evolution and systematics

There has been a long standing controversy as to whether the Pinnipedia is diphyletic (arising from two lines) or monophyletic (arising from a single line). The majority of morphological and DNA evidence now supports monophyly, with an arctoid ancestor (probably ursid, but could be mustelid or procyonid). However, still uncertain is where odobenids fit within this lineage. Most morphological evidence supports a closer relationship between odobenids and phocids although at least one morphological study places the odobenids and otariids closer together. Molecular genetic studies generally support a closer relationship between the odobenids and otariids, but there are some studies that suggest the relationship with phocids. In short, additional study is required to clarify the evolutionary position of the Odobenidae within the Pinnipedia. Currently three subspecies of walrus are recognized, the Pacific, Atlantic, and Laptev walruses, although there is disagreement on whether the Laptev group is distinct enough to be considered a subspecies.

The taxonomy for this species is *Odobenus rosmarus* (Linnaeus, 1758), "intra zonam arcticam Europae, Asiae, Americae."

A male Pacific walrus (*Odobenus rosmarus*) swimming and exhaling in Alaska. (Photo by © Keven Schafer/Peter Arnold, Inc. Reproduced by permission.)

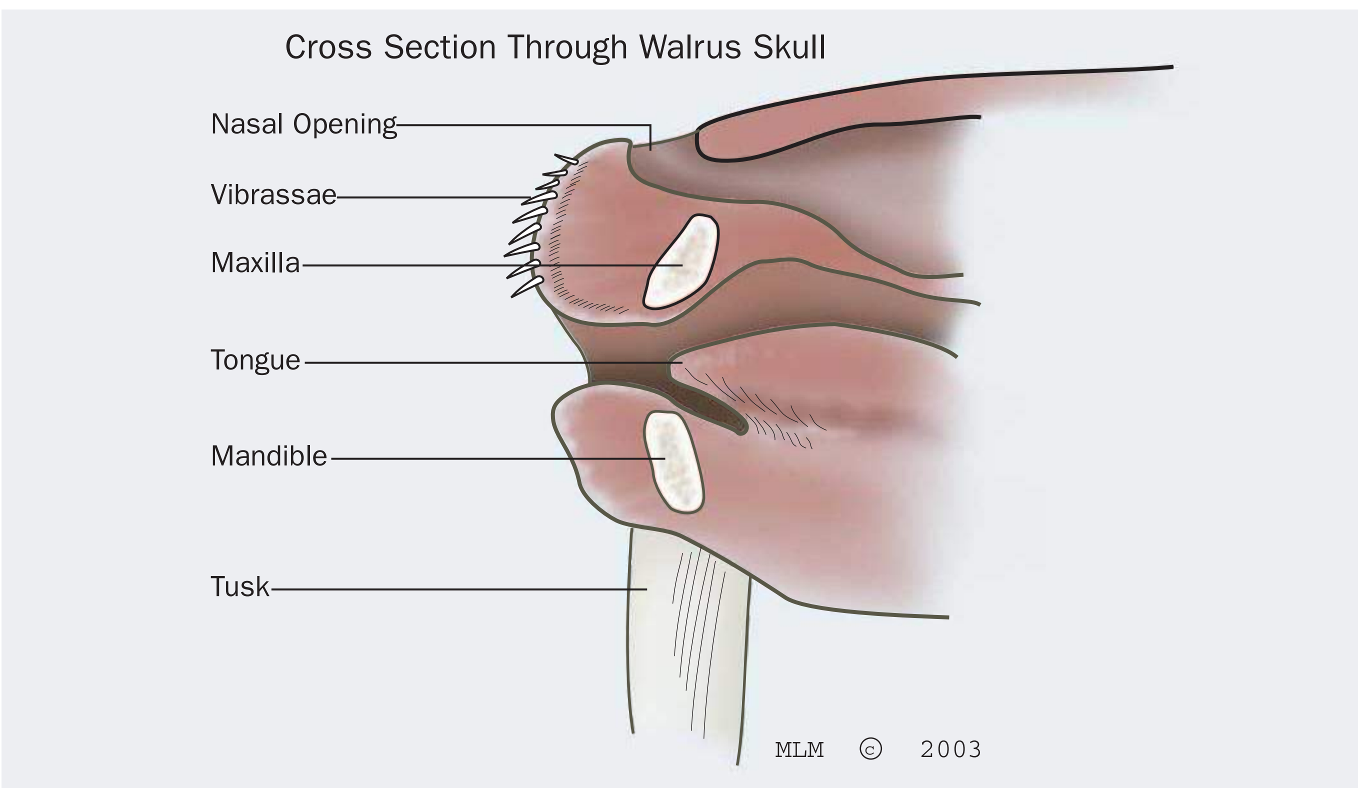
Physical characteristics

Walruses are large mammals. They are probably most noted for the extended size of their upper canines that protrude externally from the mouth as tusks. The tusks occur

Walrus calf rides on its mother's back. (Illustration by Michelle Meneghini)

Atlantic walrus (*Odobenus rosmarus rosmarus*) near the Arctic Ocean. (Photo by Dotte Larson. Bruce Coleman, Inc. Reproduced by permission.)

in both males and females, although those of males tend to be larger in diameter and shorter than those of females. The snout of the walrus distinguishes it from other seals in that it is flat or "pug nosed" and contains a pad of mustacial vibrissae (whiskers) that are short and stout. These whiskers are used in detecting prey. There are no external pinnae, i.e. ears.



Walrus mouth and snout anatomy allows for specialized finding and feeding on mollusks. (Illustration by Michelle Meneghini)

The walrus (*Odobenus rosmarus*) uses its tusks to aid in locomotion. (Photo by John Giustina. Bruce Coleman, Inc. Reproduced by permission.)

Walruses have a coat of hair covering most of their body, although some regions such as the neck and flippers are either sparse with hair or devoid of it completely. When dry, the hair is a light brown but it is darker in appearance when wet. Male walruses have large fibrous tubercles (bumps) around the neck region. The absence of these among females suggests a secondary sexual function for them.

The rotund appearance of walruses is a result of the thick layer of subcutaneous blubber. Adult females have a slightly thicker layer of blubber, being nearly twice as thick as males during the breeding period.

Like the otariids, walruses rotate the rear flippers under their body and lift themselves off the ground to walk on land. However, for swimming at sea, walruses are more like phocids in that they move their rear flippers from side to side to propel themselves. Unlike phocids, the fore flippers are used to steer and maneuver.

The male Pacific walrus (*Odobenus rosmarus*) frequently uses its tusks for fighting when beach conditions become too crowded. (Photo by Dan Guravich/Photo Researchers, Inc. Reproduced by permission.)

Distribution

Walruses are essentially circumpolar in their distribution. The Atlantic subspecies is probably widest ranging in their distribution from the Canadian Arctic to the Kara Sea of Russia. They were once found as far south as Sable Island, off the coast of Nova Scotia and at the Magdalen Islands and Prince

Altlantic walrus (*Odobenus rosmarus rosmarus*) bachelor bulls rest on drifting ice floes along the north coast of Spitzbergen, Svalbard, in the Norwegian Arctic. (Photo by Tui De Roy. Bruce Coleman, Inc. Reproduced by permission.)

Edward Island in the Gulf of St, Lawrence. However, northern Hudson Bay is as far south as they now occur.

The Pacific subspecies primarily inhabits the Bering and Chukchi Seas. As this subspecies moves with the pack ice or floating ice, the majority of Pacific walruses are in the Bering Sea in winter and the Chukchi Sea in summer. Births occur on ice usually in the region between Nunivak and St. Lawrence Islands.

The Laptev walrus is found in the eastern Kara Sea, the Laptev Sea, and the Siberian Sea.

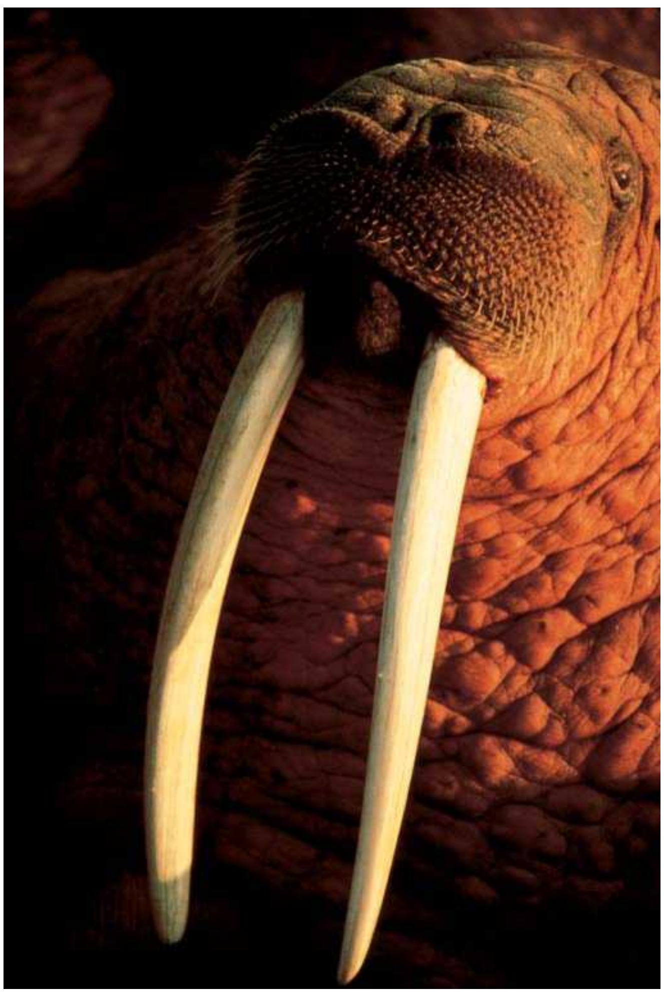
Habitat

The feeding habits of walruses restrict the habitats they use to relatively shallow water of less than 328 ft (100 m) for foraging. During the breeding season, female walruses are found on ice floes, where they give birth to their calves. Females and calves usually remain associated with floe ice, but will haul out on land when the ice is unsuitable to support their large mass or too thick (more than 8 in; 20 cm) to break through. When females are receptive, males will be found in the water off ice floes containing females and will spend long periods of time without hauling out. Outside the mating period, males have traditional haul out sites on islands with sand, cobble or boulder beaches. Round Island in Bristol Bay, Alaska is one such site where thousands of males can be seen huddled side by side, forming a churning mass of walruses. In a few places, such as Coats Island, Northwest Territories, mixed herds of males, females, and calves can be found on land in the summer.

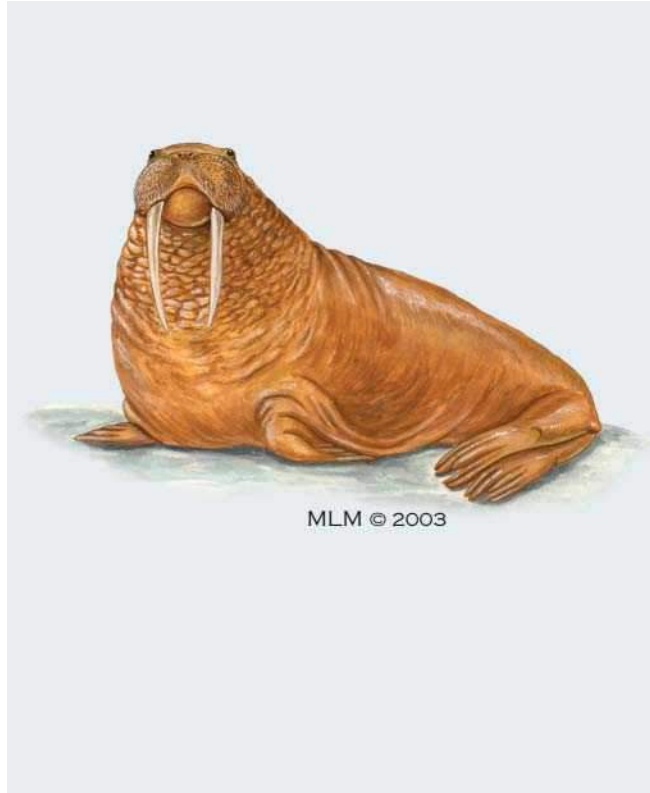
Behavior

Walruses are gregarious, traveling in small groups at sea or on ice pans and in large groups when resting or molting on land or ice. Despite the gregariousness the primary social bond seems to be that between a mother and her calf. Based on their behavior males appear to be polygynous although mating by identified animals or genetic paternity results to confirm polygyny are not available. In some situations males appear to follow females, competing directly with one another for the chance to mate. In other situations, males cluster around ice pans containing females that are likely receptive and compete through visual and vocal displays. The displays include in-air whistles and roars and underwater vocalizations that sound like taps, knocks, pulses and bells. It is thought that these sounds are made to attract females, which choose

A male walrus (*Odobenus rosmarus*) displays scars from territorial battles with other bulls. (Photo by © John Giustina. Bruce Coleman, Inc. Reproduced by permission.)



Walrus (*Odobenus rosmarus*) tusks can reach 3 ft (90 cm) and weigh over 10 lb (4.5 kg). (Photo by Jeff Foott. Bruce Coleman, Inc. Reproduced by permission.)



Male walrus (*Odobenus rosmarus*), Pacific race. (Illustration by Michelle Meneghini)

Despite its large cumbersome appearance, the walrus (*Odobenus rosmarus*) is very agile in the water. (Photo by Len Rue Jr./Photo Researchers, Inc. Reproduced by permission.)

Pacific walruses (*Odobenus rosmarus*) vary in color. When walrus are in cold water, they may appear pale brown or gray. On land, when walrus are warm, they vary from pinkish to darker brown. (Photo by Fransico Erize. Bruce Coleman, Inc. Reproduced by permission.)

among the displaying males, but it is possible that some of the vocalizations also are threats aimed at other males.

Mother walruses, unlike any other pinniped species, nurse their young at sea as well as on land. In some instances the female floats on her back and the calf suckles on top of the female. In others, the female floats vertically in the water and the calf dives underwater, upside down to suckle. Young calves sometimes ride the backs of females while traveling at sea.

Both walrus males and females use their tusks for multiple purposes. They may be displayed as threats to gain a prime position in a resting or molting group or they may strike another with them in a fight. Tusks are useful defensive weapons against predators such as polar bears and killer whales. They may also be used to produce holes in the ice and to assist in hauling out of the water onto the ice. There is no evidence that the tusks are used to dig for food in the bottom substrate.

Digging or rooting for food at the bottom is done with the snout and mustacial vibrissae. Walruses use their tongue and lips to create a suction and suck the soft parts of prey from their hard shells.

Feeding ecology and diet

Walrus calves appear to consume their mother's milk for the first 12–18 months. After that they begin to eat invertebrates as well. Walruses are generally benthic feeders (i.e., feed on organisms in the bottom substrate). The most common food items are bivalve mollusks. However, Pacific walruses have been documented to eat more than 60 genera of marine organisms. Among these organisms are corals, worms, polychaetes, crustaceans (e.g., crabs and shrimp), sea cucumbers, and other seals (e.g., ringed and spotted seals).

Walrus diets vary both seasonally and by region. This is common among other pinnipeds too. Food resources vary with differing habitats and seasons and walruses adapt to these differing conditions. There also appears to be a difference in the diets of male and female walruses. The size of prey in the stomachs of males is more than five times greater than that of females. Although based on a relatively small sample, eating other seals tends to be done more by male walruses than by females.

Reproductive biology

Walruses are long-lived animals and in keeping with such a life history, they do not begin to reproduce for several years.

Males begin to produce sperm around 7–8 years of age, but do not appear to be capable of fertilizing a female until 10–11 years old. They may not actually become competitive socially until as late as 15 years. Females become reproductive at an earlier age than males, as is often the case in mammals. The youngest females to ovulate for the first time are four year olds and most have their first ovulation between 5 and 7 years of age. First ovulations do not always lead to pregnancy, however, so a females first calf might occur slightly later. Walruses that have been studied display a polygynous mating system.

Walruses are unusual among pinnipeds in that they have a gestation that lasts for longer than a year, about 15 months. Like other pinnipeds they produce a single young during a reproductive event. Most females nurse their calf for between two and three years. As a result the interval between births for individual females is about three years. The fat content of walrus milk, based on a few samples, appears to be around 25–32% fat. This is high compared to the fat content of a lot of mammals, but low for seals. The low fat content is probably related to the long lactation period, which requires a slower rate of fattening to sustain a fast before an abrupt weaning period, as is the case with phocids or true seals with short lactation periods.

In most pinnipeds, mating immediately follows the period of births and lactation. The birth and mating periods are separated by several months in the walrus, however. Maximum known longevity in the wild is just over 40 years.

Conservation status

The major recent threat to walruses has been hunting by humans. All subspecies were hunted intensely in the 1700s and 1800s. As noted above, the Atlantic walrus used to occur in the Gulf of St. Lawrence and on Sable Island, but was hunted to extinction at these sites in the 1700s. Walruses are hunted for subsistence by indigenous peoples, but are otherwise protected globally. Threats to this species today are indirect, such as through pollution, possibly competition with fisheries, fisheries bycatch and habitat destruction from bottom fisheries. Pacific walrus recovered better from the intense hunting than did the Atlantic subspecies for unknown reasons. However, in recent years the Pacific walrus population appears to be declining. The reason for this decline is not yet known.

Significance to humans

Indigenous subsistence hunting was done initially to provide food and other materials (e.g. skin for umiak or traditional Eskimo boats, oil for fuel, and tusks for artwork). European hunters took large numbers of walruses for similar reasons, but far in excess of what could reasonably be used. Today walrus meat is eaten little by people but still used to feed dogs. Tusks and bone are still carved for artwork and sold on the world market, but under strict control by international convention.

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Books

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Daryl J. Boness, PhD

True seals

(Phocidae)

Class Mammalia

Order Carnivora

Suborder Pinnipedia

Family Phocidae

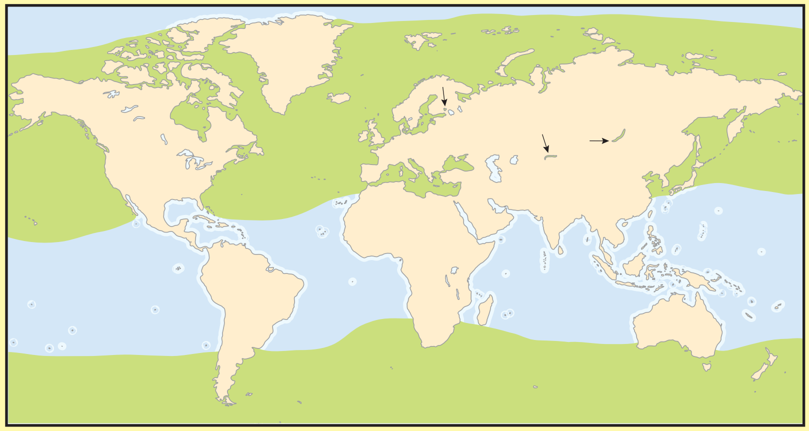
Thumbnail description
Large marine mammals that are fusiform in shape; crawls on its stomach on land or ice using either a caterpillar movement (on land) or swishing its rear end from side to side (on ice); propels itself in water by thrusting rear flippers from side to side, fanning the leading flipper and closing the trailing one; foreflippers are short and not used as rudders much in aquatic or terrestrial movement, other than to push off the ground on land; coloration varies from solid color to mottling or spotted with dark on light background or the reverse

Size
Approximately 3–15 ft (1–5 m); approximately 100–5,700 lb (45–2,600 kg)

Number of genera, species
13 genera; 19 species

Habitat
Shallow and deep marine areas, polynyas (open water within large ice masses), drifting ice floes, and island and mainland beaches (sand, cobble and rock)

Conservation status
Extinct: 1 species; Critically Endangered: 1 species; Endangered: 1 species; Vulnerable: 1 species; Near Threatened: 1 species; Data Deficient: 1 species



Distribution
Circumpolar and occupying temperate latitude waters in the Northern and Southern Hemisphere; subtropical for one species in the Pacific Ocean

Evolution and systematics

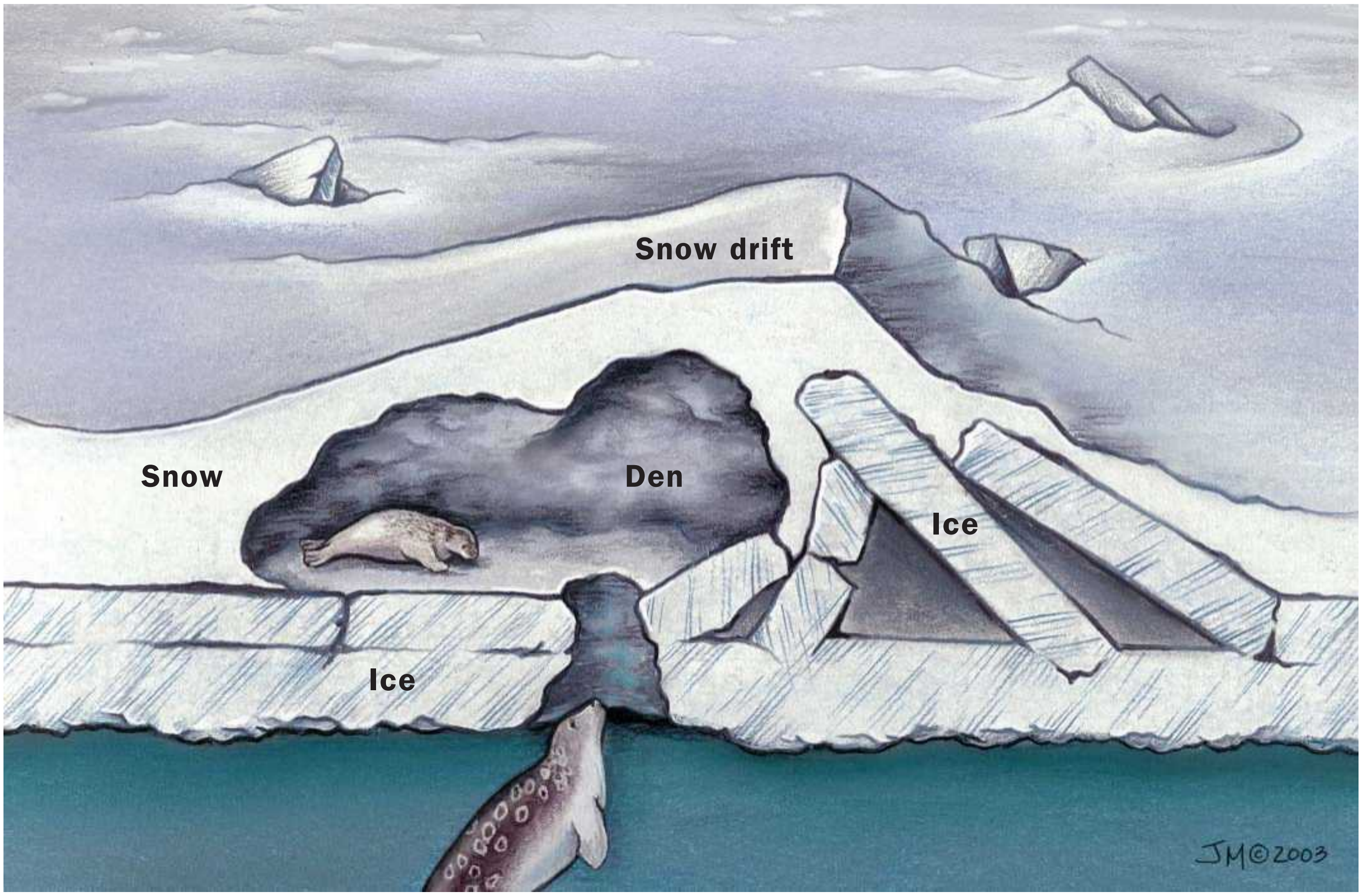
The family Phocidae is the oldest of the modern day pinnipeds, with the oldest fossil phocid reported from the late Oligocene or about 25–30 million years ago. The current phocids originated in the North Atlantic and consists of two subfamilies, the Monachinae and the Phocinae. The Phocinae contains five genera and the Monchinae six genera. The phocids along with the other two families of current pinnipeds, the otariids (fur seals and sea lions) and odobenids (walrus), appear to have evolved from a single lineage of either a bear-like, otter-like, or raccoon-like ancestor. Most evidence points toward bear or otter-like ancestry but there is conflicting evidence.

Physical characteristics

Phocid seals range from moderate to large size. Most are fusiform in shape, but the leopard seal is almost tubular looking, being longer and more slender. All phocids are characterized by having relatively short hair that lies smooth along the body, thick skin and a thick subcutaneous layer of blubber that can be 5–6 in (11–13 cm) thick to insulate the animal and provide energy stores when not foraging. The foreflippers are small while the rear flippers are large and contain webbing between the digits that expands them into paddles, which provide thrust for swimming. All phocids appear to have no neck; the head blends into the trunk of the body. They have no external pinnae (ear), minimizing structures that would produce drag during swimming. Males of some species such as elephant seals (*Mirounga* spp.), hooded seals (*Cystophora cristata*), and gray seals (*Halichoerus grypus*) have enhanced (elongated or inflatable) snouts that are used in competitive social contexts.

Distribution

The majority (14 species) of phocids are found in the Northern Hemisphere although five species occur south of



Female ring seals (*Phoca hispida*) give birth in lairs they create where snow has drifted around a pressure point in the ice. The lairs help hide the pup from polar bears, which prey on ring seals. (Illustration by Jacqueline Mahannah)

the equator. In both hemispheres many species are circumpolar or subpolar, there are a few temperate species, such as gray seals, elephant seals, and harbor seals (*Phoca vitulina*). Three species of monk seals (one of which has gone extinct in the past century) inhabit subtropical or tropical regions of the Pacific, Mediterranean and Caribbean waters. Virtually all major oceans, except the Indian Ocean, contain phocid species. There are even two species found in large inland lakes, the Baikal seal (*Phoca sibirica*) of Lake Baikal in Siberia and two subspecies of ring seal (*Phoca hispida*) found in Lake Ladoga and Lake Saimaa of Russia and Finland, respectively. There may also be a subspecies of harbor seal that inhabits inland lakes in the Ungava Peninsula of Quebec, although it is unclear if these animals are completely isolated.

Habitat

All species forage at sea but use either land or ice to produce their pups, to molt, and to rest. Mating occurs on land in a few species and in the water in most; occasional mating on ice has been seen but usually seals that give birth on ice mate in the water.

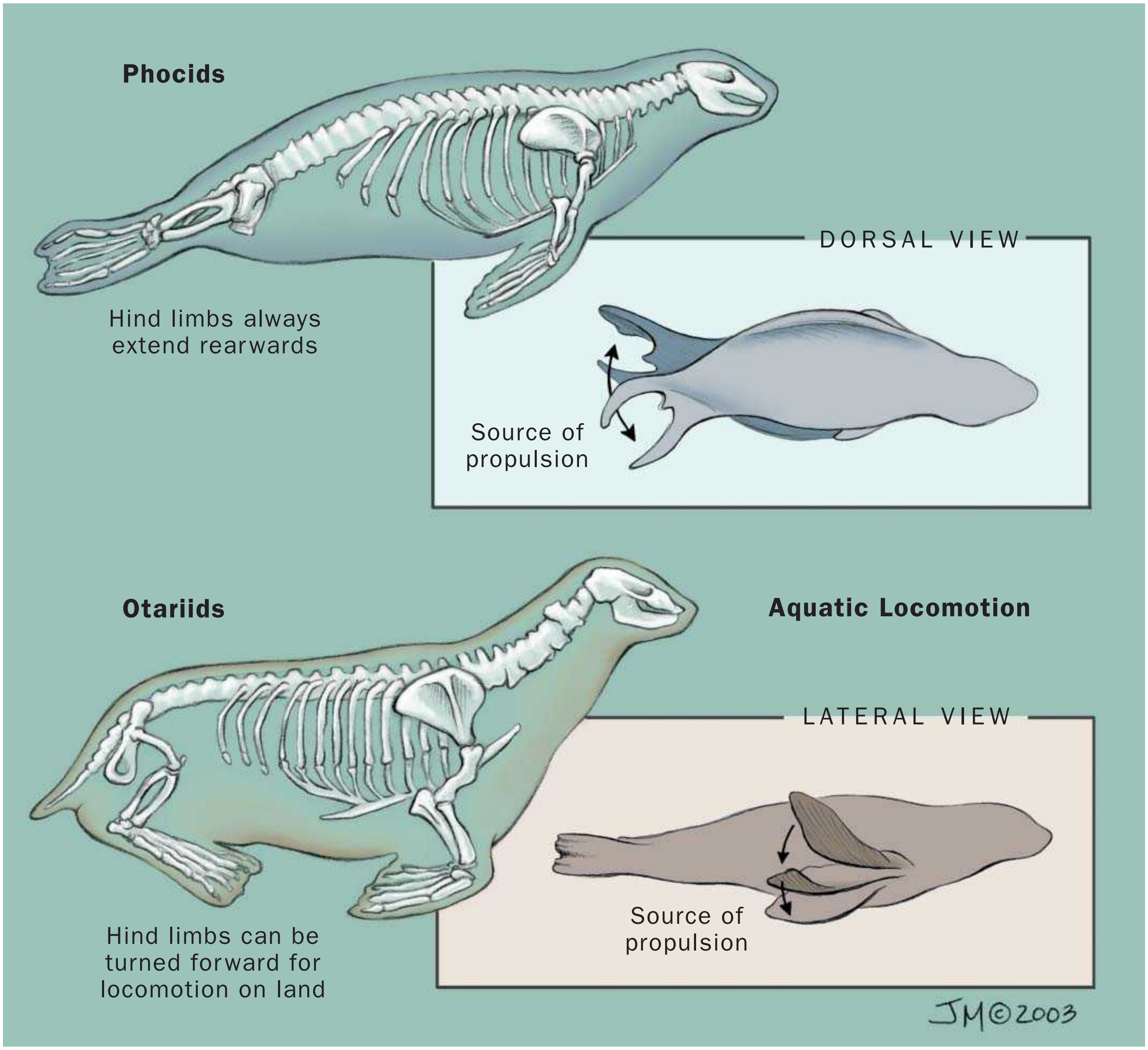
Land habitats used are variable, including sand, cobble and boulder beaches, rocky outcroppings, and caves (gray seals and Mediterranean monk seals [*Monachus monachus*]). Some species like gray and harbor seals may use all or most of these different land habitats as well as ice in some locations.

Ice habitats used by phocids include both floe ice and land fast ice. The former is free floating and the size of ice pans is highly variable. The latter consists of large ice masses affixed to land masses and are usually more stable.

Behavior

Most phocid species are gregarious during an annual molting period, when they haul out on land or ice to shed their hair and acquire a new coat. Many species form colonies during an annual breeding period, with species like elephant seals forming large dense harems of over a hundred females and a few males, all lying in contact with one another, to dispersed male-female pairs of hooded or crab-eater seals (*Lobodon carcinophagus*) a half mile (0.8 km) or more apart on floating ice pans.

Males and females of many species migrate from breeding areas to separate areas used for foraging. In some cases these migrations are associated with seasonal changes in ice patterns. Other species remain in the vicinity of the seasonal breeding areas for feeding or disperse in a more random pattern rather than migrating.



Otariid seals are better adapted to locomotion on land than are phocids. Otariids can rotate their rear flippers underneath their body and "walk" on four flippers. Phocids must crawl on their ventral surface like a caterpillar or swish their rear end from side to side for locomotion on land, likely incurring higher energy costs for movement on land than otariids. While swimming, otariids use their foreflippers in an oar-like fashion, whereas phocids use their rear flippers, thrusting them from side to side for propulsion. (Illustration by Jacqueline Mahannah)

Researchers are only beginning to learn more details about foraging tactics as a result of a few studies that have attached cameras to free-living seals to record the behavior of the seals during foraging. One such study of harbor seals shows that some males use a tactic of digging in the bottom substrate for species that bury themselves in sand while others find and follow schools of fish, picking off individual fish that leave the school and go to the bottom to avoid the seal.

Feeding ecology and diet

There is a strong link between the breeding pattern, body size, and feeding ecology in phocid seals. The relatively large size of phocids allows them to build body stores of fat that fuel breeding without foraging for periods of time (a phenomenon known as capital breeding). Some of the smaller phocids, however, such as the harbor seal, may have to forage some during the breeding period to rear their young successfully because they cannot store enough fat. The ability to store fat and fast during breeding means that foraging grounds can be separated by considerable distances from breeding grounds in these species. Northern elephant seals (*Mirounga angustirostris*), for example, are known to leave breeding and resting areas to travel about 12,000 mi (20,000 km) during two major foraging periods, after breeding and after molting.

A Hawaiian monk seal (*Monachus schauinslandi*) asleep wrapped in vines, showing shark bite scars. (Photo by Frans Lanting/Photo Researchers, Inc. Reproduced by permission.)

The diets of phocid seals may be varied both within and among species, including varying seasonally as food resources change or as the location of seals change seasonally. Crabeater seals, for example, eat krill (small shrimp-like organisms) almost exclusively, whereas leopard seals eat penguins, other seals, fish, krill, squid, octopus, and other invertebrates. Fish of one sort or another is the primary diet of most phocid species.

To obtain the energy-rich food and dense patches of fish, phocids often have to dive to considerable depths. Elephant seals will dive to depths as deep as about 5,000 ft (1,500 m), staying underwater from 20 to 60 minutes while they forage for squid. Other species, like harbor seals in some locations, regularly forage only at depths of 80–200 ft (25–60 m), whereas at other locations may forage more often at about 650–825 ft (200–250 m). The shallower dives are usually much shorter in duration, lasting more in the range of three to five minutes.

Reproductive biology

All phocids have an annual reproductive cycle in which females give birth during a fairly distinct breeding period. They are particularly noted for short lactation periods, lasting from as little as four days in the hooded seal to as long as two to three months in a couple of species. Females become receptive near the end of lactation or shortly thereafter in all species. Females of all species exhibit delayed implantation or embryonic diapause during which the fertilized ovum suspends development and remains in the uterus without implanting. This is thought to help synchronize parturition among females and produce the highly synchronous breeding seasons found in these species.

The short lactation periods of phocids are associated with fasting or feeding little during this time. Also associated with this is the buildup of extensive blubber layers by females to provide the major nutrients to produce milk for the young. Milk fat content is highest in those species with the shortest lactations, as is pup mass gain. Females may lose over 40% of their mass at the beginning of the breeding season and between 60% and 80% of that loss is in the milk transferred to the pup. Males do not participate in the care of offspring in any species.

Males of all phocids fast or feed little during the period when receptive females are available. Consequently, they too build up extensive blubber layers prior to the mating season

A leopard seal (*Hydrurga leptonyx*) slides on the snow in Antartica. (Photo by Tim Davis/Photo Researchers, Inc. Reproduced by permission.)

to fuel the energy-intense competition for access females. Mass loss as a percentage of initial body mass in males, however, is not as great as it is in females. Among several species for which there are such data, the average percentage loss is between 15% and 35% compared to the values given above for females.

Mating patterns in phocids is best known among the three species that mate on land: gray seals and the northern and southern elephant seals. In these cases, the primary mating tactic is one of defending females directly. Recent studies, which use genetic paternity analyses, show that there may be alternative tactics that are more opportunistic but are also

A northern elephant seal (*Mirounga angustirostris*) showing a threat display. (Photo by J & D Bartlett. Bruce Coleman, Inc. Reproduced by permission.)

A harp seal (*Pagophilus groenlandicus*) mother and pup. (Photo by Tom Brakefield. Bruce Coleman, Inc. Reproduced by permission.)

Female harp seal (*Pagophilus groenlandicus*) recognition behavior at the entry hole in the Gulf of St. Lawrence. (Photo by Dan Guravich/Photo Researchers, Inc. Reproduced by permission.)

successful, even if to a lesser degree. For example, gray seal males that defend and mate with females before they depart only fertilize about 22% of them and males that capture and mate with departing females, fertilize about 9% of the females they capture. A few studies of a couple of species that mate at sea suggest that males may be more likely to engage in efforts to attract females by displaying than guarding them directly; such a mating system is known as a lek-type system. Females may actually choose their mates in this system, although the evidence for female choice is not strong for any of these species yet.

Females begin producing a single young each year from four to seven years of age, whereas males become sexually mature a couple of years later than females in many species. Furthermore, males do not become socially competitive for several additional years; they may be 10 years old or more before they succeed in mating. Research seems to indicate that both males and females are potentially reproductively active until they die. There is some evidence in a few species to suggest older females may not perform as well as middle-aged females in rearing fat, healthy pups. The youngest and inexperienced mothers may also perform poorly.

Conservation status

The main factor leading to extinction, endangered, or threatened status of phocids has been hunting pressures from humans within the past century or two. More recently, the Hawaiian monk seal (*Monachus schauinslandi*), which was showing signs of coming back in the mid-1900s, was probably disturbed by military operations on the small islands used for breeding and molting, and produced poor recruitment into the breeding population. Subsequently, signs of environmental regime shifts that have caused a change in carrying capacity may be inhibiting the return of this species. It is currently listed as Endangered. Likewise the Mediterranean monk seal is Critically Endangered, and continuing to decline to near extinction (fewer than 500 seals remaining) despite protection, because of degradation in its environment. Recent disease problems producing mass die-offs can probably be attributed to the poor state of the environment. One species has gone extinct in the past 100 years, the West Indian monk seal (*Monachus tropicalis*). It is the cousin to the other two monk seals. The cause of this extinction was likely hunting pressure. Additionally, the Caspian seal is listed as Vulnerable, and the Baikal seal is listed as Lower Risk/Near Threatened by the IUCN.

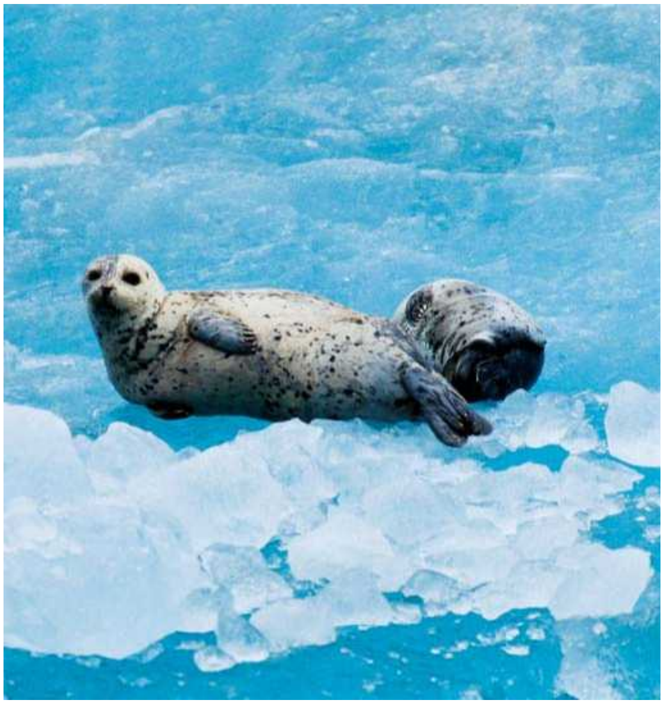
Northern elephant seal (*Mirounga angustirostris*) bulls sparring. (Photo by Tom & Pat Leeson/Photo Researchers, Inc. Reproduced by permission.)

Significance to humans

True seals have been hunted for hundreds of years, serving as a source of food, oil, and hides or furs. In recent years, these products have been boycotted as a result of public pres-

Southern elephant seal (*Mirounga leonina*) mother and pup in the South Orkney Islands. (Photo by D. Larsen. Bruce Coleman, Inc. Reproduced by permission.)

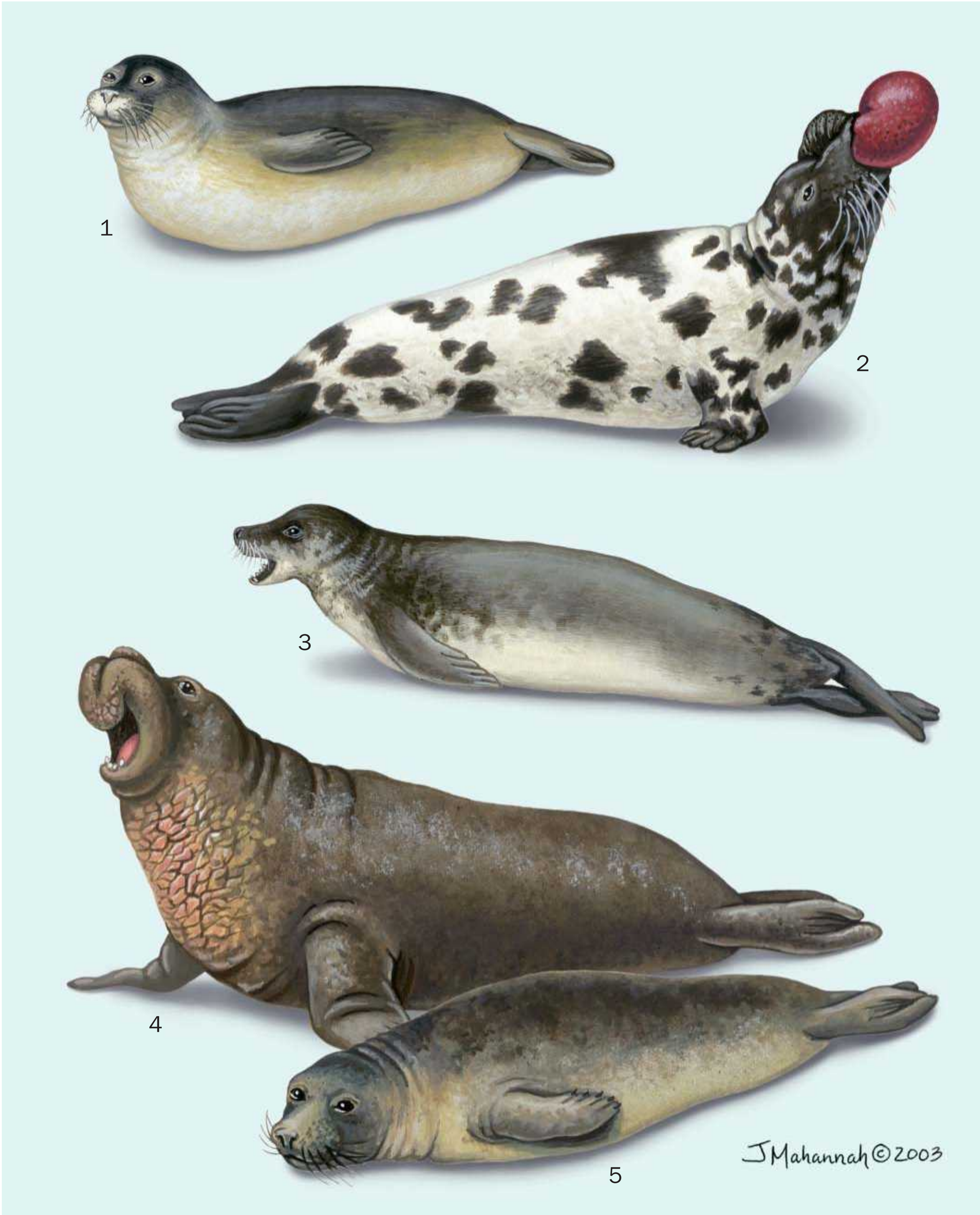
A Weddell seal (*Leptonychotes weddellii*) sleeping on Paulet Island, Antartic Peninsula. (Photo by Rod Planck/Photo Researchers, Inc. Reproduced by permission.)



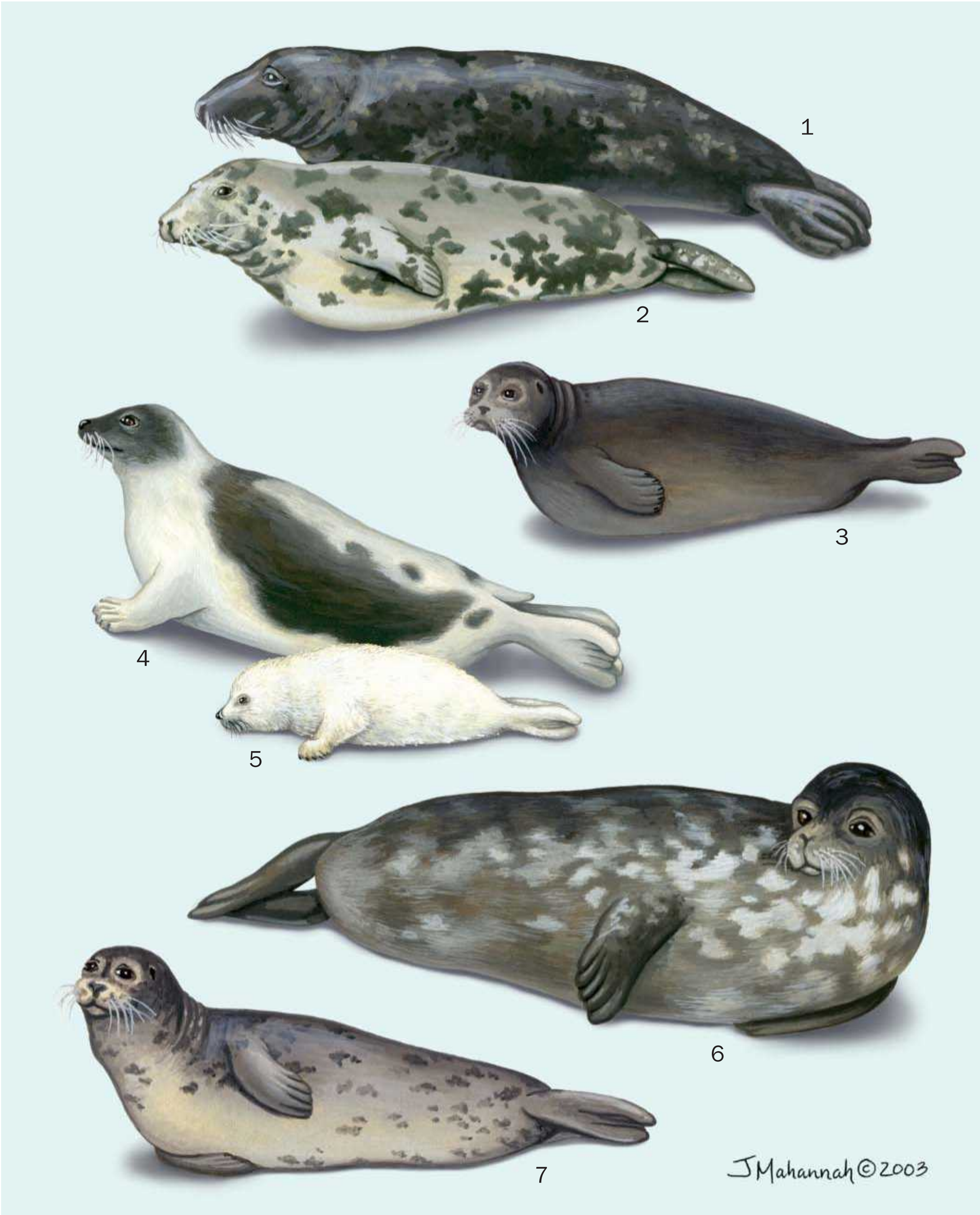
Harbor seal (*Phoca vitulina*) mother and pup resting on an iceberg, South Sawyer Glacier, Alaska, USA. (Photo by John Hyde. Bruce Coleman, Inc. Reproduced by permission.)

A harbor seal (*Phoca vitulina*) basking on land. (Photo by Joe McDonald. Bruce Coleman, Inc. Reproduced by permission.)

sure against clubbing pups, and the market for these items has nearly vanished. Subsistence hunting of some species occurs on a very small scale. Commercial hunting of at least two species, harp and hooded seals, continues annually, but at a very reduced level. These hunts take many fewer pups than in the past and have a small market for the products. One offshoot of the pressure against hunting has been the evolution of a small eco-tourism industry centered on trips to the pack ice during the harp seal breeding season. As these trips are expensive, the industry is likely to remain small for species such as harp seals. However, for species like the northern elephant seal, which now breeds in accessible mainland colonies, controlled nature programs have become successful educational experiences.



1. Hawaiian monk seal (*Monachus schauinslandi*); 2. Male hooded seal (*Cystophora cristata*); 3. Crab-eater seal (*Lobodon carcinophagus*); 4. Male northern elephant seal (*Mirounga angustirostris*); 5. Female northern elephant seal. (Illustration by Jacqueline Mahannah)



1. Male gray seal (*Halichoerus grypus*); 2. Female gray seal (*H. grypus*); 3. Baikal seal (*Phoca sibirica*); 4. Harp seal (*Pagophilus groenlandicus*); 5. Harp seal pup; 6. Weddell seal (*Leptonychotes weddellii*); 7. Harbor seal (*Phoca vitulina*). (Illustration by Jacqueline Mahannah)

Species accounts

Gray seal

Halichoerus grypus

SUBFAMILY

Phocinae

TAXONOMY

Halichoerus grypus (Fabricius, 1791), "Greenland."

OTHER COMMON NAMES

English: Horsehead seal, Atlantic seal, Atlantic gray seal, Baltic gray seal.

PHYSICAL CHARACTERISTICS

Males: 7.1 ft (2.3 m); 595 lb (271 kg); Females: 6.2 ft (2 m); 455 lb (207 kg). Males are noted for their large curved snout, which females do not have. Males generally have a dark pelage (black or charcoal gray) that is sometimes mottled with gray patterns; females generally have lighter gray pelage that is usually mottled with black patterns. Both show considerable variation. Pups are born with white lanugo.

DISTRIBUTION

Eastern and western North Atlantic Ocean, Baltic Sea.

HABITAT

Breed on island beaches (sand, cobble, boulders) and on ice floes. Forage in waters ranging from 124 to 775 ft (40–250 m) deep.

BEHAVIOR

Breed in colonies of varying densities. Ice-breeding colonies are usually less dense. Individuals tend to return to the same breeding colony every year. Large molting groups form on islands during the spring and early summer.

FEEDING ECOLOGY AND DIET

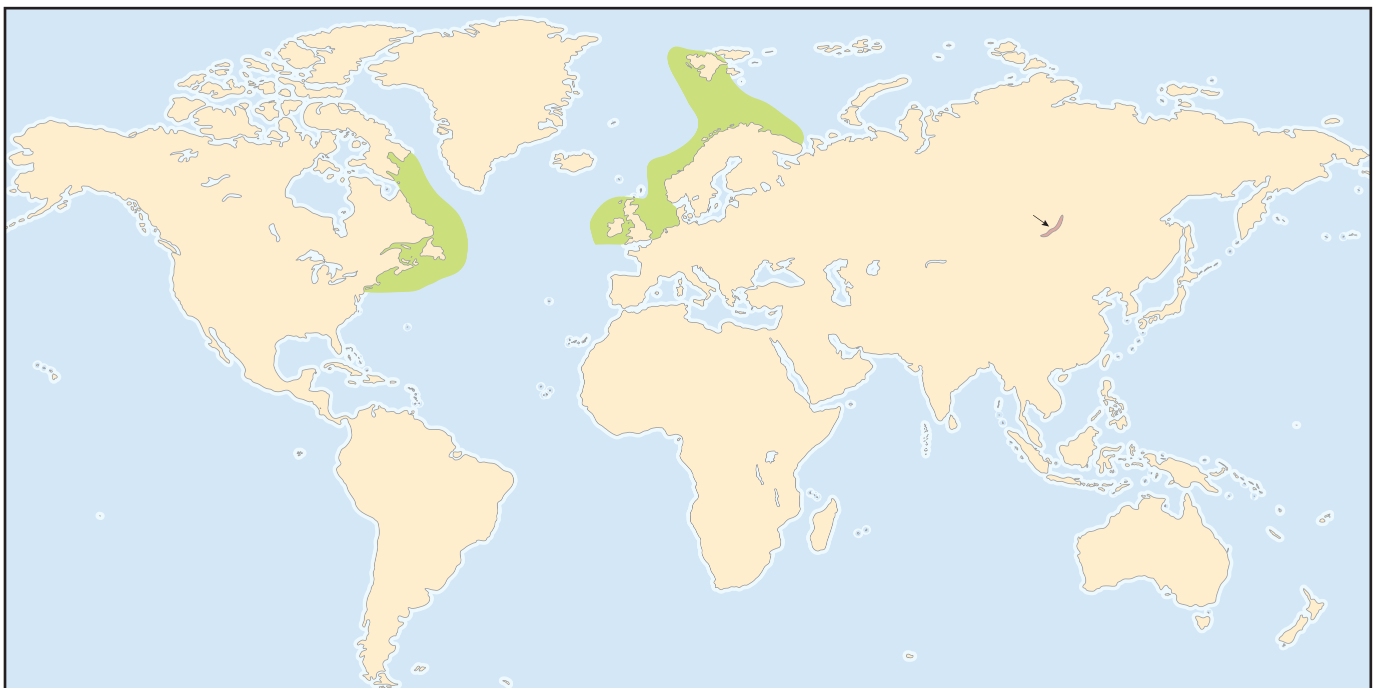
Considerable individual variation in foraging strategy, ranging from migrating to a foraging ground, randomly searching and coming and going from a fixed resting place to a particular foraging patch. Primarily eat fish; the principal species eaten varies by location, but includes cod (*Gadus morhua*), capelin (*Mallotus villosus*), and sand eels (*Ammodytes* spp.).

REPRODUCTIVE BIOLOGY

Males are polygynous with the most successful males defending clusters of females, but other successful tactics involve mating opportunistically with departing females that have already mated. Males do not succeed in mating until age 12–15 years. Females produce a single pup annually beginning at about age four to six years. Lactation lasts about 17 days and pups are fed milk that is about 60% fat.

CONSERVATION STATUS

Not threatened. Populations are protected and growing at substantial rates of greater than 12% annually. In 2002, the largest breeding colony, Sable Island, Nova Scotia, produced 50,000 pups.



Halichoerus grypus

Phoca sibirica

SIGNIFICANCE TO HUMANS
At one time they were hunted for their pelts and blubber (rendered into oil). They are no longer hunted and in some instances have become a nuisance to aquaculture and certain fisheries. ◆

Harbor seal
Phoca vitulina

SUBFAMILY
Phocinae

TAXONOMY
Phoca vitulina Linnaeus, 1758, "in mari Europaeligo."

OTHER COMMON NAMES
English: Common seal, kuril seal, island seal, spotted seal.

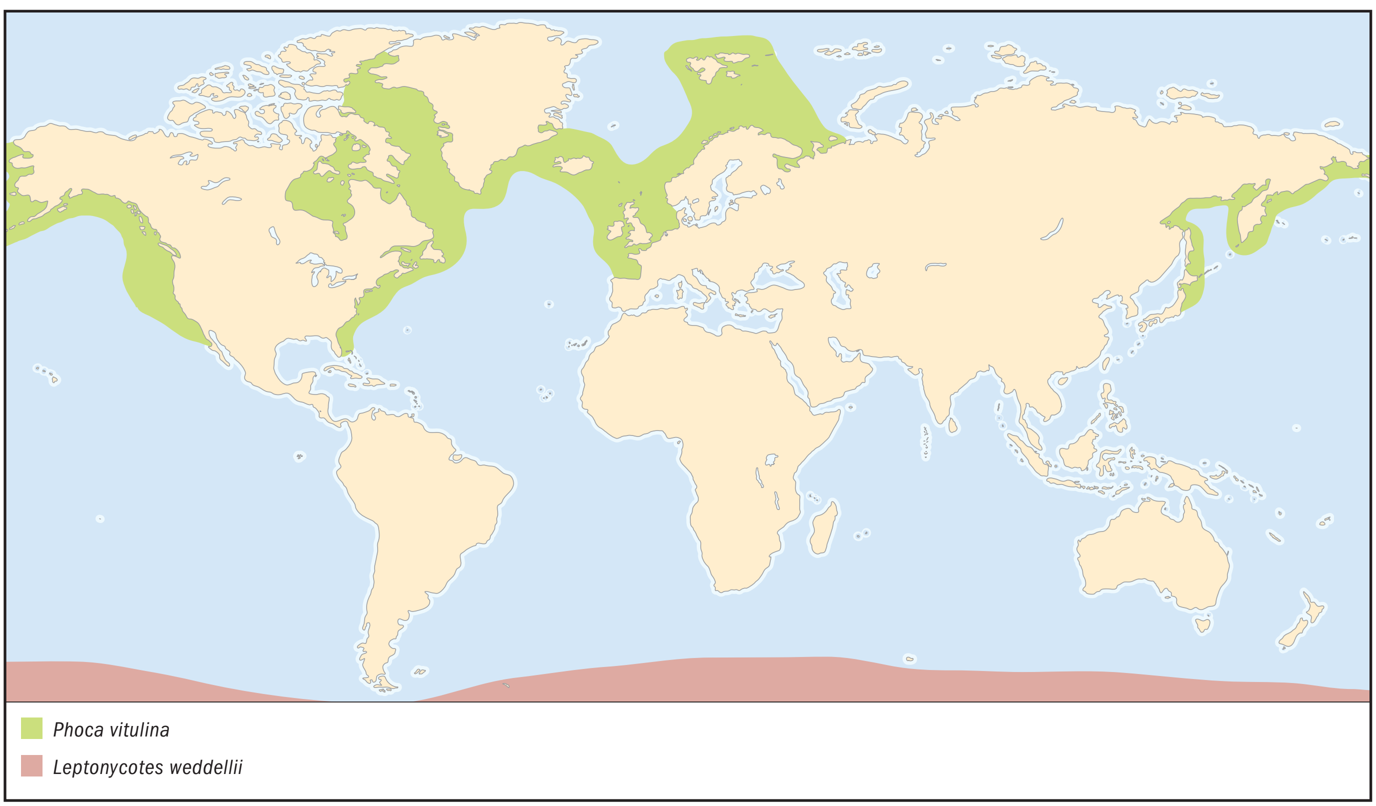
PHYSICAL CHARACTERISTICS
Males: 5.3–6.3 ft (1.6–1.9 m); 194–312 lb (88–142 kg); Females: 4.9–5.6 ft (1.5–1.7 m); 143–235 lb (65–107 kg). There is considerable variation in pelage coloration both within and among the five subspecies of this species; there is no difference between the sexes. The Atlantic subspecies have background color of various shades of gray or cream covered with dark spots. The Pacific subspecies have light and dark variants of coat color. The dark pelage consists of dense black spots, some of which are outlined by a silver ring. The light pelage has a darker upper body but the sides and underbody have a silvery background with dark spots. Most pups are born without a white natal coat, which has been shed in utero. Consequently, they look like miniature adults.

DISTRIBUTION
These seals are found broadly in the Northern Hemisphere in coastal areas of both the east and west Atlantic Ocean and of the east and west Pacific Ocean.

HABITAT
Breed, rest and molt on sand and cobble beaches, rocky islets, sand bars and occasionally ice floes. They may forage in estuaries, along the continental shelf or in deeper waters off the shelf. One population is found in an inland lake.

BEHAVIOR
During the breeding season, males and females with pups form small mixed groups on land in areas traditionally used for pupping. There is no clear organizational structure to these groups. Males spend less time on land at this time than do females with pups. Several weeks after breeding, both sexes haul out to molt. Molting groups may be much larger than the size of groups during breeding. During intensive foraging between breeding and molting, seals disperse to forage rather than migrate to specific forage areas. Harbor seals engage in little in-air vocalizations, but during the mating period males appear to use underwater displays that have visual and vocal components. Females of this species make foraging trips during lactation, similar to those seen in otariid seals.

FEEDING ECOLOGY AND DIET
Foraging patterns and diets of this species are highly variable and depend on local environments. Around Sable Island in Atlantic Canada, foraging is typically at depths of 66–165 ft (20–50 m), whereas in areas of the Pacific it is not uncommon for foraging depths to exceed 330 ft (150 m). The primary food for this species is small to medium size fishes followed by cephalopods (such as squid and octopus). While there may be many species identified as prey items for a given population,



there is usually a couple of species that predominate and this may vary seasonally and inter-annually. At Sable Island, sand eels (*Ammodytes* spp.) predominate. Around the Aleutian Islands in the Pacific, Atka mackerel (*Pleurogrammus monopterygius*) is the main fish eaten. On another level, diets in the Moray Firth of Scotland showed Atlantic cod (*Gadus morhua*) as the main food in January, whereas in June cod was the dominant prey. In January two years later herring (*Clupea harengus*) was the major food.

REPRODUCTIVE BIOLOGY
Mating in this species occurs at sea so it has been difficult to study the mating system. Recent studies using dive recorders, video cameras, hydrophones, and DNA analyses have begun to reveal some information. Males appear to be polygynous, but at a fairly low level (maximum success of fertilizing five females). In some locations, males may defend territories to control access to females and in others males may display (blowing bubbles and vocalizing) from aquatic positions to attract females. Much more research is needed to confirm such patterns. Males produce sperm about three to seven years of age but do not become successful breeders until older, probably at least 10 years of age. Females give birth for the first time from three to seven years of age, and give birth to a single young annually. Lactation is about 24 days and females produce milk averaging 50% fat. As noted above, females do not fast entirely during lactation and begin regular foraging trips to supplement blubber stores to fuel the production of milk during lactation.

CONSERVATION STATUS
This species is not threatened, but several major die-offs have occurred in recent years with thousands of seals dying from diseases not previously known to be a problem. The coastal nature of this species makes them particularly vulnerable to human-induced impacts such as pollution.

SIGNIFICANCE TO HUMANS
There are small amounts of subsistence hunting of these seals for food and hides, but the species is of no major significance to humans. ◆

Harp seal
Pagophilus groenlandicus

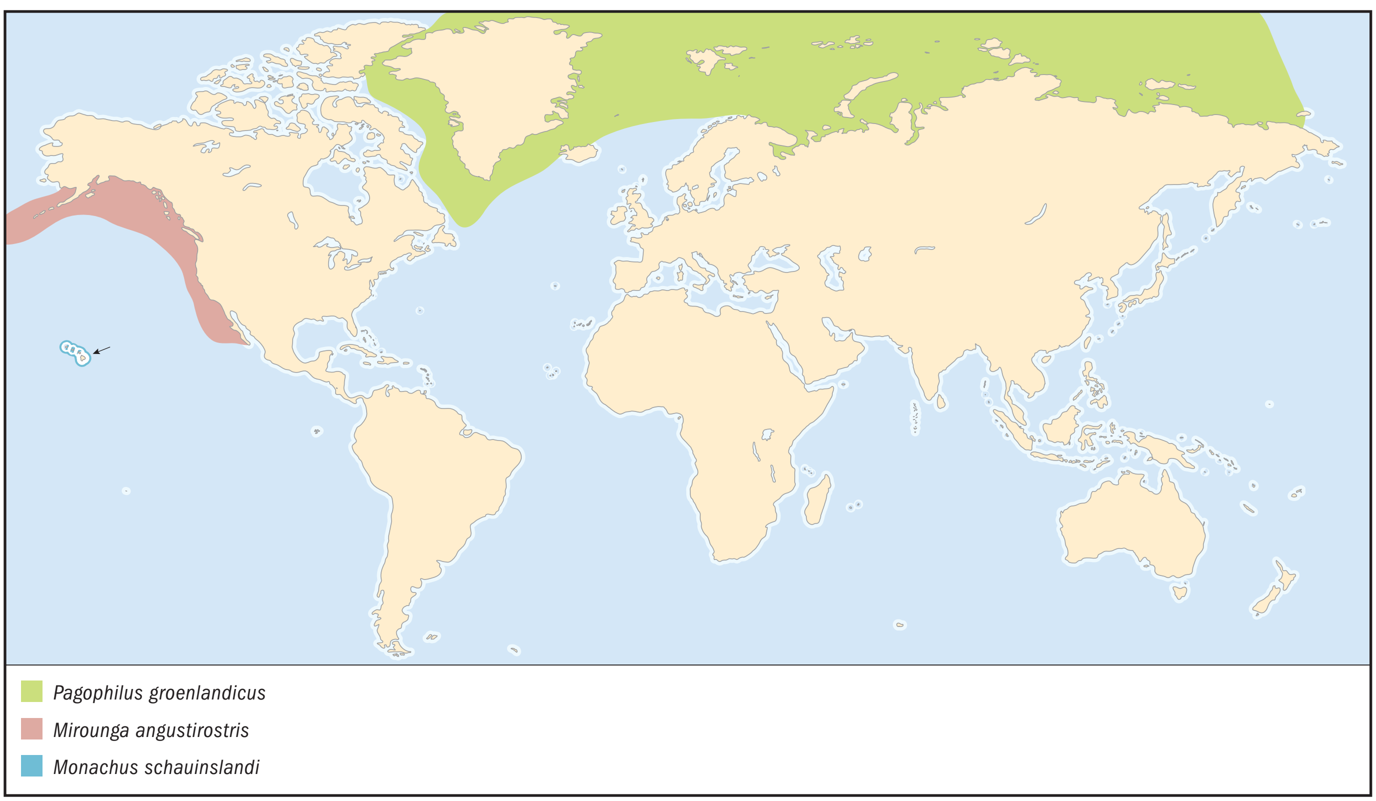
SUBFAMILY
Phocinae

TAXONOMY
Pagophilus groenlandicus (Erxleben, 1777), "in Groenlandiaet Newfoundland."

OTHER COMMON NAMES
English: Fjord seal, jar seal; Eskimo: Natchik.

PHYSICAL CHARACTERISTICS
Males: 5.6 ft (1.7 m); 297 lb (135 kg); Females: 5.6 ft (1.7 m); 240 lb (109 kg). Young adults of both sexes have a silvery gray coat with dark spots. Older adult males have basic pelage that is cream color over which is a black face to the top of the head and a matching harp or saddle pattern of black running along each side. Older females have a similar pattern but the harp pattern and face may not be as dark and sometimes it is broken into smaller patterns. Pups are born with a white natal coat.

DISTRIBUTION
There are three major breeding areas, one off the coast of northeastern Canada, another off the east coast of Greenland, and the third in the White Sea off the northwest coast of Russia. Outside of the breeding season seals may be found mainly in subarctic areas of the North Atlantic Ocean.



HABITAT
Breed on ice floes and remain in association with pack ice for resting and molting. They forage in open water or under the ice. Their ice-breeding habit makes this species particularly prone to polar bear predation during breeding.

BEHAVIOR
Females form large aggregations on floating ice during the breeding season but are not densely clumped like in some species. Males spend little time on the ice during this time. After the breeding period, both sexes haul out in groups on the ice to molt. After molting, seals migrate northward with the recession of the ice to areas where they forage intensively, having foraged little during breeding and molting. In-air vocalizations are relatively uncommon although females will give shrill calls when another animal approaches their pup too closely. Underwater around the breeding grounds there is a cacophony of sounds, most likely emanating from males although it is difficult to identify who is doing the vocalizing. Weaned pups remain on the ice and fast for several weeks before they depart to begin foraging.

FEEDING ECOLOGY AND DIET
Diets of this species have been extensively studied from stomach samples of shot seals, but only recently have dive recorders been used to determine at what depth seals feed. Moreover these data are only available during the breeding season, which may be expected to be different than at other times. During this period, seals are moderate divers potentially foraging at depths averaging 100 ft (30 m) and reaching a maximum of 300 ft (90 m). These dives typically last about four minutes, but may last as long as 13 minutes. The diet is broad and known to vary seasonally. Nearly 70 species of fish and 70 species of invertebrates have been found in the stomachs of these seals. The most predominant species are capelin (*Mallosus villosus*), and Arctic (*Boreogadus saida*), and polar cod (*Arctogadus glacialis*).

REPRODUCTIVE BIOLOGY
The mating system is poorly studied in this species. Males are believed to be polygynous, but whether they defend positions, territories, or females directly, or display to attract females is unclear. Mating occurs in the water. Males produce sperm about four to five years of age, although may not become successful breeders until older. Females give birth for the first time from four to seven years of age, and give birth to a single young annually. Lactation is about 12 days during which females produce a milk averaging 48% fat.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
These seals are hunted for meat, fur, and oil on a small scale. Also a small eco-tourism industry has evolved out of the efforts to replace the lost economy from boycotts of seal products resulting from hunting. ◆

Baikal seal
Phoca sibirica

SUBFAMILY
Phocinae

TAXONOMY
Phoca sibirica Gmelin, 1788, Lake Baikal.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Length 3.4–4.3 ft (1.1–1.4 m); weight 100–285 lb (45–130 kg); pelage is silver gray on back and yellowish white on the belly. Pups are born with a white natal coat.

DISTRIBUTION
Lake Baikal, Siberia.

HABITAT
This species is unusual in that it is one of two known to inhabit freshwater (or brackish water) exclusively. It uses ice lairs or dens in the fast ice to breed and haul out on to molt in the spring. Baikal seals haul out on lake shore or rocky outcroppings to rest in the summer.

BEHAVIOR
Seals are dispersed during breeding, occupying birth lairs that occur where ice hummocks form. Resting and molting groups form after breeding. These groups may contain several hundred seals.

FEEDING ECOLOGY AND DIET
There are no other mammalian carnivores with which this seal competes for food and are capable of eating most fish species available except perhaps a large sturgeon (*Acipenser baeri*). The four main fish species in the diet are the greater golomyanka (*Comephorus baicalensis*), the lesser golmyanka (*C. dybowskii*), the Baikal yellow fin sculpin (*Cottocomephorus grewingki*), and the longfin sculpin (*C. comephoroides*). The diets are more variable in the summer than in the fall.

REPRODUCTIVE BIOLOGY
Males are thought to be polygynous but little detailed information is available because mating occurs underwater or in breeding lairs. Male wounds are uncommon compared to other species where males compete aggressively for females. Males produce sperm by seven years of age but by what age they are socially active is not known. Females begin to produce pups at five to six years of age and continue until about 30 years of age. They give birth to a single young annually. Lactation is imprecisely known, being reported to last from between 1.5 to 2.5 months.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN.

SIGNIFICANCE TO HUMANS
Hunted for subsistence but of no major significance. ◆

Weddell seal
Leptonychotes weddellii

SUBFAMILY
Monachinae

TAXONOMY
Leptonychotes weddellii (Lesson, 1826), South Orkney Island.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Males: 8.0 ft (2.4 m); 748 lb (340 kg); Females: 8.3 ft (2.5 m); 836 lb (380 kg). Pelage of both sexes is usually black with grayish silver streaks. Pups are born with a grayish natal coat that has a darker stripe on top of the back.

DISTRIBUTION
Circumpolar around Antarctica.

HABITAT
Inhabits fast ice exclusively although individual animals may occasionally be seen on island beaches.

BEHAVIOR
Breed in colonies where both males and females spend time on the ice and in the water, although younger males are usually not tolerated on the ice with females. Females take their pups into the water within two weeks of birth. Males fight under water and give loud trilling vocalizations that may be advertisements to females or other males. There is not a routine migration from breeding sites. Seasonal movement usually follows the expansion and recession of the ice.

FEEDING ECOLOGY AND DIET
Data from dive recorders show that seals dive to depths of 1,150–1,480 ft (350–450 m) in the spring and early summer but to shallower depths 164–660 ft (50–200 m) in late summer, suggesting possible seasonal changes in diets. Their diet is broad, consisting of fish, cephalopods (squid and octopus), krill (*Euphausa superba*), and other invertebrates. Consistent with seasonal changes in dive profiles, one study found bottom and near bottom species in spring stomach samples collected and mid-water species in later summer.

REPRODUCTIVE BIOLOGY
Males are polygynous and defend positions in the water where there are traditional openings in the ice every year. These positions may be exclusive territories, but data are not sufficient to be conclusive. Mating occurs in the water. Males produce sperm about three to six years but do not become successful breeders until older. Females give birth for the first time from three to seven years of age. They give birth to a single pup annually. Lactation is about 58 days and females produce a milk averaging 48% fat.

CONSERVATION STATUS
Not threatened, but are protected by the international Antarctic Treaty.

SIGNIFICANCE TO HUMANS
These seals are of not particular value to humans. ◆

Northern elephant seal
Mirounga angustirostris

SUBFAMILY
Monachinae

TAXONOMY
Mirounga angustirostris (Gill, 1866), California.

OTHER COMMON NAMES
English: Northern sea elephant.

PHYSICAL CHARACTERISTICS
Males: 13.2 ft (4.0 m); 3,750 lb (1,704 kg); Females: 10.6 ft (3.2 m); 1,122 lb (510 kg). Males differ from females in that they have an enlarged proboscis and more highly developed neck with thickened skin than females. The pelage of males is dark gray upper and lighter gray under; females are browner than males and darker. Pups are born with a near black natal coat.

DISTRIBUTION
The breeding range is from northern California to the Baja Peninsula in Mexico. During foraging periods, seals migrate north as far as the Gulf of Alaska and the Aleutian Islands.

HABITAT
Breed and molt on mainland and island beaches of sand and cobble. Forage in deep ocean waters.

BEHAVIOR
Breed in dense colonies where both males and females show strong site fidelity from one season to the next. Males make a distinct vocalization during breeding using the proboscis as a resonating chamber. These calls have dialects for different locations. Animals migrate after breeding to foraging areas and return to the breeding location to molt. After the molt, animals again migrate, making a double roundtrip of over 6,000 miles (10,000 km) each.

FEEDING ECOLOGY AND DIET
Males and females forage in different locations and in different ways. Male go further away from breeding grounds and forage at shallower depths on average than females, and males forage on the edge of the continental shelf, whereas females forage more in open ocean. By two years of age, young seals show similar patterns to adults. Feed mostly on cephalopods (such as squid and octopus) and Pacific whiting fish. The diving pattern of these seals is remarkable. They dive continuously for weeks remaining underwater for 30–120 minutes and going to depths as deep as about 5,000 ft (1,500 m), averaging about 1,650 ft (500 m) for females and 1,090 ft (330 m) for males.

REPRODUCTIVE BIOLOGY
Males are polygynous and in most areas defend harems or large groups of densely packed females. Mating occurs on land and females often mate with males other than the harem master as they leave for sea. Males produce sperm about five years of age but do not become successful breeders until 10 to 12 years. Successful males may only breed for two to four years before they are displaced. Females give birth for the first time from three to seven years of age. They give birth to a single young annually. Lactation is about 27 days and females produce a milk averaging 54% fat.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
These seals are of no particular value to humans other than as an educational experience. Their approachability and close proximity to urban areas allow for controlled visits to learn about their biology and natural history. ◆

Hawaiian monk seal
Monachus schauinslandi

SUBFAMILY
Monachinae

TAXONOMY
Monachus schauinslandi Matschie, 1905, Laysan Island, United States.

OTHER COMMON NAMES
Spanish: Foca fraile de Hawaii.

PHYSICAL CHARACTERISTICS
Males: 6.9 ft (2.1 m); 385 lb (175 kg); Females: 7.5 ft (2.3 m); 528 lb (270 kg). Males and females are similarly colored slate gray on the upper part of their body and a light silvery gray below. Pups are born with a black natal coat.

DISTRIBUTION
This species occurs only in the Hawaiian Archipelago. Its current distribution is mainly at a chain of small, remote islands known as the northwestern Hawaiian Islands, although it has recently begun to re-inhabit the main Hawaiian Islands in small numbers. In the past, they may have occupied islands outside the Hawaiian Archipelago such as Johnston Atoll, Wake Island, and Palmyra Atoll.

HABITAT
The small islands and atolls used by monk seals for breeding, molting and resting are made up of coral sand. The parts of islands used for breeding usually have a shallow coral shelf where females and pups can cool off during the peak heat of the day and be afforded protection from large sharks that prey upon the pups. Foraging habitat appears to be primarily among the coral reef habitat although some areas of open ocean off the shelf may also be used.

BEHAVIOR
During the breeding season females haul out on islands, remaining close to the water and tend to be evenly dispersed rather than clustered. Males spend little time hauled out on these beaches with females, but periodically visit them to check their reproductive status. During molting, males and females tend to be more aggregated on land than during breeding. Seals do not migrate from their breeding or molting beaches to forage. They forage in or near the atolls or islands where they rest, molt, and breed. The subtropical latitude inhabited by monk seals requires spending time in the water daily to keep cool. As a result, few animals are hauled out during the middle part of the day when temperatures and solar radiation are at their highest levels.

FEEDING ECOLOGY AND DIET
The monk seal diet is varied and differs among the islands and the different age groups of seals. Over 40 species have been recorded from scats. The most common type of food is marine eels (Congridae, Muraenidae, and Ophicthidae), and various reef fishes such as wrass (Labridae), squirrelfish and soldierfish (Holocentridae), and triggerfish (Balistidae). Much smaller amounts of squid, octopus and lobster were also found. Recent studies using a video camera attached to a small number of free-ranging seals showed most foraging to occur at or near the bottom, and provided images of seals turning over rocks and debris on the bottom. From these camera studies and studies using dive recorders, the depths at which foraging occurs is highly variable. For some individuals it may be well under 330 ft (100 m) and for others it may be in excess of 495–990 ft (150–300 m). This is an area of study needing further effort.

REPRODUCTIVE BIOLOGY
Males are believed to be polygynous, however, mating is seen infrequently because it occurs in the water. Some evidence suggests that individual males may follow individual receptive females at sea for a period of time until mating with them, a tactic known as roving or scramble competition. More studies are necessary to gain a better understanding of mating tactics and success. The age at which males produce sperm is not well known. Females give birth for the first time from about five to six years of age. They give birth to a single young annually. Lactation is about 44 days but the milk's fat content is not known in this species. A highly unusual pattern of switching of pups occurs frequently in this species. As many as 87% of the females in a colony will switch pups during the breeding season at least once following fights between females. The reasons for this behavior are unclear, although higher-density colonies have higher rates of switching. The behavior does not appear to effect pup survival. The breeding season of monk seals is much more extended than in most other phocids, lasting six months or more.

CONSERVATION STATUS
This species is Endangered. For the past decade, the population has hovered around 1,500 seals. It is likely to decline dramatically over the next decade because of a lack of young cohorts being recruited into the breeding population. As older breeding animals die there will be few new ones at many of the colonies. Past declines may have been related to human disturbance by military installations on some of the islands, but those have been controlled or removed for some years, yet the population fails to expand. Major environmental changes, called regime shifts, may have affected the capacity of the environment to provide adequate food for this species. There may also be indirect effects from humans, too; entanglement in discard nets are known to kill monk seals and poor fisheries management (e.g., lobsters) may have helped to diminish monk seal food resources.

SIGNIFICANCE TO HUMANS
In recent times monk seals have been of no significance to humans. A current problem is arising with the increased use of the main Hawaiian Islands by monk seals. They are hauling out on major tourist beaches, and their protective status as an endangered species has resulted in the closure or restriction of the use of these beaches. Managing such situations presents a challenge so as to not turn the public against this fragile species, which could easily become extinct before the end of this century. ◆

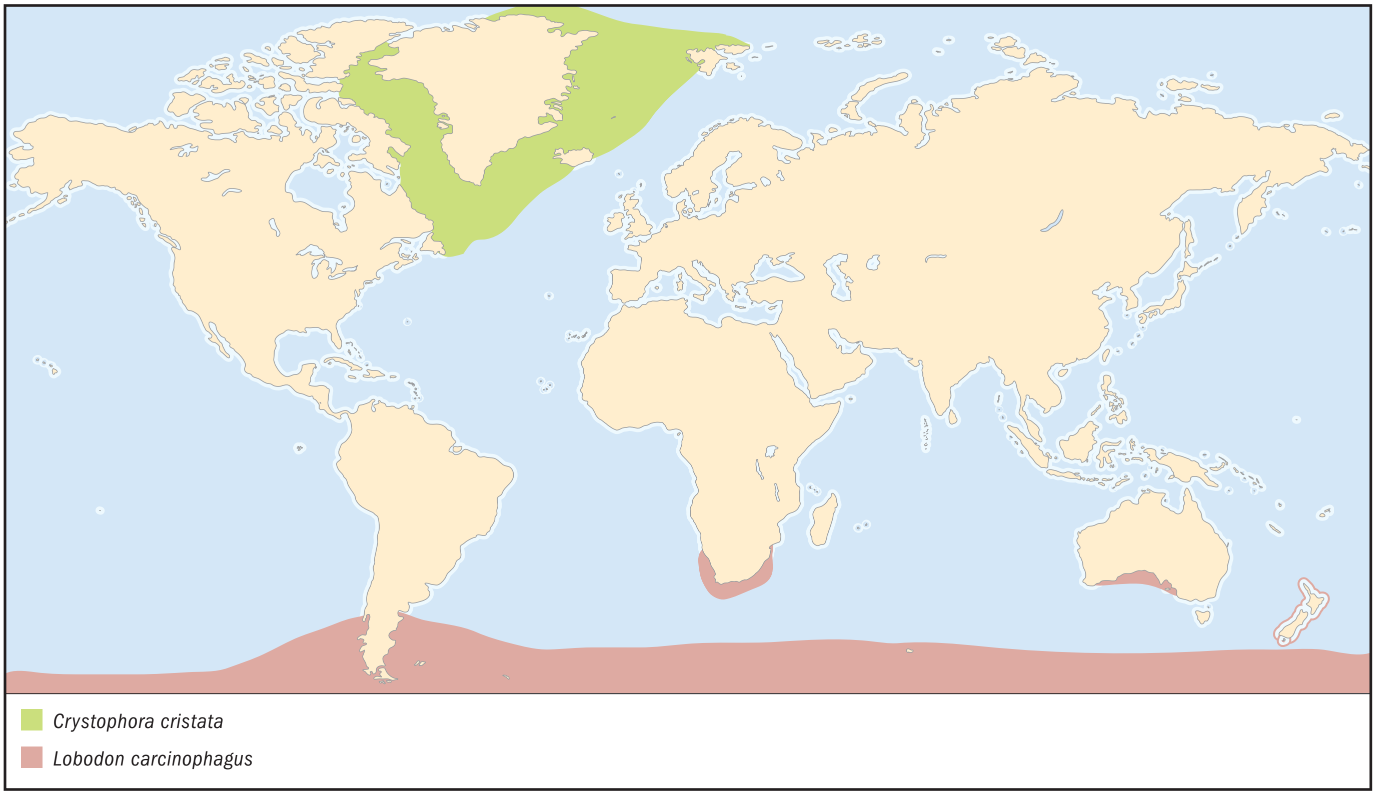
Hooded seal
Cystophora cristata

SUBFAMILY
Monachinae

TAXONOMY
Cystophora cristata (Erxleben, 1777), south Greenland and Newfoundland.

OTHER COMMON NAMES
English: Bladdernose seal.

PHYSICAL CHARACTERISTICS
Males: 8.3 ft (2.5 m); 660 lb (300 kg); Females: 7.3 ft (2.2 m); 440 lb (200 kg). Males and females have similar pelage that is a gray background with black patches. Pups are born with a coat that is blue-gray above and creamy color below. It is not the natal coat as found in most other phocids. The real natal coat in this species is shed in utero. The name hooded seal is derived from the enlarged naval cavity of adult males that can be inflated into a hood. The nasal septum membrane of males can also be inflated and extruded into a balloon-like structure. Females do not have these structures and the structures are not adequately developed in young males to be inflated.



DISTRIBUTION
There are four major breeding areas: two on ice off northeastern Canada (the Gulf of St. Lawrence and off Newfoundland/Labrador) and two on ice around Greenland (off the west coast and off the east coast). Molting occurs primarily on ice off the east coast of Greenland and near Iceland in the Denmark Strait. Foraging areas range from Labrador, around Greenland and Iceland to Spitsbergen.

HABITAT
Breed on ice floes and remain in association with pack ice for resting and molting. They forage in open water along the ice edge. Their ice-breeding habit makes them particularly prone to polar bear predation during breeding.

BEHAVIOR
Females are highly dispersed on floating ice during the breeding season, although occasionally two or three females may be within 100 ft (30 m) of one another. Males spend brief periods of time on the ice during this time. After the breeding period, both sexes migrate, probably feeding as they travel, to traditional areas where they haul out in groups on the ice to molt. Following molting, seals disperse to feed, moving with the recession of the ice to forage along the ice edge. Weaned pups remain on the ice fasting for several weeks before they depart to begin foraging.

FEEDING ECOLOGY AND DIET
Little information on diet is available but these seals are known to forage on fish and squid in deep water. They typically dive to depths of 330–1,980 ft (100–600 m), remaining underwater for more than 50 minutes. They have been known to forage at depths of over a 3,300 ft (1,000 m) and remain underwater for over an hour. Among the fish species in their diet are redfish (*Sebastes* spp.), (capelin *Mallotus villosus*), herring (*Clupea harengus*), Arctic cod (*Boreogadus saida*), and Atlantic cod (*Gadus morhua*).

REPRODUCTIVE BIOLOGY
Males are polygynous, with successful individuals moving from female to female and fighting with other males to maintain access to a female until she is mated. Through this sequential defense of females, an individual male may succeed in mating with as many as eight or more females during the short two-week mating period. This competition among males and mating occurs mostly in the water. Males produce sperm about four to six years of age, but do not become successful breeders until older. Females give birth for the first time from four to nine years of age. They give birth to a single young annually and have the shortest lactation known for any mammal. Pups are nursed for only four days before being weaned abruptly. Females produce a milk averaging 61% fat, allowing pups to gain 15.5 lbs (7 kg) per day and more than double their mass before being weaned.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
These seals are hunted for meat, fur, and oil on a small scale. ◆

Crab-eater seal
Lobodon carcinophagus

SUBFAMILY
Monachinae

TAXONOMY
Phoca carcinophaga (Hombron and Jaquinot, 1842), Scotia Sea (midway between South Orkney and South Sandwich Islands).

OTHER COMMON NAMES
English: White seal.

PHYSICAL CHARACTERISTICS
Males and females are similar in size: 7.6 ft (2.3 m); 490 lb (223 kg). Adult pelage is silvery with patches of brown on the upper body and leading edges of the foreflipper. The pelage fades to a creamy white before the next molt. Pups are born with a light brown natal coat. Body shape is less fusiform and more tubular.

DISTRIBUTION
Circumpolar among the floe ice in the Southern Hemisphere.

HABITAT
Remain among the pack ice for breeding, molting, and foraging.

BEHAVIOR
Females with pups and males are dispersed as trios during the breeding period. Large groups of seals are not seen even during the molting period in January, although the numbers of seals seen in an area increases during this period. Little is known about the behavior of this species because of their dispersed distribution in the pack ice. They are migratory by virtue of moving with the seasonal changes in the distribution of the ice.

FEEDING ECOLOGY AND DIET
These seals are specialized in their diet, feeding almost exclusively on Antarctic krill *Euphausa superba*, and do not change their diet seasonally. About 5% of their diet consists of fish and squid species. Most foraging is done at night, when the vertically migrating krill are at shallower depths. Only a few seals have been outfitted with dive recorders and these animals typically dived to less than 165 ft (50 m) with a maximum depth of about 2,750 ft (530 m).

REPRODUCTIVE BIOLOGY
Males may be polygynous but studies following known individuals have not been done, nor have DNA analyses examined paternities. Males do guard females, following the females as they wean their pup. To what extent males sequentially guard different females as in hooded seals needs to be determined. Males produce sperm about two to six years of age and may not become successful breeders until much later. Females give birth for the first time from three to seven years of age. They give birth to a single young annually. Good data on lactation length are not available nor have analyses of milk composition been done.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Bearded seal *Erignathus barbaus* Spanish: Foca barbuda	Both sexes are gray with a brownish or reddish tinge on head. Prominent, bushy moustache. Adult total length 98 in (250 cm), weight 551–717 lb (250–325 kg).	Prefers shallow waters near coasts that are free of fast ice in winter, gravel beaches, and ice floes that are not too far out to sea. Advances and retreats each winter and summer as ice pack moves. Solitary, except during mating seasons.	Along coasts and ice floes in Arctic Ocean and adjoining seas, as far south as the Sea of Okhotsk, Hokkaido, Hudson Bay, and the Gulf of St. Lawrence.	Bottom-living animals, such as shrimp, crabs, holothurians, clams, welks, snails, octopus, and bottom fishes, such as sculpin, flounder, and polar cod.	Not threatened
Leopard seal *Hydrurga leptonyx* Spanish: Leopardo marino	Gray dorsal parts, very light gray ventral parts. Black, dark gray, and light gray spots on throat, shoulders, sides. Long, slim body, large head, wide gape. Adult male head and body length 118–122 in (300–310 cm), weight 595 lb (270 kg).	Outer fringes of ice pack. Migratory and ranges widely to most subantarctic islands in winter. Solitary, but groups of up to 250 individuals found in some areas.	Waters around Antarctica and most subantarctic islands, as well as southern Australia, New Zealand, the Cook Islands, southern South America, and South Africa.	Penguins, seals, krill, and the crab-eater seal.	Not threatened
Southern elephant seal *Mirounga leonina* German: Südlichen See-Elefanten; Spanish: Elefante marino antártico	Males dark gray, but grayish brown after molting. Females are darker and browner than males. Both have large, trunk-like proboscis. Usually scarring in neck region from fighting. Adult male length 217–236 in (550–600 cm), weight up to 8,160 lb (3,700 kg). Females smaller, length 122–146 in (310–370 cm), weight 1,984 lb (900 kg).	Breeds on islands, usually on beaches or in rookeries. Social hierarchy exists among bulls. Each female bears a single pup. Relatively short lived.	Most subantarctic islands, coast of southern Argentina, waters south to the edge of Antarctic ice at 78°S, occasionally as far north as Saint Helena and Mauritius.	Consists of deep-water, bottom-dwelling marine life, including ratfish, swellsharks, spiny dogfish, cusk-eels, various species of rockfish, and squid.	Not threatened
Mediterranean monk seal *Monachus monachus* French: Phoque moine de la Méditerrané; Spanish: Foca del Mediterráneo	Chocolate brown dorsally, gray ventrally. Sometimes there is a centrally placed white patch. Largest of *Monachus* species. Total length 118 in (300 cm).	Usually found on sandy beaches and in shoreline vegetation. Found on archipelagos coastline, and/or cliff-bound mainland coastlines. Not migratory, pups born between September and October. Diurnal.	Mediterranean and Black Seas, Atlantic coast of Morocco and western Sahara, Madeira and Canary Islands.	Consists of wide variety of fish and invertebrates, including eels, octopus, and lobsters.	Critically Endangered
West Indian monk seal *Monachus tropicalis* English: Caribbean monk seal; Spanish: Foca del Caribe	Grayish brown on back side, yellowish white on ventral side. Average length 79 in (200 cm).	Usually found on sandy beaches and in shoreline vegetation. Found on archipelagos coastline, and/or cliff-bound mainland coastlines. Not migratory, pups born between September and October. Diurnal.	Originally found throughout the West Indies and along coasts of Florida, United States, Yucatán, Mexico, and eastern Central America.	Mainly fish.	Extinct
Ross seal *Ommatophoca rossii* Spanish: Elefantos marinos	Large, plump body with short, wide head. Coloration is dark gray, darker along middle of back, ventral area is whitish. Large flippers, rather small mouth, protruding eyes. Average male length 79 in (200 cm), average male weight 375 lb (170 kg).	Prefers heavy consolidated ice pack around the edge of the Antarctic continent. Solitary, nonmigratory. Nothing known about reproductive habits.	Pack ice of the Antarctic.	Mainly cephalopods, but also krill and fish.	Not threatened
Ring seal *Phoca hispida* Spanish: Foca anillada	Belly is gray, dorsal side is pale gray with dark spots surrounded by pale colored rings. Females are usually slightly smaller. Average length 55–59 in (140–150 cm), weight 143–209 lb (65–95 kg).	Found on seasonally shifting ice packs and on fast ice around the arctic region. Maintains breathing holes by abrading ice with claws.	Palearctic and Nearctic in the Arctic Ocean.	Consists of saffron cod, various shrimps, hypeni amphipods, and euphausiids.	Not threatened
Caspian seal *Phoca caspica* Spanish: Foca del Caspio	Grayish yellow, irregularly spotted with black. Head and body length 51–59 in (130–150 cm), average weight 110–132 lb (50–60 kg).	Found in Caspian Sea, a land-locked body of salt water bordered by Russia, Azerbaijan, Iran, Turkmenistan, and Kazakhstan. Generally found on rocky islands and floating ice, sometimes shoreline. Pups born from late January to early February. Spend most of their time in large colonies.	Caspian Sea.	Consists of a wide variety of fish and various types of crabs. May also consume kilka, silverside, roach, pike perch, asp, and gobies.	Vulnerable

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Glossary

Adaptive radiation—Diversification of a species or single ancestral type into several forms that are each adaptively specialized to a specific niche.

Agonistic—Behavioral patterns that are aggressive in context.

Allopatric—Occurring in separate, nonoverlapping geographic areas.

Alpha breeder—The reproductively dominant member of a social unit.

Altricial—An adjective referring to a mammal that is born with little, if any, hair, is unable to feed itself, and initially has poor sensory and thermoregulatory abilities.

Amphibious—Refers to the ability of an animal to move both through water and on land.

Austral—May refer to "southern regions," typically meaning Southern Hemisphere. May also refer to the geographical region included within the Transition, Upper Austral, and Lower Austral Life Zones as defined by C. Hart Merriam in 1892–1898. These zones are often characterized by specific plant and animal communities and were originally defined by temperature gradients especially in the mountains of southwestern North America.

Bergmann's rule—Within a species or among closely related species of mammals, those individuals in colder environments often are larger in body size. Bergmann's rule is a generalization that reflects the ability of endothermic animals to more easily retain body heat (in cold climates) if they have a high body surface to body volume ratio, and to more easily dissipate excess body heat (in hot environments) if they have a low body surface to body volume ratio.

Bioacoustics—The study of biological sounds such as the sounds produced by bats or other mammals.

Biogeographic region—One of several major divisions of the earth defined by a distinctive assemblage of animals and plants. Sometimes referred to as "zoogeographic regions or realms" (for animals) or "phytogeographic regions or realms" (for plants). Such terminology dates from the late nineteenth century and varies considerably. Major biogeographic regions each have a somewhat distinctive flora and fauna. Those generally recognized include Nearctic, Neotropical, Palearctic, Ethiopian, Oriental, and Australian.

Blow—Cloud of vapor and sea water exhaled by cetaceans.

Boreal—Often used as an adjective meaning "northern"; also may refer to the northern climatic zone immediately south of the Arctic; may also include the Arctic, Hudsonian, and Canadian Life Zones described by C. Hart Merriam.

Brachiating ancestor—Ancestor that swung around by the arms.

Breaching—A whale behavior—leaping above the water's surface, then falling back into the water, landing on its back or side.

Cephalopod—Member of the group of mollusks such as squid and octopus.

Cladistic—Evolutionary relationships suggested as "tree" branches to indicate lines of common ancestry.

Cline—A gradient in a measurable characteristic, such as size and color, showing geographic differentiation. Various patterns of geographic variation are reflected as clines or clinal variation, and have been described as "ecogeographic rules."

Cloaca—A common opening for the digestive, urinary, and reproductive tracts found in monotreme mammals.

Colony—A group of mammals living in close proximity, interacting, and usually aiding in early warning of the presence of predators and in group defense.

Commensal—A relationship between species in which one benefits and the other is neither benefited nor harmed.

Congeneric—Descriptive of two or more species that belong to the same genus.

Conspecific—Descriptive of two or more individuals or populations that belong to the same species.

Contact call—Simple vocalization used to maintain communication or physical proximity among members of a social unit.

Convergent evolution—When two evolutionarily unrelated groups of organisms develop similar characteristics due to adaptation to similar aspects of their environment or niche.

Coprophagy—Reingestion of feces to obtain nutrients that were not ingested the first time through the digestive system.

Cosmopolitan—Adjective describing the distribution pattern of an animal found around the world in suitable habitats.

Crepuscular—Active at dawn and at dusk.

Critically Endangered—A technical category used by IUCN for a species that is at an extremely high risk of extinction in the wild in the immediate future.

Cryptic—Hidden or concealed; i.e., well-camouflaged patterning.

Dental formula—A method for describing the number of each type of tooth found in an animal's mouth: incisors (I), canines (C), premolars (P), and molars (M). The formula gives the number of each tooth found in an upper and lower quadrant of the mouth, and the total is multiplied by two for the total number of teeth. For example, the formula for humans is: I2/2 C1/1 P2/2 M3/3 (total, 16, times two is 32 teeth).

Dimorphic—Occurring in two distinct forms (e.g., in reference to the differences in size between males and females of a species).

Disjunct—A distribution pattern characterized by populations that are geographically separated from one another.

Diurnal—Active during the day.

DNA-DNA hybridization—A technique whereby the genetic similarity of different animal groups is determined based on the extent to which short stretches of their DNA, when mixed together in solution in the laboratory, are able to join with each other.

Dominance hierarchy—The social status of individuals in a group; each animal can usually dominate those animals below it in a hierarchy.

Dorso-ventrally—From back to front.

Duetting—Male and female singing and integrating their songs together.

Echolocation—A method of navigation used by some mammals (e.g., bats and marine mammals) to locate objects and investigate surroundings. The animals emit audible "clicks" and determine pathways by using the echo of the sound from structures in the area.

Ecotourism—Travel for the primary purpose of viewing nature. Ecotourism is now "big business" and is used as a non-consumptive but financially rewarding way to protect important areas for conservation.

Ectothermic—Using external energy and behavior to regulate body temperature. "Cold-blooded."

Endangered—A term used by IUCN and also under the Endangered Species Act of 1973 in the United States in reference to a species that is threatened with imminent extinction or extirpation over all or a significant portion of its range.

Endemic—Native to only one specific area.

Endothermic—Maintaining a constant body-temperature using metabolic energy. "Warm-blooded."

Eocene—Geological time period; subdivision of the Tertiary, from about 55.5 to 33.7 million years ago.

Ethology—The study of animal behavior.

Exotic—Not native.

Extant—Still in existence; not destroyed, lost, or extinct.

Extinct—Refers to a species that no longer survives anywhere.

Extirpated—Referring to a local extinction of a species that can still be found elsewhere.

Feral—A population of domesticated animal that lives in the wild.

Flehmen—Lip curling and head raising after sniffing a female's urine.

Forb—Any herb that is not a grass or grass-like.

Fossorial—Adapted for digging.

Frugivorous—Feeds on fruit.

Granivorous—Feeding on seeds.

Gravid—Pregnant.

Gregarious—Occuring in large groups.

Hibernation—A deep state of reduced metabolic activity and lowered body temperature that may last for weeks or months.

Holarctic—The Palearctic and Nearctic bigeographic regions combined.

Hybrid—The offspring resulting from a cross between two different species (or sometimes between distinctive subspecies).

Innate—An inherited characteristic.

Insectivorous—Technically refers to animals that eat insects; generally refers to animals that feed primarily on insects and other arthropods.

Introduced species—An animal or plant that has been introduced to an area where it normally does not occur.

Iteroparous—Breeds in multiple years.

Jacobson's organ—Olfactory organ found in the upper palate that first appeared in amphibians and is most developed in these and in reptiles, but is also found in some birds and mammals.

Kiva—A large chamber wholly or partly underground, and often used for religious ceremonies in Pueblo Indian villages.

Mandible—Technically an animal's lower jaw. The plural, mandibles, is used to refer to both the upper and lower jaw. The upper jaw is technically the maxilla, but often called the "upper mandible."

Marsupial—A mammal whose young complete their embryonic development outside of the mother's body, within a maternal pouch.

Matrilineal—Describing a social unit in which group members are descended from a single female.

Melon—The fat-filled forehead of aquatic mammals of the order Cetacea.

Metabolic rate—The rate of chemical processes in living organisms, resulting in energy expenditure and growth. Metabolic rate decreases when an animal is resting and increases during activity.

Migration—A two-way movement in some mammals, often dramatically seasonal. Typically latitudinal, though in some species is altitudinal or longitudinal. May be short-distance or long-distance.

Miocene—The geological time period that lasted from about 23.8 to 5.6 million years ago.

Molecular phylogenetics—The use of molecular (usually genetic) techniques to study evolutionary relationships between or among different groups of organisms.

Monestrous—Experiencing estrus just once each year or breeding season.

Monogamous—A breeding system in which a male and female mate only with one another.

Monophyletic—A group (or clade) that shares a common ancestor.

Monotypic—A taxonomic category that includes only one form (e.g., a genus that includes only one species; a species that includes no subspecies).

Montane—Of or inhabiting the biogeographic zone of relatively moist, cool upland slopes below timberline dominated by large coniferous trees.

Morphology—The form and structure of animals and plants.

Mutualism—Ecological relationship between two species in which both gain benefit.

Near Threatened—A category defined by the IUCN suggesting possible risk of extinction in the medium term (as opposed to long or short term) future.

Nearctic—The biogeographic region that includes temperate North America. faunal region.

Neotropical—The biogeographic region that includes South and Central America, the West Indies, and tropical Mexico.

New World—A general descriptive term encompassing the Nearctic and Neotropical biogeographic regions.

Niche—The role of an organism in its environment; multi-dimensional, with habitat and behavioral components.

Nocturnal—Active at night.

Old World—A general term that usually describes a species or group as being from Eurasia or Africa.

Oligocene—The geologic time period occurring from about 33.7 to 23.8 million years ago.

Omnivorous—Feeding on a broad range of foods, both plant and animal matter.

Palearctic—A biogeographic region that includes temperate Eurasia and Africa north of the Sahara.

Paleocene—Geological period, subdivision of the Tertiary, from 65 to 55.5 million years ago.

Pelage—Coat, skin, and hair.

Pelagic—An adjective used to indicate a relationship to the open sea.

Pestiferous—Troublesome or annoying; nuisance.

Phylogeny—A grouping of taxa based on evolutionary history.

Piscivorous—Fish-eating.

Placental—A mammal whose young complete their embryonic development within the mother's uterus, joined to her by a placenta.

Pleistocene—In general, the time of the great ice ages; geological period variously considered to include the last 1 to 1.8 million years.

Pliocene—The geological period preceding the Pleistocence; the last subdivision of what is known as the Tertiary; lasted from 5.5 to 1.8 million years ago.

Polyandry—A breeding system in which one female mates with two or more males.

Polygamy—A breeding system in which either or both male and female may have two or more mates.

Polygyny—A breeding system in which one male mates with two or more females.

Polyphyletic—A taxonomic group that is believed to have originated from more than one group of ancestors.

Post-gastric digestion—Refers to the type of fermentative digestion of vegetative matter found in tapirs and other animals by which microorganisms decompose food in a caecum. This is not as thorough a decomposition as occurs in ruminant digesters.

Precocial—An adjective used to describe animals that are born in an advanced state of development such that they generally can leave their birth area quickly and obtain their own food, although they are often led to food and guarded by a parent.

Proboscis—The prehensile trunk (a muscular hydrostat) found in tapirs, elephants, etc.

Quaternary—The geological period, from 1.8 million years ago to the present, usually including two subdivisions: the Pleistocene, and the Holocene.

Refugium (pl. refugia) —An area relatively unaltered during a time of climatic change, from which dispersion and speciation may occur after the climate readjusts.

Reproductive longevity—The length of an animal's life over which it is capable of reproduction.

Ruminant—An even-toed, hoofed mammal with a four-chambered stomach that eats rapidly to regurgitate its food and chew the cud later.

Scansorial—Specialized for climbing.

Seed dispersal—Refers to how tapirs and other animals transport viable seeds from their source to near or distant, suitable habitats where they can successfully germinate. Such dispersal may occur through the feces, through sputum, or as the seeds are attached and later released from fur, etc.

Semelparity—A short life span, in which a single instance of breeding is followed by death in the first year of life.

Sexual dimorphism—Male and female differ in morphology, such as size, feather size or shape, or bill size or shape.

Sibling species—Two or more species that are very closely related, presumably having differentiated from a common ancestor in the recent past; often difficult to distinguish, often interspecifically territorial.

Sonagram—A graphic representation of sound.

Speciation—The evolution of new species.

Spy-hopping—Positioning the body vertically in the water, with the head raised above the sea surface, sometimes while turning slowly.

Steppe—Arid land with vegetation that can thrive with very little moisture; found usually in regions of extreme temperature range.

Suspensory—Moving around or hanging by the arms.

Sympatric—Inhabiting the same range.

Systematist—A specialist in the classification of organisms; systematists strive to classify organisms on the basis of their evolutionary relationships.

Taxon (pl. taxa) —Any unit of scientific classification (e.g., species, genus, family, order).

Taxonomist—A specialist in the naming and classification of organisms. (See also Systematist. Taxonomy is the older science of naming things; identification of evolutionary relationships has not always been the goal of taxonomists. The modern science of systematics generally incorporates taxonomy with the search for evolutionary relationships.)

Taxonomy—The science of identifying, naming, and classifying organisms into groups.

Territoriality—Refers to an animal's defense of a certain portion of its habitat against other conspecifics. This is often undertaken by males in relation to one another and as a lure to females.

Territory—Any defended area. Territorial defense is typically male against male, female against female, and within a species or between sibling species. Area defended varies greatly among taxa, seasons, and habitats. A territory may include the entire home range, only the area immediately around a nest, or only a feeding area.

Tertiary—The geological period including most of the Cenozoic; from about 65 to 1.8 million years ago.

Thermoregulation—The ability to regulate body temperature; can be either behavioral or physiological.

Tribe—A unit of classification below the subfamily and above the genus.

Truncal erectness—Sitting, hanging, arm-swinging (brachiating), walking bipedally with the backbone held vertical.

Ungulate—A hoofed mammal.

Upper cone—The circle in which the arm can rotate when raised above the head.

Viable population—A population that is capable of maintaining itself over a period of time. One of the major conservation issues of the twenty-first century is determining what is a minimum viable population size. Population geneticists have generally come up with estimates of about 500 breeding pairs.

Vulnerable—A category defined by IUCN as a species that is not Critically Endangered or Endangered, but is still facing a threat of extinction.

Mammals species list

Monotremata [Order]

Tachyglossidae [Family]
Tachyglossus [Genus]
T. aculeatus [Species]
Zaglossus [Genus]
Z. bruijni [Species]

Ornithorhynchidae [Family]
Ornithorhynchus [Genus]
O. anatinus [Species]

Didelphimorphia [Order]

Didelphidae [Family]
Caluromys [Genus]
C. derbianus [Species]
C. lanatus
C. philander
Caluromysiops [Genus]
C. irrupta [Species]
Chironectes [Genus]
C. minimus [Species]
Didelphis [Genus]
D. albiventris [Species]
D. aurita
D. marsupialis
D. virginiana
Glironia [Genus]
G. venusta [Species]
Gracilinanus [Genus]
G. aceramarcae [Species]
G. agilis
G. dryas
G. emiliae
G. marica
G. microtarsus
Lestodelphys [Genus]
L. halli [Species]
Lutreolina [Genus]
L. crassicaudata [Species]
Marmosa [Genus]
M. andersoni [Species]
M. canescens
M. lepida
M. mexicana
M. murina
M. robinsoni
M. rubra
M. tyleriana
M. xerophila
Marmosops [Genus]
M. cracens [Species]
M. dorothea
M. fuscatus
M. handleyi
M. impavidus
M. incanus
M. invictus
M. noctivagus
M. parvidens
Metachirus [Genus]
M. nudicaudatus [Species]
Micoureus [Genus]
M. alstoni [Species]
M. constantiae
M. demerarae
M. regina
Monodelphis [Genus]
M. adusta [Species]
M. americana
M. brevicaudata
M. dimidiata
M. domestica
M. emiliae
M. iheringi
M. kunsi
M. maraxina
M. osgoodi
M. rubida
M. scalops
M. sorex
M. theresa
M. unistriata
Philander [Genus]
P. andersoni [Species]
P. opossum
Thylamys [Genus]
T. elegans [Species]
T. macrura
T. pallidior
T. pusilla
T. velutinus

Paucituberculata [Order]

Caenolestidae [Family]
Caenolestes [Genus]
C. caniventer [Species]
C. convelatus
C. fuliginosus
Lestoros [Genus]
L. inca [Species]
Rhyncholestes [Genus]
R. raphanurus [Species]

Microbiotheria [Order]

Microbiotheriidae [Family]
Dromiciops [Genus]
D. gliroides [Species]

Dasyuromorphia [Order]

Dasyuridae [Family]
Antechinus [Genus]
A. bellus [Species]
A. flavipes
A. godmani
A. leo
A. melanurus
A. minimus
A. naso
A. stuartii
A. swainsonii
A. wilhelmina
Dasycercus [Genus]
D. byrnei [Species]
D. cristicauda
Dasykaluta [Genus]
D. rosamondae [Species]
Dasyurus [Genus]
D. albopunctatus [Species]
D. geoffroii
D. hallucatus

D. maculatus
D. spartacus
D. viverrinus
Murexia [Genus]
M. longicaudata [Species]
M. rothschildi
Myoictis [Genus]
M. melas [Species]
Neophascogale [Genus]
N. lorentzi [Species]
Ningaui [Genus]
N. ridei [Species]
N. timealeyi
N. yvonnae
Parantechinus [Genus]
P. apicalis [Species]
P. bilarni
Phascogale [Genus]
P. calura [Species]
P. tapoatafa
Phascolosorex [Genus]
P. doriae [Species]
P. dorsalis
Planigale [Genus]
P. gilesi [Species]
P. ingrami
P. maculata
P. novaeguineae
P. tenuirostris
Pseudantechinus [Genus]
P. macdonnellensis [Species]
P. ningbing
P. woolleyae
Sarcophilus [Genus]
S. laniarius [Species]
Sminthopsis [Genus]
S. aitkeni [Species]
S. archeri
S. butleri
S. crassicaudata
S. dolichura
S. douglasi
S. fuliginosus
S. gilberti
S. granulipes
S. griseoventer
S. hirtipes
S. laniger
S. leucopus
S. longicaudata
S. macroura
S. murina
S. ooldea
S. psammophila
S. virginiae
S. youngsoni

Myrmecobiidae [Family]
Myrmecobius [Genus]
M. fasciatus [Species]

Thylacinidae [Family]
Thylacinus [Genus]
T. cynocephalus [Species]

Peramelemorphia [Order]

Peramelidae [Family]
Chaeropus [Genus]
C. ecaudatus [Species]
Isoodon [Genus]
I. auratus [Species]
I. macrourus
I. obesulus
Macrotis [Genus]
M. lagotis [Species]
M. leucura
Perameles [Genus]
P. bougainville [Species]
P. eremiana
P. gunnii
P. nasuta

Peroryctidae [Family]
Echymipera [Genus]
E. clara [Species]
E. davidi
E. echinista
E. kalubu
E. rufescens
Microperoryctes [Genus]
M. longicauda [Species]
M. murina
M. papuensis
Peroryctes [Genus]
P. broadbenti [Species]
P. raffrayana
Rhynchomeles [Genus]
R. prattorum [Species]

Notoryctemorphia [Order]

Notoryctidae [Family]
Notoryctes [Genus]
N. caurinus [Species]
N. typhlops

Diprotodontia [Order]

Phascolarctidae [Family]
Phascolarctos [Genus]
P. cinereus [Species]

Vombatidae [Family]
Lasiorhinus [Genus]
L. krefftii [Species]
L. latifrons
Vombatus [Genus]
V. ursinus [Species]

Phalangeridae [Family]
Ailurops [Genus]
A. ursinus [Species]
Phalanger [Genus]
P. carmelitae [Species]
P. lullulae
P. matanim
P. orientalis
P. ornatus
P. pelengensis
P. rothschildi
P. sericeus
P. vestitus
Spilocuscus [Genus]
S. maculatus [Species]
S. rufoniger
Strigocuscus [Genus]
S. celebensis [Species]
S. gymnotis
Trichosurus [Genus]
T. arnhemensis [Species]
T. caninus
T. vulpecula
Wyulda [Genus]
W. squamicaudata [Species]

Hypsiprymnodontidae [Family]
Hypsiprymnodon [Genus]
H. moschatus [Species]

Potoroidae [Family]
Aepyprymnus [Genus]
A. rufescens [Species]
Bettongia [Genus]
B. gaimardi [Species]
B. lesueur
B. penicillata
Caloprymnus [Genus]
C. campestris [Species]
Potorous [Genus]
P. longipes [Species]
P. platyops
P. tridactylus

Macropodidae [Family]
Dendrolagus [Genus]
D. bennettianus [Species]
D. dorianus
D. goodfellowi
D. inustus
D. lumholtzi
D. matschiei
D. scottae
D. spadix
D. ursinus
Dorcopsis [Genus]
D. atrata [Species]
D. hageni
D. luctuosa
D. muelleri
Dorcopsulus [Genus]
D. macleayi [Species]
D. vanheurni
Lagorchestes [Genus]

L. asomatus [Species]
L. conspicillatus
L. hirsutus
L. leporides
Lagostrophus [Genus]
L. fasciatus [Species]
Macropus [Genus]
M. agilis [Species]
M. antilopinus
M. bernardus
M. dorsalis
M. eugenii
M. fuliginosus
M. giganteus
M. greyi
M. irma
M. parma
M. parryi
M. robustus
M. rufogriseus
M. rufus
Onychogalea [Genus]
O. fraenata [Species]
O. lunata
O. unguifera
Petrogale [Genus]
P. assimilis [Species]
P. brachyotis
P. burbidgei
P. concinna
P. godmani
P. inornata
P. lateralis
P. penicillata
P. persephone
P. rothschildi
P. xanthopus
Setonix [Genus]
S. brachyurus [Species]
Thylogale [Genus]
T. billardierii [Species]
T. brunii
T. stigmatica
T. thetis
Wallabia [Genus]
W. bicolor [Species]

Burramyidae [Family]
Burramys [Genus]
B. parvus [Species]
Cercartetus [Genus]
C. caudatus [Species]
C. concinnus
C. lepidus
C. nanus

Pseudocheiridae [Family]
Hemibelideus [Genus]
H. lemuroides [Species]
Petauroides [Genus]
P. volans [Species]
Petropseudes [Genus]
P. dahli [Species]
Pseudocheirus [Genus]
P. canescens [Species]
P. caroli
P. forbesi
P. herbertensis
P. mayeri
P. peregrinus
P. schlegeli
Pseudochirops [Genus]
P. albertisii [Species]
P. archeri
P. corinnae
P. cupreus

Petauridae [Family]
Dactylopsila [Genus]
D. megalura [Species]
D. palpator
D. tatei
D. trivirgata
Gymnobelideus [Genus]
G. leadbeateri [Species]
Petaurus [Genus]
P. abidi [Species]
P. australis
P. breviceps
P. gracilis
P. norfolcensis

Tarsipedidae [Family]
Tarsipes [Genus]
T. rostratus [Species]

Acrobatidae [Family]
Acrobates [Genus]
A. pygmaeus [Species]
Distoechurus [Genus]
D. pennatus [Species]

Xenarthra [Order]

Megalonychidae [Family]
Choloepus [Genus]
C. didactylus [Species]
C. hoffmanni

Bradypodidae [Family]
Bradypus [Genus]
B. torquatus [Species]
B. tridactylus
B. variegatus

Myrmecophagidae [Family]
Cyclopes [Genus]
C. didactylus [Species]
Myrmecophaga [Genus]
M. tridactyla [Species]
Tamandua [Genus]
T. mexicana [Species]
T. tetradactyla

Dasypodidae [Family]
Chlamyphorus [Genus]
C. retusus [Species]
C. truncatus
Cabassous [Genus]
C. centralis [Species]
C. chacoensis
C. tatouay
C. unicinctus
Chaetophractus [Genus]
C. nationi [Species]
C. vellerosus
C. villosus
Dasypus [Genus]
D. hybridus [Species]
D. kappleri
D. novemcinctus
D. pilosus
D. sabanicola
D. septemcinctus
Euphractus [Genus]
E. sexcinctus [Species]
Priodontes [Genus]
P. maximus [Species]
Tolypeutes [Genus]
T. matacus [Species]
T. tricinctus
Zaedyus [Genus]
Z. pichiy [Species]

Insectivora [Order]

Erinaceidae [Family]
Atelerix [Genus]
A. albiventris [Species]
A. algirus
A. frontalis
A. sclateri
Erinaceus [Genus]
E. amurensis [Species]
E. concolor
E. europaeus
Hemiechinus [Genus]
H. aethiopicus [Species]
H. auritus
H. collaris
H. hypomelas
H. micropus
H. nudiventris
Mesechinus [Genus]
M. dauuricus [Species]
M. hughi
Echinosorex [Genus]
E. gymnura [Species]
Hylomys [Genus]
H. hainanensis [Species]
H. sinensis
H. suillus
Podogymnura [Genus]
P. aureospinula [Species]
P. truei

Chrysochloridae [Family]
Amblysomus [Genus]
A. gunningi [Species]
A. hottentotus
A. iris
A. julianae
Calcochloris [Genus]
C. obtusirostris [Species]
Chlorotalpa [Genus]
C. arendsi [Species]
C. duthieae
C. leucorhina
C. sclateri
C. tytonis
Chrysochloris [Genus]
C. asiatica [Species]
C. stuhlmanni
C. visagiei
Chrysospalax [Genus]
C. trevelyani [Species]
C. villosus
Cryptochloris [Genus]
C. wintoni [Species]
C. zyli
Eremitalpa [Genus]
E. granti [Species]

Tenrecidae [Family]
Echinops [Genus]
E. telfairi [Species]
Geogale [Genus]
G. aurita [Species]
Hemicentetes [Genus]
H. semispinosus [Species]
Limnogale [Genus]
L. mergulus [Species]
Microgale [Genus]
M. brevicaudata [Species]
M. cowani
M. dobsoni
M. dryas
M. gracilis
M. longicaudata
M. parvula
M. principula
M. pulla
M. pusilla
M. talazaci
M. thomasi
Micropotamogale [Genus]
M. lamottei [Species]
M. ruwenzorii
Oryzorictes [Genus]
O. hova [Species]
O. talpoides
O. tetradactylus
Potamogale [Genus]
P. velox [Species]
Setifer [Genus]
S. setosus [Species]
Tenrec [Genus]
T. ecaudatus [Species]

Solenodontidae [Family]
Solenodon [Genus]
S. cubanus [Species]
S. marcanoi
S. paradoxus

Nesophontidae [Family]
Nesophontes [Genus]
N. edithae [Species]
N. hypomicrus
N. longirostris
N. major
N. micrus
N. paramicrus
N. submicrus
N. zamicrus

Soricidae [Family]
Anourosorex [Genus]
A. squamipes [Species]
Blarina [Genus]
B. brevicauda [Species]
B. carolinensis
B. hylophaga
Blarinella [Genus]
B. quadraticauda [Species]
B. wardi
Chimarrogale [Genus]
C. hantu [Species]
C. himalayica
C. phaeura
C. platycephala
C. styani
C. sumatrana
Congosorex [Genus]
C. polli [Species]
Crocidura [Genus]
C. aleksandrisi [Species]
C. allex
C. andamanensis
C. ansellorum
C. arabica
C. armenica
C. attenuata
C. attila
C. baileyi
C. batesi
C. beatus
C. beccarii
C. bottegi
C. bottegoides
C. buettikoferi
C. caliginea
C. canariensis
C. cinderella
C. congobelgica
C. cossyrensis
C. crenata
C. crossei
C. cyanea
C. denti
C. desperata
C. dhofarensis
C. dolichura
C. douceti
C. dsinezumi
C. eisentrauti
C. elgonius
C. elongata
C. erica
C. fischeri
C. flavescens
C. floweri
C. foxi
C. fuliginosa
C. fulvastra
C. fumosa
C. fuscomurina
C. glassi
C. goliath
C. gracilipes
C. grandiceps
C. grandis
C. grassei
C. grayi
C. greenwoodi
C. gueldenstaedtii
C. harenna
C. hildegardeae
C. hirta
C. hispida
C. horsfieldii
C. jacksoni
C. jenkinsi
C. kivuana
C. lamottei
C. lanosa
C. lasiura
C. latona
C. lea
C. leucodon
C. levicula
C. littoralis
C. longipes
C. lucina
C. ludia
C. luna
C. lusitania
C. macarthuri
C. macmillani
C. macowi
C. malayana
C. manengubae
C. maquassiensis
C. mariquensis
C. maurisca
C. maxi
C. mindorus

C. minuta
C. miya
C. monax
C. monticola
C. montis
C. muricauda
C. mutesae
C. nana
C. nanilla
C. neglecta
C. negrina
C. nicobarica
C. nigeriae
C. nigricans
C. nigripes
C. nigrofusca
C. nimbae
C. niobe
C. obscurior
C. olivieri
C. orii
C. osorio
C. palawanensis
C. paradoxura
C. parvipes
C. pasha
C. pergrisea
C. phaeura
C. picea
C. pitmani
C. planiceps
C. poensis
C. polia
C. pullata
C. raineyi
C. religiosa
C. rhoditis
C. roosevelti
C. russula
C. selina
C. serezkyensis
C. sibirica
C. sicula
C. silacea
C. smithii
C. somalica
C. stenocephala
C. suaveolens
C. susiana
C. tansaniana
C. tarella
C. tarfayensis
C. telfordi
C. tenuis
C. thalia
C. theresae
C. thomensis
C. turba
C. ultima
C. usambarae
C. viaria
C. voi
C. whitakeri
C. wimmeri
C. xantippe
C. yankariensis
C. zaphiri
C. zarudnyi
C. zimmeri
C. zimmermanni
Cryptotis [Genus]
C. avia [Species]
C. endersi
C. goldmani
C. goodwini
C. gracilis
C. hondurensis
C. magna
C. meridensis
C. mexicana
C. montivaga
C. nigrescens
C. parva
C. squamipes
C. thomasi
Diplomesodon [Genus]
D. pulchellum [Species]
Feroculus [Genus]
F. feroculus [Species]
Megasorex [Genus]
M. gigas [Species]
Myosorex [Genus]
M. babaulti [Species]
M. blarina
M. cafer
M. eisentrauti
M. geata
M. longicaudatus
M. okuensis
M. rumpii
M. schalleri
M. sclateri
M. tenuis
M. varius
Nectogale [Genus]
N. elegans [Species]
Neomys [Genus]
N. anomalus [Species]
N. fodiens
N. schelkovnikovi
Notiosorex [Genus]
N. crawfordi [Species]
Paracrocidura [Genus]
P. graueri [Species]
P. maxima
P. schoutedeni
Ruwenzorisorex [Genus]
R. suncoides [Species]
Scutisorex [Genus]
S. somereni [Species]
Solisorex [Genus]
S. pearsoni [Species]
Sorex [Genus]
S. alaskanus [Species]
S. alpinus
S. araneus
S. arcticus
S. arizonae
S. asper
S. bairdii
S. bedfordiae
S. bendirii
S. buchariensis
S. caecutiens
S. camtschatica
S. cansulus
S. cinereus
S. coronatus
S. cylindricauda
S. daphaenodon
S. dispar
S. emarginatus
S. excelsus
S. fumeus
S. gaspensis
S. gracillimus
S. granarius
S. haydeni
S. hosonoi
S. hoyi
S. hydrodromus
S. isodon
S. jacksoni
S. kozlovi
S. leucogaster
S. longirostris
S. lyelli
S. macrodon
S. merriami
S. milleri
S. minutissimus
S. minutus
S. mirabilis
S. monticolus
S. nanus
S. oreopolus
S. ornatus
S. pacificus
S. palustris
S. planiceps
S. portenkoi
S. preblei
S. raddei
S. roboratus
S. sadonis
S. samniticus
S. satunini
S. saussurei
S. sclateri
S. shinto

S. sinalis
S. sonomae
S. stizodon
S. tenellus
S. thibetanus
S. trowbridgii
S. tundrensis
S. ugyunak
S. unguiculatus
S. vagrans
S. ventralis
S. veraepacis
S. volnuchini
Soriculus [Genus]
S. caudatus [Species]
S. fumidus
S. hypsibius
S. lamula
S. leucops
S. macrurus
S. nigrescens
S. parca
S. salenskii
S. smithii
Suncus [Genus]
S. ater [Species]
S. dayi
S. etruscus
S. fellowesgordoni
S. hosei
S. infinitesimus
S. lixus
S. madagascariensis
S. malayanus
S. mertensi
S. montanus
S. murinus
S. remyi
S. stoliczkanus
S. varilla
S. zeylanicus
Surdisorex [Genus]
S. norae [Species]
S. polulus
Sylvisorex [Genus]
S. granti [Species]
S. howelli
S. isabellae
S. johnstoni
S. lunaris
S. megalura
S. morio
S. ollula
S. oriundus
S. vulcanorum

Talpidae [Family]
Desmana [Genus]
D. moschata [Species]
Galemys [Genus]
G. pyrenaicus [Species]
Condylura [Genus]
C. cristata [Species]
Euroscaptor [Genus]
E. grandis [Species]
E. klossi
E. longirostris
E. micrura
E. mizura
E. parvidens
Mogera [Genus]
M. etigo [Species]
M. insularis
M. kobeae
M. minor
M. robusta
M. tokudae
M. wogura
Nesoscaptor [Genus]
N. uchidai [Species]
Neurotrichus [Genus]
N. gibbsii [Species]
Parascalops [Genus]
P. breweri [Species]
Parascaptor [Genus]
P. leucura [Species]
Scalopus [Genus]
S. aquaticus [Species]
Scapanulus [Genus]
S. oweni [Species]
Scapanus [Genus]
S. latimanus [Species]
S. orarius
S. townsendii
Scaptochirus [Genus]
S. moschatus [Species]
Scaptonyx [Genus]
S. fusicaudus [Species]
Talpa [Genus]
T. altaica [Species]
T. caeca
T. caucasica
T. europaea
T. levantis
T. occidentalis
T. romana
T. stankovici
T. streeti
Urotrichus [Genus]
U. pilirostris [Species]
U. talpoides
Uropsilus [Genus]
U. andersoni [Species]
U. gracilis
U. investigator
U. soricipes

Scandentia [Order]

Tupaiidae [Family]
Anathana [Genus]
A. ellioti [Species]
Dendrogale [Genus]
D. melanura [Species]
D. murina
Ptilocercus [Genus]
P. lowii [Species]
Tupaia [Genus]
T. belangeri [Species]
T. chrysogaster
T. dorsalis
T. glis
T. gracilis
T. javanica
T. longipes
T. minor
T. montana
T. nicobarica
T. palawanensis
T. picta
T. splendidula
T. tana
Urogale [Genus]
U. everetti [Species]

Dermoptera [Order]

Cynocephalidae [Family]
Cynocephalus [Genus]
C. variegatus [Species]
C. volans

Chiroptera [Order]

Pteropodidae [Family]
Acerodon [Genus]
A. celebensis [Species]
A. humilis
A. jubatus
A. leucotis
A. lucifer
A. mackloti
Aethalops [Genus]
A. alecto [Species]
Alionycteris [Genus]
A. paucidentata [Species]
Aproteles [Genus]
A. bulmerae [Species]
Balionycteris [Genus]
B. maculata [Species]
Boneia [Genus]
B. bidens [Species]
Casinycteris [Genus]
C. argynnis [Species]
Chironax [Genus]
C. melanocephalus [Species]
Cynopterus [Genus]
C. brachyotis [Species]
C. horsfieldi
C. nusatenggara
C. sphinx
C. titthaecheileus
Dobsonia [Genus]

D. beauforti [Species]
D. chapmani
D. emersa
D. exoleta
D. inermis
D. minor
D. moluccensis
D. pannietensis
D. peroni
D. praedatrix
D. viridis
Dyacopterus [Genus]
D. spadiceus [Species]
Eidolon [Genus]
E. dupreanum [Species]
E. helvum
Eonycteris [Genus]
E. major [Species]
E. spelaea
Epomophorus [Genus]
E. angolensis [Species]
E. gambianus
E. grandis
E. labiatus
E. minimus
E. wahlbergi
Epomops [Genus]
E. buettikoferi [Species]
E. dobsoni
E. franqueti
Haplonycteris [Genus]
H. fischeri [Species]
Harpyionycteris [Genus]
H. celebensis [Species]
H. whiteheadi
Hypsignathus [Genus]
H. monstrosus [Species]
Latidens [Genus]
L. salimalii [Species]
Macroglossus [Genus]
M. minimus [Species]
M. sobrinus
Megaerops [Genus]
M. ecaudatus [Species]
M. kusnotoi
M. niphanae
M. wetmorei
Megaloglossus [Genus]
M. woermanni [Species]
Melonycteris [Genus]
M. aurantius [Species]
M. melanops
M. woodfordi
Micropteropus [Genus]
M. intermedius [Species]
M. pusillus
Myonycteris [Genus]
M. brachycephala [Species]
M. relicta
M. torquata
Nanonycteris [Genus]
N. veldkampi [Species]
Neopteryx [Genus]
N. frosti [Species]
Notopteris [Genus]
N. macdonaldi [Species]
Nyctimene [Genus]
N. aello [Species]
N. albiventer
N. celaeno
N. cephalotes
N. certans
N. cyclotis
N. draconilla
N. major
N. malaitensis
N. masalai
N. minutus
N. rabori
N. robinsoni
N. sanctacrucis
N. vizcaccia
Otopteropus [Genus]
O. cartilagonodus [Species]
Paranyctimene [Genus]
P. raptor [Species]
Penthetor [Genus]
P. lucasi [Species]
Plerotes [Genus]
P. anchietai [Species]
Ptenochirus [Genus]
P. jagori [Species]
P. minor
Pteralopex [Genus]
P. acrodonta [Species]
P. anceps
P. atrata
P. pulchra
Pteropus [Genus]
P. admiralitatum [Species]
P. aldabrensis
P. alecto
P. anetianus
P. argentatus
P. brunneus
P. caniceps
P. chrysoproctus
P. conspicillatus
P. dasymallus
P. faunulus
P. fundatus
P. giganteus
P. gilliardi
P. griseus
P. howensis
P. hypomelanus
P. insularis
P. leucopterus
P. livingstonei
P. lombocensis
P. lylei
P. macrotis
P. mahaganus
P. mariannus
P. mearnsi
P. melanopogon
P. melanotus
P. molossinus
P. neohibernicus
P. niger
P. nitendiensis
P. ocularis
P. ornatus
P. personatus
P. phaeocephalus
P. pilosus
P. pohlei
P. poliocephalus
P. pselaphon
P. pumilus
P. rayneri
P. rodricensis
P. rufus
P. samoensis
P. sanctacrucis
P. scapulatus
P. seychellensis
P. speciosus
P. subniger
P. temmincki
P. tokudae
P. tonganus
P. tuberculatus
P. vampyrus
P. vetulus
P. voeltzkowi
P. woodfordi
Rousettus [Genus]
R. aegyptiacus [Species]
R. amplexicaudatus
R. angolensis
R. celebensis
R. lanosus
R. leschenaulti
R. madagascariensis
R. obliviosus
R. spinalatus
Scotonycteris [Genus]
S. ophiodon [Species]
S. zenkeri
Sphaerias [Genus]
S. blanfordi [Species]
Styloctenium [Genus]
S. wallacei [Species]
Syconycteris [Genus]
S. australis [Species]
S. carolinae
S. hobbit
Thoopterus [Genus]
T. nigrescens [Species]

Rhinopomatidae [Family]
Rhinopoma [Genus]
R. hardwickei [Species]
R. microphyllum
R. muscatellum

Emballonuridae [Family]
Balantiopteryx [Genus]
B. infusca [Species]
B. io
B. plicata
Centronycteris [Genus]
C. maximiliani [Species]
Coleura [Genus]
C. afra [Species]
C. seychellensis
Cormura [Genus]
C. brevirostris [Species]
Cyttarops [Genus]
C. alecto [Species]
Diclidurus [Genus]
D. albus [Species]
D. ingens
D. isabellus
D. scutatus
Emballonura [Genus]
E. alecto [Species]
E. atrata
E. beccarii
E. dianae
E. furax
E. monticola
E. raffrayana
E. semicaudata
Mosia [Genus]
M. nigrescens [Species]
Peropteryx [Genus]
P. kappleri [Species]
P. leucoptera
P. macrotis
Rhynchonycteris [Genus]
R. naso [Species]
Saccolaimus [Genus]
S. flaviventris [Species]
S. mixtus
S. peli
S. pluto
S. saccolaimus
Saccopteryx [Genus]
S. bilineata [Species]
S. canescens
S. gymnura
S. leptura
Taphozous [Genus]
T. australis [Species]
T. georgianus
T. hamiltoni
T. hildegardeae
T. hilli
T. kapalgensis
T. longimanus
T. mauritianus
T. melanopogon
T. nudiventris
T. perforatus
T. philippinensis
T. theobaldi

Craseonycteridae [Family]
Craseonycteris [Genus]
C. thonglongyai [Species]

Nycteridae [Family]
Nycteris [Genus]
N. arge [Species]
N. gambiensis
N. grandis
N. hispida
N. intermedia
N. javanica
N. macrotis
N. major
N. nana
N. thebaica
N. tragata
N. woodi

Megadermatidae [Family]
Cardioderma [Genus]
C. cor [Species]
Lavia [Genus]
L. frons [Species]
Macroderma [Genus]
M. gigas [Species]
Megaderma [Genus]
M. lyra [Species]
M. spasma

Rhinolophidae [Family]
Rhinolophus [Genus]
R. acuminatus [Species]
R. adami
R. affinis
R. alcyone
R. anderseni
R. arcuatus
R. blasii
R. borneensis
R. canuti
R. capensis
R. celebensis
R. clivosus
R. coelophyllus
R. cognatus
R. cornutus
R. creaghi
R. darlingi
R. deckenii
R. denti
R. eloquens
R. euryale
R. euryotis
R. ferrumequinum
R. fumigatus
R. guineensis
R. hildebrandti
R. hipposideros
R. imaizumii
R. inops
R. keyensis
R. landeri
R. lepidus
R. luctus
R. maclaudi
R. macrotis
R. malayanus
R. marshalli
R. megaphyllus
R. mehelyi
R. mitratus
R. monoceros
R. nereis
R. osgoodi
R. paradoxolophus
R. pearsoni
R. philippinensis
R. pusillus
R. rex
R. robinsoni
R. rouxi
R. rufus
R. sedulus
R. shameli
R. silvestris
R. simplex
R. simulator
R. stheno
R. subbadius
R. subrufus
R. swinnyi
R. thomasi
R. trifoliatus
R. virgo
R. yunanensis

Hipposideridae [Family]
Anthops [Genus]
A. ornatus [Species]
Asellia [Genus]
A. patrizii [Species]
A. tridens
Aselliscus [Genus]
A. stoliczkanus [Species]
A. tricuspidatus
Cloeotis [Genus]
C. percivali [Species]
Coelops [Genus]
C. frithi [Species]
C. hirsutus
C. robinsoni
Hipposideros [Genus]
H. abae [Species]
H. armiger

H. ater
H. beatus
H. bicolor
H. breviceps
H. caffer
H. calcaratus
H. camerunensis
H. cervinus
H. cineraceus
H. commersoni
H. coronatus
H. corynophyllus
H. coxi
H. crumeniferus
H. curtus
H. cyclops
H. diadema
H. dinops
H. doriae
H. dyacorum
H. fuliginosus
H. fulvus
H. galeritus
H. halophyllus
H. inexpectatus
H. jonesi
H. lamottei
H. lankadiva
H. larvatus
H. lekaguli
H. lylei
H. macrobullatus
H. maggietaylorae
H. marisae
H. megalotis
H. muscinus
H. nequam
H. obscurus
H. papua
H. pomona
H. pratti
H. pygmaeus
H. ridleyi
H. ruber
H. sabanus
H. schistaceus
H. semoni
H. speoris
H. stenotis
H. turpis
H. wollastoni
Paracoelops [Genus]
P. megalotis [Species]
Rhinonicteris [Genus]
R. aurantia [Species]
Triaenops [Genus]
T. furculus [Species]
T. persicus

Phyllostomidae [Family]
Ametrida [Genus]
A. centurio [Species]
Anoura [Genus]
A. caudifer [Species]
A. cultrata
A. geoffroyi
A. latidens
Ardops [Genus]
A. nichollsi [Species]
Ariteus [Genus]
A. flavescens [Species]
Artibeus [Genus]
A. amplus [Species]
A. anderseni
A. aztecus
A. cinereus
A. concolor
A. fimbriatus
A. fraterculus
A. glaucus
A. hartii
A. hirsutus
A. inopinatus
A. jamaicensis
A. lituratus
A. obscurus
A. phaeotis
A. planirostris
A. toltecus
Brachyphylla [Genus]
B. cavernarum [Species]
B. nana
Carollia [Genus]
C. brevicauda [Species]
C. castanea
C. perspicillata
C. subrufa
Centurio [Genus]
C. senex [Species]
Chiroderma [Genus]
C. doriae [Species]
C. improvisum
C. salvini
C. trinitatum
C. villosum
Choeroniscus [Genus]
C. godmani [Species]
C. intermedius
C. minor
C. periosus
Choeronycteris [Genus]
C. mexicana [Species]
Chrotopterus [Genus]
C. auritus [Species]
Desmodus [Genus]
D. rotundus [Species]
Diaemus [Genus]
D. youngi [Species]
Diphylla [Genus]
D. ecaudata [Species]
Ectophylla [Genus]
E. alba [Species]
Erophylla [Genus]
E. sezekorni [Species]
Glossophaga [Genus]
G. commissarisi [Species]
G. leachii
G. longirostris
G. morenoi
G. soricina
Hylonycteris [Genus]
H. underwoodi [Species]
Leptonycteris [Genus]
L. curasoae [Species]
L. nivalis
Lichonycteris [Genus]
L. obscura [Species]
Lionycteris [Genus]
L. spurrelli [Species]
Lonchophylla [Genus]
L. bokermanni [Species]
L. dekeyseri
L. handleyi
L. hesperia
L. mordax
L. robusta
L. thomasi
Lonchorhina [Genus]
L. aurita [Species]
L. fernandezi
L. marinkellei
L. orinocensis
Macrophyllum [Genus]
M. macrophyllum [Species]
Macrotus [Genus]
M. californicus [Species]
M. waterhousii
Mesophylla [Genus]
M. macconnelli [Species]
Micronycteris [Genus]
M. behnii [Species]
M. brachyotis
M. daviesi
M. hirsuta
M. megalotis
M. minuta
M. nicefori
M. pusilla
M. schmidtorum
M. sylvestris
Mimon [Genus]
M. bennettii [Species]
M. crenulatum
Monophyllus [Genus]
M. plethodon [Species]
M. redmani
Musonycteris [Genus]
M. harrisoni [Species]
Phylloderma [Genus]
P. stenops [Species]
Phyllonycteris [Genus]

P. aphylla [Species]
P. poeyi
Phyllops [Genus]
P. falcatus [Species]
Phyllostomus [Genus]
P. discolor [Species]
P. elongatus
P. hastatus
P. latifolius
Platalina [Genus]
P. genovensium [Species]
Platyrrhinus [Genus]
P. aurarius [Species]
P. brachycephalus
P. chocoensis
P. dorsalis
P. helleri
P. infuscus
P. lineatus
P. recifinus
P. umbratus
P. vittatus
Pygoderma [Genus]
P. bilabiatum [Species]
Rhinophylla [Genus]
R. alethina [Species]
R. fischerae
R. pumilio
Scleronycteris [Genus]
S. ega [Species]
Sphaeronycteris [Genus]
S. toxophyllum [Species]
Stenoderma [Genus]
S. rufum [Species]
Sturnira [Genus]
S. aratathomasi [Species]
S. bidens
S. bogotensis
S. erythromos
S. lilium
S. ludovici
S. luisi
S. magna
S. mordax
S. nana
S. thomasi
S. tildae
Tonatia [Genus]
T. bidens [Species]
T. brasiliense
T. carrikeri
T. evotis
T. schulzi
T. silvicola
Trachops [Genus]
T. cirrhosus [Species]
Uroderma [Genus]
U. bilobatum [Species]
U. magnirostrum
Vampyressa [Genus]
V. bidens [Species]
V. brocki
V. melissa
V. nymphaea
V. pusilla
Vampyrodes [Genus]
V. caraccioli [Species]
Vampyrum [Genus]
V. spectrum [Species]

Mormoopidae [Family]
Mormoops [Genus]
M. blainvillii [Species]
M. megalophylla
Pteronotus [Genus]
P. davyi [Species]
P. gymnonotus
P. macleayii
P. parnellii
P. personatus
P. quadridens

Noctilionidae [Family]
Noctilio [Genus]
N. albiventris [Species]
N. leporinus

Mystacinidae [Family]
Mystacina [Genus]
M. robusta [Species]
M. tuberculata

Natalidae [Family]
Natalus [Genus]
N. lepidus [Species]
N. micropus
N. stramineus
N. tumidifrons
N. tumidirostris

Furipteridae [Family]
Amorphochilus [Genus]
A. schnablii [Species]
Furipterus [Genus]
F. horrens [Species]

Thyropteridae [Family]
Thyroptera [Genus]
T. discifera [Species]
T. tricolor

Myzopodidae [Family]
Myzopoda [Genus]
M. aurita [Species]

Molossidae [Family]
Chaerephon [Genus]
C. aloysiisabaudiae [Species]
C. ansorgei
C. bemmeleni
C. bivittata
C. chapini
C. gallagheri
C. jobensis
C. johorensis
C. major
C. nigeriae
C. plicata
C. pumila
C. russata
Cheiromeles [Genus]
C. torquatus [Species]
Eumops [Genus]
E. auripendulus [Species]
E. bonariensis
E. dabbenei
E. glaucinus
E. hansae
E. maurus
E. perotis
E. underwoodi
Molossops [Genus]
M. abrasus [Species]
M. aequatorianus
M. greenhalli
M. mattogrossensis
M. neglectus
M. planirostris
M. temminckii
Molossus [Genus]
M. ater [Species]
M. bondae
M. molossus
M. pretiosus
M. sinaloae
Mops [Genus]
M. brachypterus [Species]
M. condylurus
M. congicus
M. demonstrator
M. midas
M. mops
M. nanulus
M. niangarae
M. niveiventer
M. petersoni
M. sarasinorum
M. spurrelli
M. thersites
M. trevori
Mormopterus [Genus]
M. acetabulosus [Species]
M. beccarii
M. doriae
M. jugularis
M. kalinowskii
M. minutus
M. norfolkensis
M. petrophilus
M. phrudus
M. planiceps
M. setiger
Myopterus [Genus]

M. daubentonii [Species]
M. whitleyi
Nyctinomops [Genus]
N. aurispinosus [Species]
N. femorosaccus
N. laticaudatus
N. macrotis
Otomops [Genus]
O. formosus [Species]
O. martiensseni
O. papuensis
O. secundus
O. wroughtoni
Promops [Genus]
P. centralis [Species]
P. nasutus
Tadarida [Genus]
T. aegyptiaca [Species]
T. australis
T. brasiliensis
T. espiritosantensis
T. fulminans
T. lobata
T. teniotis
T. ventralis

Vespertilionidae [Family]
Antrozous [Genus]
A. dubiaquercus [Species]
A. pallidus
Barbastella [Genus]
B. barbastellus [Species]
B. leucomelas
Chalinolobus [Genus]
C. alboguttatus [Species]
C. argentatus
C. beatrix
C. dwyeri
C. egeria
C. gleni
C. gouldii
C. kenyacola
C. morio
C. nigrogriseus
C. picatus
C. poensis
C. superbus
C. tuberculatus
C. variegatus
Eptesicus [Genus]
E. baverstocki [Species]
E. bobrinskoi
E. bottae
E. brasiliensis
E. brunneus
E. capensis
E. demissus
E. diminutus
E. douglasorum
E. flavescens
E. floweri
E. furinalis
E. fuscus
E. guadeloupensis
E. guineensis
E. hottentotus
E. innoxius
E. kobayashii
E. melckorum
E. nasutus
E. nilssoni
E. pachyotis
E. platyops
E. pumilus
E. regulus
E. rendalli
E. sagittula
E. serotinus
E. somalicus
E. tatei
E. tenuipinnis
E. vulturnus
Euderma [Genus]
E. maculatum [Species]
Eudiscopus [Genus]
E. denticulus [Species]
Glischropus [Genus]
G. javanus [Species]
G. tylopus
Harpiocephalus [Genus]
H. harpia [Species]
Hesperoptenus [Genus]
H. blanfordi [Species]
H. doriae
H. gaskelli
H. tickelli
H. tomesi
Histiotus [Genus]
H. alienus [Species]
H. macrotus
H. montanus
H. velatus
Ia [Genus]
I. io [Species]
Idionycteris [Genus]
I. phyllotis [Species]
Kerivoula [Genus]
K. aerosa [Species]
K. africana
K. agnella
K. argentata
K. atrox
K. cuprosa
K. eriophora
K. flora
K. hardwickei
K. intermedia
K. jagori
K. lanosa
K. minuta
K. muscina
K. myrella
K. papillosa
K. papuensis
K. pellucida
K. phalaena
K. picta
K. smithi
K. whiteheadi
Laephotis [Genus]
L. angolensis [Species]
L. botswanae
L. namibensis
L. wintoni
Lasionycteris [Genus]
L. noctivagans [Species]
Lasiurus [Genus]
L. borealis [Species]
L. castaneus
L. cinereus
L. ega
L. egregius
L. intermedius
L. seminolus
Mimetillus [Genus]
M. moloneyi [Species]
Miniopterus [Genus]
M. australis [Species]
M. fraterculus
M. fuscus
M. inflatus
M. magnater
M. minor
M. pusillus
M. robustior
M. schreibersi
M. tristis
Murina [Genus]
M. aenea [Species]
M. aurata
M. cyclotis
M. florium
M. fusca
M. grisea
M. huttoni
M. leucogaster
M. puta
M. rozendaali
M. silvatica
M. suilla
M. tenebrosa
M. tubinaris
M. ussuriensis
Myotis [Genus]
M. abei [Species]
M. adversus
M. aelleni
M. albescens
M. altarium
M. annectans
M. atacamensis

M. auriculus
M. australis
M. austroriparius
M. bechsteini
M. blythii
M. bocagei
M. bombinus
M. brandti
M. californicus
M. capaccinii
M. chiloensis
M. chinensis
M. cobanensis
M. dasycneme
M. daubentoni
M. dominicensis
M. elegans
M. emarginatus
M. evotis
M. findleyi
M. formosus
M. fortidens
M. frater
M. goudoti
M. grisescens
M. hasseltii
M. horsfieldii
M. hosonoi
M. ikonnikovi
M. insularum
M. keaysi
M. keenii
M. leibii
M. lesueuri
M. levis
M. longipes
M. lucifugus
M. macrodactylus
M. macrotarsus
M. martiniquensis
M. milleri
M. montivagus
M. morrisi
M. muricola
M. myotis
M. mystacinus
M. nattereri
M. nesopolus
M. nigricans
M. oreias
M. oxyotus
M. ozensis
M. peninsularis
M. pequinius
M. planiceps
M. pruinosus
M. ricketti
M. ridleyi
M. riparius
M. rosseti
M. ruber
M. schaubi
M. scotti
M. seabrai
M. sicarius
M. siligorensis
M. simus
M. sodalis
M. stalkeri
M. thysanodes
M. tricolor
M. velifer
M. vivesi
M. volans
M. welwitschii
M. yesoensis
M. yumanensis
Nyctalus [Genus]
N. aviator [Species]
N. azoreum
N. lasiopterus
N. leisleri
N. montanus
N. noctula
Nycticeius [Genus]
N. balstoni [Species]
N. greyii
N. humeralis
N. rueppellii
N. sanborni
N. schlieffeni
Nyctophilus [Genus]
N. arnhemensis [Species]
N. geoffroyi
N. gouldi
N. heran
N. microdon
N. microtis
N. timoriensis
N. walkeri
Otonycteris [Genus]
O. hemprichi [Species]
Pharotis [Genus]
P. imogene [Species]
Philetor [Genus]
P. brachypterus [Species]
Pipistrellus [Genus]
P. aegyptius [Species]
P. aero
P. affinis
P. anchietai
P. anthonyi
P. arabicus
P. ariel
P. babu
P. bodenheimeri
P. cadornae
P. ceylonicus
P. circumdatus
P. coromandra
P. crassulus
P. cuprosus
P. dormeri
P. eisentrauti
P. endoi
P. hesperus
P. imbricatus
P. inexspectatus
P. javanicus
P. joffrei
P. kitcheneri
P. kuhlii
P. lophurus
P. macrotis
P. maderensis
P. mimus
P. minahassae
P. mordax
P. musciculus
P. nanulus
P. nanus
P. nathusii
P. paterculus
P. peguensis
P. permixtus
P. petersi
P. pipistrellus
P. pulveratus
P. rueppelli
P. rusticus
P. savii
P. societatis
P. stenopterus
P. sturdeei
P. subflavus
P. tasmaniensis
P. tenuis
Plecotus [Genus]
P. auritus [Species]
P. austriacus
P. mexicanus
P. rafinesquii
P. taivanus
P. teneriffae
P. townsendii
Rhogeessa [Genus]
R. alleni [Species]
R. genowaysi
R. gracilis
R. minutilla
R. mira
R. parvula
R. tumida
Scotoecus [Genus]
S. albofuscus [Species]
S. hirundo
S. pallidus
Scotomanes [Genus]
S. emarginatus [Species]
S. ornatus

Scotophilus [Genus]
S. borbonicus [Species]
S. celebensis
S. dinganii
S. heathi
S. kuhlii
S. leucogaster
S. nigrita
S. nux
S. robustus
S. viridis
Tomopeas [Genus]
T. ravus [Species]
Tylonycteris [Genus]
T. pachypus [Species]
T. robustula
Vespertilio [Genus]
V. murinus [Species]
V. superans

Primates [Order]

Lorisidae [Family]
Arctocebus [Genus]
A. aureus [Species]
A. calabarensis
Loris [Genus]
L. tardigradus [Species]
Nycticebus [Genus]
N. coucang [Species]
N. pygmaeus
Perodicticus [Genus]
P. potto [Species]

Galagidae [Family]
Euoticus [Genus]
E. elegantulus [Species]
E. pallidus
Galago [Genus]
G. alleni [Species]
G. gallarum
G. matschiei
G. moholi
G. senegalensis
Galagoides [Genus]
G. demidoff [Species]
G. zanzibaricus
Otolemur [Genus]
O. crassicaudatus [Species]
O. garnettii

Cheirogaleidae [Family]
Allocebus [Genus]
A. trichotis [Species]
Cheirogaleus [Genus]
C. major [Species]
C. medius
Microcebus [Genus]
Microcebus coquereli [Species]
Microcebus murinus
Microcebus rufus
Phaner [Genus]
P. furcifer [Species]

Lemuridae [Family]
Eulemur [Genus]
E. coronatus [Species]
E. fulvus
E. macaco
E. mongoz
E. rubriventer
Hapalemur [Genus]
H. aureus [Species]
H. griseus
H. simus
Lemur [Genus]
L. catta [Species]
Varecia [Genus]
V. variegata [Species]

Indriidae [Family]
Avahi [Genus]
A. laniger [Species]
Indri [Genus]
I. indri [Species]
Propithecus [Genus]
P. diadema [Species]
P. tattersalli
P. verreauxi

Lepilemuridae [Family]
Lepilemur [Genus]
L. dorsalis [Species]
L. edwardsi
L. leucopus
L. microdon
L. mustelinus
L. ruficaudatus
L. septentrionalis

Daubentoniidae [Family]
Daubentonia [Genus]
D. madagascariensis [Species]

Tarsiidae [Family]
Tarsius [Genus]
T. bancanus [Species]
T. dianae
T. pumilus
T. spectrum
T. syrichta

Cebidae [Family]
Alouatta [Genus]
A. belzebul [Species]
A. caraya
A. coibensis
A. fusca
A. palliata
A. pigra
A. sara
A. seniculus
Callicebus [Genus]
C. brunneus [Species]
C. caligatus
C. cinerascens
C. cupreus
C. donacophilus
C. dubius
C. hoffmannsi
C. modestus
C. moloch
C. oenanthe
C. olallae
C. personatus
C. torquatus
Cebus [Genus]
C. albifrons [Species]
C. apella
C. capucinus
C. olivaceus
Saimiri [Genus]
S. boliviensis [Species]
S. oerstedii
S. sciureus
S. ustus
S. vanzolinii

Callitrichidae [Family]
Callimico [Genus]
C. goeldii [Species]
Callithrix [Genus]
C. argentata [Species]
C. aurita
C. flaviceps
C. geoffroyi
C. humeralifer
C. jacchus
C. kuhlii
C. penicillata
C. pygmaea
Leontopithecus [Genus]
L. caissara [Species]
L. chrysomela
L. chrysopygus
L. rosalia
Saguinus [Genus]
S. bicolor [Species]
S. fuscicollis
S. geoffroyi
S. imperator
S. inustus
S. labiatus
S. leucopus
S. midas
S. mystax
S. nigricollis
S. oedipus
S. tripartitus

Aotidae [Family]
Aotus [Genus]
A. azarai [Species]
A. brumbacki

A. hershkovitzi
A. infulatus
A. lemurinus
A. miconax
A. nancymaae
A. nigriceps
A. trivirgatus
A. vociferans

Pitheciidae [Family]
Cacajao [Genus]
C. calvus [Species]
C. melanocephalus
Chiropotes [Genus]
C. albinasus [Species]
C. satanas
Pithecia [Genus]
P. aequatorialis [Species]
P. albicans
P. irrorata
P. monachus
P. pithecia

Atelidae [Family]
Ateles [Genus]
A. belzebuth [Species]
A. chamek
A. fusciceps
A. geoffroyi
A. marginatus
A. paniscus
Brachyteles [Genus]
B. arachnoides [Species]
Lagothrix [Genus]
L. flavicauda [Species]
L. lagotricha

Cercopithecidae [Family]
Allenopithecus [Genus]
A. nigroviridis [Species]
Cercocebus [Genus]
C. agilis [Species]
C. galeritus
C. torquatus
Cercopithecus [Genus]
C. ascanius [Species]
C. campbelli
C. cephus
C. diana
C. dryas
C. erythrogaster
C. erythrotis
C. hamlyni
C. lhoesti
C. mitis
C. mona
C. neglectus
C. nictitans
C. petaurista
C. pogonias
C. preussi
C. sclateri
C. solatus
C. wolfi
Chlorocebus [Genus]
C. aethiops [Species]
Colobus [Genus]
C. angolensis [Species]
C. guereza
C. polykomos
C. satanas
Erythrocebus [Genus]
E. patas [Species]
Lophocebus [Genus]
L. albigena [Species]
Macaca [Genus]
M. arctoides [Species]
M. assamensis
M. cyclopis
M. fascicularis
M. fuscata
M. maura
M. mulatta
M. nemestrina
M. nigra
M. ochreata
M. radiata
M. silenus
M. sinica
M. sylvanus
M. thibetana
M. tonkeana
Mandrillus [Genus]
M. leucophaeus [Species]
M. sphinx
Miopithecus
M. talapoin
Nasalis [Genus]
N. concolor [Species]
N. larvatus
Papio [Genus]
P. hamadryas [Species]
Presbytis [Genus]
P. comata [Species]
P. femoralis
P. frontata
P. hosei
P. melalophos
P. potenziani
P. rubicunda
P. thomasi
Procolobus [Genus]
P. badius [Species]
P. pennantii
P. preussi
P. rufomitratus
P. verus
Pygathrix [Genus]
P. avunculus [Species]
P. bieti
P. brelichi
P. nemaeus
P. roxellana
Semnopithecus [Genus]
S. entellus [Species]
Theropithecus [Genus]
T. gelada [Species]
Trachypithecus [Genus]
T. auratus [Species]
T. cristatus
T. francoisi
T. geei
T. johnii
T. obscurus
T. phayrei
T. pileatus
T. vetulus

Hylobatidae [Family]
Hylobates [Genus]
H. agilis [Species]
H. concolor
H. gabriellae
H. hoolock
H. klossii
H. lar
H. leucogenys
H. moloch
H. muelleri
H. pileatus
H. syndactylus

Hominidae [Family]
Gorilla [Genus]
G. gorilla [Species]
Homo [Genus]
H. sapiens [Species]
Pan [Genus]
P. paniscus [Species]
P. troglodytes
Pongo [Genus]
P. pygmaeus [Species]

Carnivora [Order]

Canidae [Family]
Alopex [Genus]
A. lagopus [Species]
Atelocynus
A. microtis
Canis [Genus]
C. adustus [Species]
C. aureus
C. latrans
C. lupus
C. mesomelas
C. rufus
C. simensis
Cerdocyon [Genus]
C. thous [Species]
Chrysocyon [Genus]
C. brachyurus [Species]
Cuon [Genus]

C. alpinus [Species]
Dusicyon [Genus]
D. australis [Species]
Lycaon [Genus]
L. pictus [Species]
Nyctereutes [Genus]
N. procyonoides [Species]
Otocyon [Genus]
O. megalotis [Species]
Pseudalopex [Genus]
P. culpaeus [Species]
P. griseus
P. gymnocercus
P. sechurae
P. vetulus
Speothos [Genus]
S. venaticus [Species]
Urocyon [Genus]
U. cinereoargenteus [Species]
U. littoralis
Vulpes [Genus]
V. bengalensis [Species]
V. cana
V. chama
V. corsac
V. ferrilata
V. pallida
V. rueppelli
V. velox
V. vulpes
V. zerda

Ursidae [Family]
Ailuropoda [Genus]
A. melanoleuca [Species]
Ailurus [Genus]
A. fulgens [Species]
Helarctos [Genus]
H. malayanus [Species]
Melursus [Genus]
M. ursinus [Species]
Tremarctos [Genus]
T. ornatus [Species]
Ursus [Genus]
U. americanus [Species]
U. arctos
U. maritimus
U. thibetanus

Procyonidae [Family]
Bassaricyon [Genus]
B. alleni [Species]
B. beddardi
B. gabbii
B. lasius
B. pauli
Potos [Genus]
P. flavus [Species]
Bassariscus [Genus]
B. astutus [Species]
B. sumichrasti
Nasua [Genus]
N. narica [Species]
N. nasua
Nasuella [Genus]
N. olivacea [Species]
Procyon [Genus]
P. cancrivorus [Species]
P. gloveralleni
P. insularis
P. lotor
P. maynardi
P. minor
P. pygmaeus

Mustelidae [Family]
Amblonyx [Genus]
A. cinereus [Species]
Aonyx [Genus]
A. capensis [Species]
A. congicus
Arctonyx [Genus]
A. collaris [Species]
Conepatus [Genus]
C. chinga [Species]
C. humboldtii
C. leuconotus
C. mesoleucus
C. semistriatus
Eira [Genus]
E. barbara [Species]
Enhydra [Genus]
E. lutris [Species]
Galictis [Genus]
G. cuja [Species]
G. vittata
Gulo [Genus]
G. gulo [Species]
Ictonyx [Genus]
I. libyca [Species]
I. striatus
Lontra [Genus]
L. canadensis [Species]
L. felina
L. longicaudis
L. provocax
Lutra [Genus]
L. lutra [Species]
L. maculicollis
L. sumatrana
Lutrogale [Genus]
L. perspicillata [Species]
Lyncodon [Genus]
L. patagonicus [Species]
Martes [Genus]
M. americana [Species]
M. flavigula
M. foina
M. gwatkinsii
M. martes
M. melampus
M. pennanti
M. zibellina
Meles [Genus]
M. meles [Species]
Mellivora [Genus]
M. capensis [Species]
Melogale [Genus]
M. everetti [Species]
M. moschata
M. orientalis
M. personata
Mephitis [Genus]
M. macroura [Species]
M. mephitis
Mustela [Genus]
M. africana [Species]
M. altaica
M. erminea
M. eversmannii
M. felipei
M. frenata
M. kathiah
M. lutreola
M. lutreolina
M. nigripes
M. nivalis
M. nudipes
M. putorius
M. sibirica
M. strigidorsa
M. vison
Mydaus [Genus]
M. javanensis [Species]
M. marchei
Poecilogale [Genus]
P. albinucha [Species]
Pteronura [Genus]
P. brasiliensis [Species]
Spilogale [Genus]
S. putorius [Species]
S. pygmaea
Taxidea [Genus]
T. taxus [Species]
Vormela [Genus]
V. peregusna [Species]

Viverridae [Family]
Arctictis [Genus]
A. binturong [Species]
Arctogalidia [Genus]
A. trivirgata [Species]
Chrotogale [Genus]
C. owstoni [Species]
Civettictis [Genus]
C. civetta [Species]
Cryptoprocta [Genus]
C. ferox [Species]
Cynogale [Genus]
C. bennettii [Species]
Diplogale [Genus]
D. hosei [Species]
Eupleres [Genus]

E. goudotii [Species]
Fossa [Genus]
F. fossana [Species]
Genetta [Genus]
G. abyssinica [Species]
G. angolensis
G. genetta
G. johnstoni
G. maculata
G. servalina
G. thierryi
G. tigrina
G. victoriae
Hemigalus [Genus]
H. derbyanus [Species]
Nandinia [Genus]
N. binotata [Species]
Macrogalidia [Genus]
M. musschenbroekii [Species]
Paguma [Genus]
P. larvata [Species]
Paradoxurus [Genus]
P. hermaphroditus [Species]
P. jerdoni
P. zeylonensis
Osbornictis [Genus]
O. piscivora [Species]
Poiana [Genus]
P. richardsonii [Species]
Prionodon [Genus]
P. linsang [Species]
P. pardicolor
Viverra [Genus]
V. civettina [Species]
V. megaspila
V. tangalunga
V. zibetha
Viverricula [Genus]
V. indica [Species]

Herpestidae [Family]
Atilax [Genus]
A. paludinosus [Species]
Bdeogale [Genus]
B. crassicauda [Species]
B. jacksoni
B. nigripes
Crossarchus [Genus]
C. alexandri [Species]
C. ansorgei
C. obscurus
Cynictis [Genus]
C. penicillata [Species]
Dologale [Genus]
D. dybowskii [Species]
Galerella [Genus]
G. flavescens [Species]
G. pulverulenta
G. sanguinea
G. swalius
Galidia [Genus]
G. elegans [Species]
Galidictis [Genus]
G. fasciata [Species]
G. grandidieri
Helogale [Genus]
H. hirtula [Species]
H. parvula
Herpestes [Genus]
H. brachyurus [Species]
H. edwardsii
H. ichneumon
H. javanicus
H. naso
H. palustris
H. semitorquatus
H. smithii
H. urva
H. vitticollis
Ichneumia [Genus]
I. albicauda [Species]
Liberiictis [Genus]
L. kuhni [Species]
Mungos [Genus]
M. gambianus [Species]
M. mungo
Mungotictis [Genus]
M. decemlineata [Species]
Paracynictis [Genus]
P. selousi [Species]
Rhynchogale [Genus]
R. melleri [Species]
Salanoia [Genus]
S. concolor [Species]
Suricata [Genus]
S. suricatta [Species]

Hyaenidae [Family]
Crocuta [Genus]
C. crocuta [Species]
Hyaena [Genus]
H. hyaena [Species]
Parahyaena [Genus]
P. brunnea [Species]
Proteles [Genus]
P. cristatus [Species]

Felidae [Family]
Acinonyx [Genus]
A. jubatus [Species]
Caracal [Genus]
C. caracal [Species]
Catopuma [Genus]
C. badia [Species]
C. temminckii
Felis [Genus]
F. bieti [Species]
F. chaus
F. margarita
F. nigripes
F. silvestris
Herpailurus [Genus]
H. yaguarondi [Species]
Leopardus [Genus]
L. pardalis [Species]
L. tigrinus
L. wiedii
Leptailurus [Genus]
L. serval [Species]
Lynx [Genus]
L. canadensis [Species]
L. lynx
L. pardinus
L. rufus
Neofelis [Genus]
N. nebulosa [Species]
Oncifelis [Genus]
O. colocolo [Species]
O. geoffroyi
O. guigna
Oreailurus [Genus]
O. jacobita [Species]
Otocolobus [Genus]
O. manul [Species]
Panthera [Genus]
P. leo [Species]
P. onca
P. pardus
P. tigris
Pardofelis
P. marmorata
Prionailurus [Genus]
P. bengalensis [Species]
P. planiceps
P. rubiginosus
P. viverrinus
Profelis [Genus]
P. aurata [Species]
Puma [Genus]
P. concolor [Species]
Uncia [Genus]
U. uncia [Species]

Otariidae [Family]
Arctocephalus [Genus]
A. australis [Species]
A. forsteri
A. galapagoensis
A. gazella
A. philippii
A. pusillus
A. townsendi
A. tropicalis
Callorhinus [Genus]
C. ursinus [Species]
Eumetopias [Genus]
E. jubatus [Species]
Neophoca [Genus]
N. cinerea [Species]
Otaria [Genus]
O. byronia [Species]

Phocarctos [Genus]
P. hookeri [Species]
Zalophus [Genus]
Z. californianus [Species]

Odobenidae [Family]
Odobenus [Genus]
O. rosmarus [Species]

Phocidae [Family]
Cystophora [Genus]
C. cristata [Species]
Erignathus [Genus]
E. barbatus [Species]
Halichoerus [Genus]
H. grypus [Species]
Hydrurga [Genus]
H. leptonyx [Species]
Leptonychotes [Genus]
L. weddellii [Species]
Lobodon [Genus]
L. carcinophagus [Species]
Mirounga [Genus]
M. angustirostris [Species]
M. leonina
Monachus [Genus]
M. monachus [Species]
M. schauinslandi
M. tropicalis
Ommatophoca [Genus]
O. rossii [Species]
Phoca [Genus]
P. caspica [Species]
P. fasciata
P. groenlandica
P. hispida
P. largha
P. sibirica
P. vitulina

Cetacea [Order]

Platanistidae [Family]
Platanista [Genus]
P. gangetica [Species]
P. minor

Lipotidae [Family]
Lipotes [Genus]
L. vexillifer [Species]

Pontoporiidae [Family]
Pontoporia [Genus]
P. blainvillei [Species]

Iniidae [Family]
Inia [Genus]
I. geoffrensis [Species]

Phocoenidae [Family]
Australophocaena [Genus]
A. dioptrica [Species]
Neophocaena [Genus]
N. phocaenoides [Species]
Phocoena [Genus]
P. phocoena [Species]
P. sinus
P. spinipinnis
Phocoenoides [Genus]
P. dalli [Species]

Delphinidae [Family]
Cephalorhynchus [Genus]
C. commersonii [Species]
C. eutropia
C. heavisidii
C. hectori
Delphinus [Genus]
D. delphis [Species]
Feresa [Genus]
F. attenuata [Species]
Globicephala [Genus]
G. macrorhynchus [Species]
G. melas
Grampus [Genus]
G. griseus [Species]
Lagenodelphis [Genus]
L. hosei [Species]
Lagenorhynchus [Genus]
L. acutus [Species]
L. albirostris
L. australis
L. cruciger
L. obliquidens
L. obscurus
Lissodelphis [Genus]
L. borealis [Species]
L. peronii
Orcaella [Genus]
O. brevirostris [Species]
Orcinus [Genus]
O. orca [Species]
Peponocephala [Genus]
P. electra [Species]
Pseudorca [Genus]
P. crassidens [Species]
Sotalia [Genus]
S. fluviatilis [Species]
Sousa [Genus]
S. chinensis [Species]
S. teuszii
Stenella [Genus]
S. attenuata [Species]
S. clymene
S. coeruleoalba
S. frontalis
S. longirostris
Steno [Genus]
S. bredanensis [Species]
Tursiops [Genus]
T. truncatus [Species]

Ziphiidae [Family]
Berardius [Genus]
B. arnuxii [Species]
B. bairdii
Hyperoodon [Genus]
H. ampullatus [Species]
H. planifrons
Indopacetus [Genus]
I. pacificus [Species]
Mesoplodon [Genus]
M. bidens [Species]
M. bowdoini
M. carlhubbsi
M. densirostris
M. europaeus
M. ginkgodens
M. grayi
M. hectori
M. layardii
M. mirus
M. peruvianus
M. stejnegeri
Tasmacetus [Genus]
T. shepherdi [Species]
Ziphius [Genus]
Z. cavirostris [Species]

Physeteridae [Family]
Kogia [Genus]
K. breviceps [Species]
K. simus
Physeter [Genus]
P. catodon [Species]

Monodontidae [Family]
Delphinapterus [Genus]
D. leucas [Species]
Monodon [Genus]
M. monoceros [Species]

Eschrichtiidae [Family]
Eschrichtius [Genus]
E. robustus [Species]

Neobalaenidae [Family]
Caperea [Genus]
C. marginata [Species]

Balaenidae [Family]
Balaena [Genus]
B. mysticetus [Species]
Eubalaena [Genus]
E. australis [Species]
E. glacialis

Balaenopteridae [Family]
Balaenoptera [Genus]
B. acutorostrata [Species]
B. borealis
B. edeni
B. musculus
B. physalus
Megaptera [Genus]
M. novaeangliae [Species]

Tubulidentata [Order]

Orycteropodidae [Family]
Orycteropus [Genus]
O. afer [Species]

Proboscidea [Order]

Elephantidae [Family]
Elephas [Genus]
E. maximus [Species]
Loxodonta [Genus]
L. africana [Species]
L. cyclotis

Hyracoidea [Order]

Procaviidae [Family]
Dendrohyrax [Genus]
D. arboreus [Species]
D. dorsalis
D. validus
Heterohyrax [Genus]
H. antineae [Species]
H. brucei
Procavia [Genus]
P. capensis [Species]

Sirenia [Order]

Dugongidae [Family]
Dugong [Genus]
D. dugon [Species]
Hydrodamalis [Genus]
H. gigas [Species]

Trichechidae [Family]
Trichechus [Genus]
T. inunguis [Species]
T. manatus
T. senegalensis

Perissodactyla [Order]

Equidae [Family]
Equus [Genus]
E. asinus [Species]
E. burchellii
E. caballus
E. grevyi
E. hemionus
E. kiang
E. onager
E. quagga
E. zebra

Tapiridae [Family]
Tapirus [Genus]
T. bairdii [Species]
T. indicus
T. pinchaque
T. terrestris

Rhinocerotidae [Family]
Ceratotherium [Genus]
C. simum [Species]
Dicerorhinus [Genus]
D. sumatrensis [Species]
Diceros [Genus]
D. bicornis [Species]
Rhinoceros [Genus]
R. sondaicus [Species]
R. unicornis

Artiodactyla [Order]

Suidae [Family]
Babyrousa [Genus]
B. babyrussa [Species]
Phacochoerus [Genus]
P. aethiopicus [Species]
P. africanus
Hylochoerus [Genus]
H. meinertzhageni [Species]
Potamochoerus [Genus]
P. larvatus [Species]
P. porcus
Sus [Genus]
S. barbatus [Species]
S. bucculentus
S. cebifrons
S. celebensis
S. heureni
S. philippensis
S. salvanius
S. scrofa
S. timoriensis
S. verrucosus

Tayassuidae [Family]
Catagonus [Genus]
C. wagneri [Species]
Pecari [Genus]
P. tajacu [Species]
Tayassu [Genus]
T. pecari [Species]

Hippopotamidae [Family]
Hexaprotodon [Genus]
H. liberiensis [Species]
H. madagascariensis
Hippopotamus [Genus]
H. amphibius [Species]
H. lemerlei

Camelidae [Family]
Camelus [Genus]
C. bactrianus [Species]
C. dromedarius
Lama [Genus]
L. glama [Species]
L. guanicoe
L. pacos
Vicugna [Genus]
V. vicugna [Species]

Tragulidae [Family]
Hyemoschus [Genus]
H. aquaticus [Species]
Moschiola [Genus]
M. meminna [Species]
Tragulus [Genus]
T. javanicus [Species]
T. napu

Cervidae [Family]
Alces [Genus]
A. alces [Species]
Axis [Genus]
A. axis [Species]
A. calamianensis
A. kuhlii
A. porcinus
Blastocerus [Genus]
B. dichotomus [Species]
Capreolus [Genus]
C. capreolus [Species]
C. pygargus
Cervus [Genus]
C. albirostris [Species]
C. alfredi
C. duvaucelii
C. elaphus
C. eldii
C. mariannus
C. nippon
C. schomburgki
C. timorensis
C. unicolor
Dama [Genus]
D. dama [Species]
D. mesopotamica
Elaphodus [Genus]
E. cephalophus [Species]
Elaphurus [Genus]
E. davidianus [Species]
Hippocamelus [Genus]
H. antisensis [Species]
H. bisulcus
Hydropotes [Genus]
H. inermis [Species]
Mazama [Genus]
M. americana [Species]
M. bricenii
M. chunyi
M. gouazoupira
M. nana
M. rufina
Moschus [Genus]
M. berezovskii [Species]
M. chrysogaster
M. fuscus
M. moschiferus
Muntiacus [Genus]
M. atherodes [Species]
M. crinifrons
M. feae
M. gongshanensis

M. muntjak
M. reevesi
Odocoileus [Genus]
O. hemionus [Species]
O. virginianus
Ozotoceros [Genus]
O. bezoarticus [Species]
Pudu [Genus]
P. mephistophiles [Species]
P. puda
Rangifer [Genus]
R. tarandus [Species]

Giraffidae [Family]
Giraffa [Genus]
G. camelopardalis [Species]
Okapia [Genus]
O. johnstoni [Species]

Antilocapridae [Family]
Antilocapra [Genus]
A. americana [Species]

Bovidae [Family]
Addax [Genus]
A. nasomaculatus [Species]
Aepyceros [Genus]
A. melampus [Species]
Alcelaphus [Genus]
A. buselaphus [Species]
Ammodorcas [Genus]
A. clarkei [Species]
Ammotragus [Genus]
A. lervia [Species]
Antidorcas [Genus]
A. marsupialis [Species]
Antilope [Genus]
A. cervicapra [Species]
Bison [Genus]
B. bison [Species]
B. bonasus
Bos [Genus]
B. frontalis [Species]
B. grunniens
B. javanicus
B. sauveli
B. taurus
Boselaphus [Genus]
B. tragocamelus [Species]
Bubalus [Genus]
B. bubalis [Species]
B. depressicornis
B. mephistopheles
B. mindorensis
B. quarlesi
Budorcas [Genus]
B. taxicolor [Species]
Capra [Genus]
C. caucasica [Species]
C. cylindricornis
C. falconeri
C. hircus
C. ibex
C. nubiana
C. pyrenaica
C. sibirica
C. walie
Cephalophus [Genus]
C. adersi [Species]
C. callipygus
C. dorsalis
C. harveyi
C. jentinki
C. leucogaster
C. maxwellii
C. monticola
C. natalensis
C. niger
C. nigrifrons
C. ogilbyi
C. rubidus
C. rufilatus
C. silvicultor
C. spadix
C. weynsi
C. zebra
Connochaetes [Genus]
C. gnou [Species]
C. taurinus
Damaliscus [Genus]
D. hunteri [Species]
D. lunatus
D. pygargus
Dorcatragus [Genus]
D. megalotis [Species]
Gazella [Genus]
G. arabica [Species]
G. bennettii
G. bilkis
G. cuvieri
G. dama
G. dorcas
G. gazella
G. granti
G. leptoceros
G. rufifrons
G. rufina
G. saudiya
G. soemmerringii
G. spekei
G. subgutturosa
G. thomsonii
Hemitragus [Genus]
H. hylocrius [Species]
H. jayakari
H. jemlahicus
Hippotragus [Genus]
H. equinus [Species]
H. leucophaeus
H. niger
Kobus [Genus]
K. ellipsiprymnus [Species]
K. kob
K. leche
K. megaceros
K. vardonii
Litocranius [Genus]
L. walleri [Species]
Madoqua [Genus]
M. guentheri [Species]
M. kirkii
M. piacentinii
M. saltiana
Naemorhedus [Genus]
N. baileyi [Species]
N. caudatus
N. crispus
N. goral
N. sumatraensis
N. swinhoei
Neotragus [Genus]
N. batesi [Species]
N. moschatus
N. pygmaeus
Oreamnos [Genus]
O. americanus [Species]
Oreotragus [Genus]
O. oreotragus [Species]
Oryx [Genus]
O. dammah [Species]
O. gazella
O. leucoryx
Ourebia [Genus]
O. ourebi [Species]
Ovibos [Genus]
O. moschatus [Species]
Ovis [Genus]
O. ammon [Species]
O. aries
O. canadensis
O. dalli
O. nivicola
O. vignei
Pantholops [Genus]
P. hodgsonii [Species]
Pelea [Genus]
P. capreolus [Species]
Procapra [Genus]
P. gutturosa [Species]
P. picticaudata
P. przewalskii
Pseudois [Genus]
P. nayaur [Species]
P. schaeferi
Raphicerus [Genus]
R. campestris [Species]
R. melanotis
R. sharpei
Redunca [Genus]
R. arundinum [Species]
R. fulvorufula
R. redunca

Rupicapra [Genus]
R. pyrenaica [Species]
R. rupicapra
Saiga [Genus]
S. tatarica [Species]
Sigmoceros [Genus]
S. lichtensteinii [Species]
Sylvicapra [Genus]
S. grimmia [Species]
Syncerus [Genus]
S. caffer [Species]
Taurotragus [Genus]
T. derbianus [Species]
T. oryx
Tetracerus [Genus]
T. quadricornis [Species]
Tragelaphus [Genus]
T. angasii [Species]
T. buxtoni
T. eurycerus
T. imberbis
T. scriptus
T. spekii
T. strepsiceros

Pholidota [Order]

Manidae [Family]
Manis [Genus]
M. crassicaudata [Species]
M. gigantea
M. javanica
M. pentadactyla
M. temminckii
M. tetradactyla
M. tricuspis

Rodentia [Order]

Aplodontidae [Family]
Aplodontia [Genus]
A. rufa [Species]

Sciuridae [Family]
Aeretes [Genus]
A. melanopterus [Species]
Aeromys [Genus]
A. tephromelas [Species]
A. thomasi
Ammospermophilus [Genus]
A. harrisii [Species]
A. insularis
A. interpres
A. leucurus
A. nelsoni
Atlantoxerus [Genus]
A. getulus [Species]
Belomys [Genus]
B. pearsonii [Species]
Biswamoyopterus [Genus]
B. biswasi [Species]
Callosciurus [Genus]
C. adamsi [Species]
C. albescens
C. baluensis
C. caniceps
C. erythraeus
C. finlaysonii
C. inornatus
C. melanogaster
C. nigrovittatus
C. notatus
C. orestes
C. phayrei
C. prevostii
C. pygerythrus
C. quinquestriatus
Cynomys [Genus]
C. gunnisoni [Species]
C. leucurus
C. ludovicianus
C. mexicanus
C. parvidens
Dremomys [Genus]
D. everetti [Species]
D. lokriah
D. pernyi
D. pyrrhomerus
D. rufigenis
Epixerus [Genus]
E. ebii [Species]
E. wilsoni
Eupetaurus [Genus]
E. cinereus [Species]
Exilisciurus [Genus]
E. concinnus [Species]
E. exilis
E. whiteheadi
Funambulus [Genus]
F. layardi [Species]
F. palmarum
F. pennantii
F. sublineatus
F. tristriatus
Funisciurus [Genus]
F. anerythrus [Species]
F. bayonii
F. carruthersi
F. congicus
F. isabella
F. lemniscatus
F. leucogenys
F. pyrropus
F. substriatus
Glaucomys [Genus]
G. sabrinus [Species]
G. volans
Glyphotes [Genus]
G. simus [Species]
Heliosciurus [Genus]
H. gambianus [Species]
H. mutabilis
H. punctatus
H. rufobrachium
H. ruwenzorii
H. undulatus
Hylopetes [Genus]
H. alboniger [Species]
H. baberi
H. bartelsi
H. fimbriatus
H. lepidus
H. nigripes
H. phayrei
H. sipora
H. spadiceus
H. winstoni
Hyosciurus [Genus]
H. heinrichi [Species]
H. ileile
Iomys [Genus]
I. horsfieldi [Species]
I. sipora
Lariscus [Genus]
L. hosei [Species]
L. insignis
L. niobe
L. obscurus
Marmota [Genus]
M. baibacina [Species]
M. bobak
M. broweri
M. caligata
M. camtschatica
M. caudata
M. flaviventris
M. himalayana
M. marmota
M. menzbieri
M. monax
M. olympus
M. sibirica
M. vancouverensis
Menetes [Genus]
M. berdmorei [Species]
Microsciurus [Genus]
M. alfari [Species]
M. flaviventer
M. mimulus
M. santanderensis
Myosciurus [Genus]
M. pumilio [Species]
Nannosciurus [Genus]
N. melanotis [Species]
Paraxerus [Genus]
P. alexandri [Species]
P. boehmi
P. cepapi
P. cooperi
P. flavovittis
P. lucifer

P. ochraceus
P. palliatus
P. poensis
P. vexillarius
P. vincenti
Petaurillus [Genus]
P. emiliae [Species]
P. hosei
P. kinlochii
Petaurista [Genus]
P. alborufus [Species]
P. elegans
P. leucogenys
P. magnificus
P. nobilis
P. petaurista
P. philippensis
P. xanthotis
Petinomys [Genus]
P. crinitus [Species]
P. fuscocapillus
P. genibarbis
P. hageni
P. lugens
P. sagitta
P. setosus
P. vordermanni
Prosciurillus [Genus]
P. abstrusus [Species]
P. leucomus
P. murinus
P. weberi
Protoxerus [Genus]
P. aubinnii [Species]
P. stangeri
Pteromys [Genus]
P. momonga [Species]
P. volans
Pteromyscus [Genus]
P. pulverulentus [Species]
Ratufa [Genus]
R. affinis [Species]
R. bicolor
R. indica
R. macroura
Rheithrosciurus [Genus]
R. macrotis [Species]
Rhinosciurus [Genus]
R. laticaudatus [Species]
Rubrisciurus [Genus]
R. rubriventer [Species]
Sciurillus [Genus]
S. pusillus [Species]
Sciurotamias [Genus]
S. davidianus [Species]
S. forresti
Sciurus [Genus]
S. aberti [Species]
S. aestuans
S. alleni
S. anomalus
S. arizonensis
S. aureogaster
S. carolinensis
S. colliaei
S. deppei
S. flammifer
S. gilvigularis
S. granatensis
S. griseus
S. ignitus
S. igniventris
S. lis
S. nayaritensis
S. niger
S. oculatus
S. pucheranii
S. pyrrhinus
S. richmondi
S. sanborni
S. spadiceus
S. stramineus
S. variegatoides
S. vulgaris
S. yucatanensis
Spermophilopsis [Genus]
S. leptodactylus [Species]
Spermophilus [Genus]
S. adocetus [Species]
S. alashanicus
S. annulatus
S. armatus
S. atricapillus
S. beecheyi
S. beldingi
S. brunneus
S. canus
S. citellus
S. columbianus
S. dauricus
S. elegans
S. erythrogenys
S. franklinii
S. fulvus
S. lateralis
S. madrensis
S. major
S. mexicanus
S. mohavensis
S. mollis
S. musicus
S. parryii
S. perotensis
S. pygmaeus
S. relictus
S. richardsonii
S. saturatus
S. spilosoma
S. suslicus
S. tereticaudus
S. townsendii
S. tridecemlineatus
S. undulatus
S. variegatus
S. washingtoni
S. xanthoprymnus
Sundasciurus [Genus]
S. brookei [Species]
S. davensis
S. fraterculus
S. hippurus
S. hoogstraali
S. jentinki
S. juvencus
S. lowii
S. mindanensis
S. moellendorffi
S. philippinensis
S. rabori
S. samarensis
S. steerii
S. tenuis
Syntheosciurus [Genus]
S. brochus [Species]
Tamias [Genus]
T. alpinus [Species]
T. amoenus
T. bulleri
T. canipes
T. cinereicollis
T. dorsalis
T. durangae
T. merriami
T. minimus
T. obscurus
T. ochrogenys
T. palmeri
T. panamintinus
T. quadrimaculatus
T. quadrivittatus
T. ruficaudus
T. rufus
T. senex
T. sibiricus
T. siskiyou
T. sonomae
T. speciosus
T. striatus
T. townsendii
T. umbrinus
Tamiasciurus [Genus]
T. douglasii [Species]
T. hudsonicus
T. mearnsi
Tamiops [Genus]
T. macclellandi [Species]
T. maritimus
T. rodolphei
T. swinhoei
Trogopterus [Genus]

T. xanthipes [Species]
Xerus [Genus]
X. erythropus [Species]
X. inauris
X. princeps
X. rutilus

Castoridae [Family]
Castor [Genus]
C. canadensis [Species]
C. fiber

Geomyidae [Family]
Geomys [Genus]
G. arenarius [Species]
G. bursarius
G. personatus
G. pinetis
G. tropicalis
Orthogeomys [Genus]
O. cavator [Species]
O. cherriei
O. cuniculus
O. dariensis
O. grandis
O. heterodus
O. hispidus
O. lanius
O. matagalpae
O. thaeleri
O. underwoodi
Pappogeomys [Genus]
P. alcorni [Species]
P. bulleri
P. castanops
P. fumosus
P. gymnurus
P. merriami
P. neglectus
P. tylorhinus
P. zinseri
Thomomys [Genus]
T. bottae [Species]
T. bulbivorus
T. clusius
T. idahoensis
T. mazama
T. monticola
T. talpoides
T. townsendii
T. umbrinus
Zygogeomys [Genus]
Z. trichopus [Species]

Heteromyidae [Family]
Chaetodipus [Genus]
C. arenarius [Species]
C. artus
C. baileyi
C. californicus
C. fallax
C. formosus
C. goldmani
C. hispidus
C. intermedius
C. lineatus
C. nelsoni
C. penicillatus
C. pernix
C. spinatus
Dipodomys [Genus]
D. agilis [Species]
D. californicus
D. compactus
D. deserti
D. elator
D. elephantinus
D. gravipes
D. heermanni
D. ingens
D. insularis
D. margaritae
D. merriami
D. microps
D. nelsoni
D. nitratoides
D. ordii
D. panamintinus
D. phillipsii
D. spectabilis
D. stephensi
D. venustus
Microdipodops [Genus]
M. megacephalus [Species]
M. pallidus
Heteromys [Genus]
H. anomalus [Species]
H. australis
H. desmarestianus
H. gaumeri
H. goldmani
H. nelsoni
H. oresterus
Liomys [Genus]
L. adspersus [Species]
L. irroratus
L. pictus
L. salvini
L. spectabilis
Perognathus [Genus]
P. alticola [Species]
P. amplus
P. fasciatus
P. flavescens
P. flavus
P. inornatus
P. longimembris
P. merriami
P. parvus
P. xanthanotus

Dipodidae [Family]
Allactaga [Genus]
A. balikunica [Species]
A. bullata
A. elater
A. euphratica
A. firouzi
A. hotsoni
A. major
A. severtzovi
A. sibirica
A. tetradactyla
A. vinogradovi
Allactodipus [Genus]
A. bobrinskii [Species]
Cardiocranius [Genus]
C. paradoxus [Species]
Dipus [Genus]
D. sagitta [Species]
Eozapus [Genus]
E. setchuanus [Species]
Eremodipus [Genus]
E. lichtensteini [Species]
Euchoreutes [Genus]
E. naso [Species]
Jaculus [Genus]
J. blanfordi [Species]
J. jaculus
J. orientalis
J. turcmenicus
Napaeozapus [Genus]
N. insignis [Species]
Paradipus [Genus]
P. ctenodactylus [Species]
Pygeretmus [Genus]
P. platyurus [Species]
P. pumilio
P. shitkovi
Salpingotus [Genus]
S. crassicauda [Species]
S. heptneri
S. kozlovi
S. michaelis
S. pallidus
S. thomasi
Sicista [Genus]
S. armenica [Species]
S. betulina
S. caucasica
S. caudata
S. concolor
S. kazbegica
S. kluchorica
S. napaea
S. pseudonapaea
S. severtzovi
S. strandi
S. subtilis
S. tianshanica
Stylodipus [Genus]

S. andrewsi [Species]
S. sungorus
S. telum
Zapus [Genus]
Z. hudsonius [Species]
Z. princeps
Z. trinotatus

Muridae [Family]
Abditomys [Genus]
A. latidens [Species]
Abrawayaomys [Genus]
A. ruschii [Species]
Acomys [Genus]
A. cahirinus [Species]
A. cilicicus
A. cinerasceus
A. ignitus
A. kempi
A. louisae
A. minous
A. mullah
A. nesiotes
A. percivali
A. russatus
A. spinosissimus
A. subspinosus
A. wilsoni
Aepeomys [Genus]
A. fuscatus [Species]
A. lugens
Aethomys [Genus]
A. bocagei [Species]
A. chrysophilus
A. granti
A. hindei
A. kaiseri
A. namaquensis
A. nyikae
A. silindensis
A. stannarius
A. thomasi
Akodon [Genus]
A. aerosus [Species]
A. affinis
A. albiventer
A. azarae
A. bogotensis
A. boliviensis
A. budini
A. cursor
A. dayi
A. dolores
A. fumeus
A. hershkovitzi
A. illuteus
A. iniscatus
A. juninensis
A. kempi
A. kofordi
A. lanosus
A. latebricola
A. lindberghi
A. longipilis
A. mansoensis
A. markhami
A. mimus
A. molinae
A. mollis
A. neocenus
A. nigrita
A. olivaceus
A. orophilus
A. puer
A. sanborni
A. sanctipaulensis
A. serrensis
A. siberiae
A. simulator
A. spegazzinii
A. subfuscus
A. surdus
A. sylvanus
A. toba
A. torques
A. urichi
A. varius
A. xanthorhinus
Allocricetulus [Genus]
A. curtatus [Species]
A. eversmanni
Alticola [Genus]
A. albicauda [Species]
A. argentatus
A. barakshin
A. lemminus
A. macrotis
A. montosa
A. roylei
A. semicanus
A. stoliczkanus
A. stracheyi
A. strelzowi
A. tuvinicus
Ammodillus [Genus]
A. imbellis [Species]
Andalgalomys [Genus]
A. olrogi [Species]
A. pearsoni
Andinomys [Genus]
A. edax [Species]
Anisomys [Genus]
A. imitator [Species]
Anonymomys [Genus]
A. mindorensis [Species]
Anotomys [Genus]
A. leander [Species]
Apodemus [Genus]
A. agrarius [Species]
A. alpicola
A. argenteus
A. arianus
A. chevrieri
A. draco
A. flavicollis
A. fulvipectus
A. gurkha
A. hermonensis
A. hyrcanicus
A. latronum
A. mystacinus
A. peninsulae
A. ponticus
A. rusiges
A. semotus
A. speciosus
A. sylvaticus
A. uralensis
A. wardi
Apomys [Genus]
A. abrae [Species]
A. datae
A. hylocoetes
A. insignis
A. littoralis
A. microdon
A. musculus
A. sacobianus
Arborimus [Genus]
A. albipes [Species]
A. longicaudus
A. pomo
Archboldomys [Genus]
A. luzonensis [Species]
Arvicanthis [Genus]
A. abyssinicus [Species]
A. blicki
A. nairobae
A. niloticus
A. somalicus
Arvicola [Genus]
A. sapidus [Species]
A. terrestris
Auliscomys [Genus]
A. boliviensis [Species]
A. micropus
A. pictus
A. sublimis
Baiomys [Genus]
B. musculus [Species]
B. taylori
Bandicota [Genus]
B. bengalensis [Species]
B. indica
B. savilei
Batomys [Genus]
B. dentatus [Species]
B. granti
B. salomonseni
Beamys [Genus]
B. hindei [Species]

B. major
Berylmys [Genus]
B. berdmorei [Species]
B. bowersi
B. mackenziei
B. manipulus
Bibimys [Genus]
B. chacoensis [Species]
B. labiosus
B. torresi
Blanfordimys [Genus]
B. afghanus [Species]
B. bucharicus
Blarinomys [Genus]
B. breviceps [Species]
Bolomys [Genus]
B. amoenus [Species]
B. lactens
B. lasiurus
B. obscurus
B. punctulatus
B. temchuki
Brachiones [Genus]
B. przewalskii [Species]
Brachytarsomys [Genus]
B. albicauda [Species]
Brachyuromys [Genus]
B. betsileoensis [Species]
B. ramirohitra
Bullimus [Genus]
B. bagobus [Species]
B. luzonicus
Bunomys [Genus]
B. andrewsi [Species]
B. chrysocomus
B. coelestis
B. fratrorum
B. heinrichi
B. penitus
B. prolatus
Calomys [Genus]
C. boliviae [Species]
C. callidus
C. callosus
C. hummelincki
C. laucha
C. lepidus
C. musculinus
C. sorellus
C. tener
Calomyscus [Genus]
C. bailwardi [Species]
C. baluchi
C. hotsoni
C. mystax
C. tsolovi
C. urartensis
Canariomys [Genus]
C. tamarani [Species]
Cannomys [Genus]
C. badius [Species]
Cansumys [Genus]
C. canus [Species]
Carpomys [Genus]
C. melanurus [Species]
C. phaeurus
Celaenomys [Genus]
C. silaceus [Species]
Chelemys [Genus]
C. macronyx [Species]
C. megalonyx
Chibchanomys [Genus]
C. trichotis [Species]
Chilomys [Genus]
C. instans [Species]
Chiromyscus [Genus]
C. chiropus [Species]
Chinchillula [Genus]
C. sahamae [Species]
Chionomys [Genus]
C. gud [Species]
C. nivalis
C. roberti
Chiropodomys [Genus]
C. calamianensis [Species]
C. gliroides
C. karlkoopmani
C. major
C. muroides
C. pusillus
Chiruromys [Genus]
C. forbesi [Species]
C. lamia
C. vates
Chroeomys [Genus]
C. andinus [Species]
C. jelskii
Chrotomys [Genus]
C. gonzalesi [Species]
C. mindorensis
C. whiteheadi
Clethrionomys [Genus]
C. californicus [Species]
C. centralis
C. gapperi
C. glareolus
C. rufocanus
C. rutilus
C. sikotanensis
Coccymys [Genus]
C. albidens [Species]
C. ruemmleri
Colomys [Genus]
C. goslingi [Species]
Conilurus [Genus]
C. albipes [Species]
C. penicillatus
Coryphomys [Genus]
C. buhleri [Species]
Crateromys [Genus]
C. australis [Species]
C. paulus
C. schadenbergi
Cremnomys [Genus]
C. blanfordi [Species]
C. cutchicus
C. elvira
Cricetomys [Genus]
C. emini [Species]
C. gambianus
Cricetulus [Genus]
C. alticola [Species]
C. barabensis
C. kamensis
C. longicaudatus
C. migratorius
C. sokolovi
Cricetus [Genus]
C. cricetus [Species]
Crossomys [Genus]
C. moncktoni [Species]
Crunomys [Genus]
C. celebensis [Species]
C. fallax
C. melanius
C. rabori
Dacnomys [Genus]
D. millardi [Species]
Dasymys [Genus]
D. foxi [Species]
D. incomtus
D. montanus
D. nudipes
D. rufulus
Delanymys [Genus]
D. brooksi [Species]
Delomys [Genus]
D. dorsalis [Species]
D. sublineatus
Dendromus [Genus]
D. insignis [Species]
D. kahuziensis
D. kivu
D. lovati
D. melanotis
D. mesomelas
D. messorius
D. mystacalis
D. nyikae
D. oreas
D. vernayi
Dendroprionomys [Genus]
D. rousseloti [Species]
Deomys [Genus]
D. ferrugineus [Species]
Dephomys [Genus]
D. defua [Species]
D. eburnea
Desmodilliscus [Genus]
D. braueri [Species]

Desmodillus [Genus]
D. auricularis [Species]
Dicrostonyx [Genus]
D. exsul [Species]
D. groenlandicus
D. hudsonius
D. kilangmiutak
D. nelsoni
D. nunatakensis
D. richardsoni
D. rubricatus
D. torquatus
D. unalascensis
D. vinogradovi
Desmomys [Genus]
D. harringtoni [Species]
Dinaromys [Genus]
D. bogdanovi [Species]
Diomys [Genus]
D. crumpi [Species]
Diplothrix [Genus]
D. legatus [Species]
Echiothrix [Genus]
E. leucura [Species]
Eropeplus [Genus]
E. canus [Species]
Eligmodontia [Genus]
E. moreni [Species]
E. morgani
E. puerulus
E. typus
Eliurus [Genus]
E. majori [Species]
E. minor
E. myoxinus
E. penicillatus
E. tanala
E. webbi
Ellobius [Genus]
E. alaicus [Species]
E. fuscocapillus
E. lutescens
E. talpinus
E. tancrei
Eolagurus [Genus]
E. luteus [Species]
E. przewalskii
Eothenomys [Genus]
E. chinensis [Species]
E. custos
E. eva
E. inez
E. melanogaster
E. olitor
E. proditor
E. regulus
E. shanseius
Euneomys [Genus]
E. chinchilloides [Species]
E. fossor
E. mordax
E. petersoni
Galenomys [Genus]
G. garleppi [Species]
Geoxus [Genus]
G. valdivianus [Species]
Gerbillurus [Genus]
G. paeba [Species]
G. setzeri
G. tytonis
G. vallinus
Gerbillus [Genus]
G. acticola [Species]
G. allenbyi
G. andersoni
G. bilensis
G. bottai
G. burtoni
G. cheesmani
G. dalloni
G. diminutus
G. dunni
G. floweri
G. gerbillus
G. grobbeni
G. henleyi
G. hoogstraali
G. juliani
G. lowei
G. maghrebi
G. mesopotamiae
G. nancillus
G. nigeriae
G. percivali
G. poecilops
G. pulvinatus
G. pyramidum
G. riggenbachi
G. ruberrimus
G. somalicus
G. syrticus
G. vivax
Golunda [Genus]
G. ellioti [Species]
Grammomys [Genus]
G. aridulus [Species]
G. caniceps
G. dolichurus
G. gigas
G. macmillani
G. rutilans
Graomys [Genus]
G. domorum [Species]
G. griseoflavus
Gymnuromys [Genus]
G. roberti [Species]
Habromys [Genus]
H. chinanteco [Species]
H. lepturus
H. lophurus
H. simulatus
Hadromys [Genus]
H. humei [Species]
Haeromys [Genus]
H. margarettae [Species]
H. minahassae
H. pusillus
Hapalomys [Genus]
H. delacouri [Species]
H. longicaudatus
Heimyscus [Genus]
H. fumosus [Species]
Hodomys [Genus]
H. alleni [Species]
Holochilus [Genus]
H. brasiliensis [Species]
H. chacarius
H. magnus
H. sciureus
Hybomys [Genus]
H. basilii [Species]
H. eisentrauti
H. lunaris
H. planifrons
H. trivirgatus
H. univittatus
Hydromys [Genus]
H. chrysogaster [Species]
H. habbema
H. hussoni
H. neobrittanicus
H. shawmayeri
Hylomyscus [Genus]
H. aeta [Species]
H. alleni
H. baeri
H. carillus
H. denniae
H. parvus
H. stella
Hyomys [Genus]
H. dammermani [Species]
H. goliath
Hyperacrius [Genus]
H. fertilis [Species]
H. wynnei
Hypogeomys [Genus]
H. antimena [Species]
Ichthyomys [Genus]
I. hydrobates [Species]
I. pittieri
I. stolzmanni
I. tweedii
Irenomys [Genus]
I. tarsalis [Species]
Isthmomys [Genus]
I. flavidus [Species]
I. pirrensis
Juscelinomys [Genus]
J. candango [Species]

J. vulpinus
Kadarsanomys [Genus]
K. sodyi [Species]
Komodomys [Genus]
K. rintjanus [Species]
Kunsia [Genus]
K. fronto [Species]
K. tomentosus
Lagurus [Genus]
L. lagurus [Species]
Lamottemys [Genus]
L. okuensis [Species]
Lasiopodomys [Genus]
L. brandtii [Species]
L. fuscus
L. mandarinus
Leggadina [Genus]
L. forresti [Species]
L. lakedownensis
Leimacomys [Genus]
L. buettneri [Species]
Lemmiscus [Genus]
L. curtatus [Species]
Lemmus [Genus]
L. amurensis [Species]
L. lemmus
L. sibiricus
Lemniscomys [Genus]
L. barbarus [Species]
L. bellieri
L. griselda
L. hoogstraali
L. linulus
L. macculus
L. mittendorfi
L. rosalia
L. roseveari
L. striatus
Lenomys [Genus]
L. meyeri [Species]
Lenothrix [Genus]
L. canus [Species]
Lenoxus [Genus]
L. apicalis [Species]
Leopoldamys [Genus]
L. edwardsi [Species]
L. neilli
L. sabanus
L. siporanus
Leporillus [Genus]
L. apicalis [Species]
L. conditor
Leptomys [Genus]
L. elegans [Species]
L. ernstmayri
L. signatus
Limnomys [Genus]
L. sibuanus [Species]
Lophiomys [Genus]
L. imhausi [Species]
Lophuromys [Genus]
L. cinereus [Species]
L. flavopunctatus
L. luteogaster
L. medicaudatus
L. melanonyx
L. nudicaudus
L. rahmi
L. sikapusi
L. woosnami
Lorentzimys [Genus]
L. nouhuysi [Species]
Macrotarsomys [Genus]
M. bastardi [Species]
M. ingens
Macruromys [Genus]
M. elegans [Species]
M. major
Malacomys [Genus]
M. cansdalei [Species]
M. edwardsi
M. longipes
M. lukolelae
M. verschureni
Malacothrix [Genus]
M. typica [Species]
Mallomys [Genus]
M. aroaensis [Species]
M. gunung
M. istapantap
M. rothschildi
Malpaisomys [Genus]
M. insularis [Species]
Margaretamys [Genus]
M. beccarii [Species]
M. elegans
M. parvus
Mastomys [Genus]
M. angolensis [Species]
M. coucha
M. erythroleucus
M. hildebrandtii
M. natalensis
M. pernanus
M. shortridgei
M. verheyeni
Maxomys [Genus]
M. alticola [Species]
M. baeodon
M. bartelsii
M. dollmani
M. hellwaldii
M. hylomyoides
M. inas
M. inflatus
M. moi
M. musschenbroekii
M. ochraceiventer
M. pagensis
M. panglima
M. rajah
M. surifer
M. wattsi
M. whiteheadi
Mayermys [Genus]
M. ellermani [Species]
Megadendromus [Genus]
M. nikolausi [Species]
Megadontomys [Genus]
M. cryophilus [Species]
M. nelsoni
M. thomasi
Megalomys [Genus]
M. desmarestii [Species]
M. luciae
Melanomys [Genus]
M. caliginosus [Species]
M. robustulus
M. zunigae
Melasmothrix [Genus]
M. naso [Species]
Melomys [Genus]
M. aerosus [Species]
M. bougainville
M. burtoni
M. capensis
M. cervinipes
M. fellowsi
M. fraterculus
M. gracilis
M. lanosus
M. leucogaster
M. levipes
M. lorentzii
M. mollis
M. moncktoni
M. obiensis
M. platyops
M. rattoides
M. rubex
M. rubicola
M. rufescens
M. spechti
Meriones [Genus]
M. arimalius [Species]
M. chengi
M. crassus
M. dahli
M. hurrianae
M. libycus
M. meridianus
M. persicus
M. rex
M. sacramenti
M. shawi
M. tamariscinus
M. tristrami
M. unguiculatus
M. vinogradovi
M. zarudnyi

Mesembriomys [Genus]
M. gouldii [Species]
M. macrurus
Mesocricetus [Genus]
M. auratus [Species]
M. brandti
M. newtoni
M. raddei
Microdillus [Genus]
M. peeli [Species]
Microhydromys [Genus]
M. musseri [Species]
M. richardsoni
Micromys [Genus]
M. minutus [Species]
Microryzomys [Genus]
M. altissimus [Species]
M. minutus
Microtus [Genus]
M. abbreviatus [Species]
M. agrestis
M. arvalis
M. bavaricus
M. breweri
M. cabrerae
M. californicus
M. canicaudus
M. chrotorrhinus
M. daghestanicus
M. duodecimcostatus
M. evoronensis
M. felteni
M. fortis
M. gerbei
M. gregalis
M. guatemalensis
M. guentheri
M. hyperboreus
M. irani
M. irene
M. juldaschi
M. kermanensis
M. kirgisorum
M. leucurus
M. limnophilus
M. longicaudus
M. lusitanicus
M. majori
M. maximowiczii
M. mexicanus
M. middendorffi
M. miurus
M. mongolicus
M. montanus
M. montebelli
M. mujanensis
M. multiplex
M. nasarovi
M. oaxacensis
M. obscurus
M. ochrogaster
M. oeconomus
M. oregoni
M. pennsylvanicus
M. pinetorum
M. quasiater
M. richardsoni
M. rossiaemeridionalis
M. sachalinensis
M. savii
M. schelkovnikovi
M. sikimensis
M. socialis
M. subterraneus
M. tatricus
M. thomasi
M. townsendii
M. transcaspicus
M. umbrosus
M. xanthognathus
Millardia [Genus]
M. gleadowi [Species]
M. kathleenae
M. kondana
M. meltada
Muriculus [Genus]
M. imberbis [Species]
Mus [Genus]
M. baoulei [Species]
M. booduga
M. bufo
M. callewaerti
M. caroli
M. cervicolor
M. cookii
M. crociduroides
M. famulus
M. fernandoni
M. goundae
M. haussa
M. indutus
M. kasaicus
M. macedonicus
M. mahomet
M. mattheyi
M. mayori
M. minutoides
M. musculoides
M. musculus
M. neavei
M. orangiae
M. oubanguii
M. pahari
M. phillipsi
M. platythrix
M. saxicola
M. setulosus
M. setzeri
M. shortridgei
M. sorella
M. spicilegus
M. spretus
M. tenellus
M. terricolor
M. triton
M. vulcani
Mylomys [Genus]
M. dybowskii [Species]
Myomys [Genus]
M. albipes [Species]
M. daltoni
M. derooi
M. fumatus
M. ruppi
M. verreauxii
M. yemeni
Myopus [Genus]
M. schisticolor [Species]
Myospalax [Genus]
M. aspalax [Species]
M. epsilanus
M. fontanierii
M. myospalax
M. psilurus
M. rothschildi
M. smithii
Mystromys [Genus]
M. albicaudatus [Species]
Nannospalax [Genus]
N. ehrenbergi [Species]
N. leucodon
N. nehringi
Neacomys [Genus]
N. guianae [Species]
N. pictus
N. spinosus
N. tenuipes
Nectomys [Genus]
N. palmipes [Species]
N. parvipes
N. squamipes
Nelsonia [Genus]
N. goldmani [Species]
N. neotomodon
Neofiber [Genus]
N. alleni [Species]
Neohydromys [Genus]
N. fuscus [Species]
Neotoma [Genus]
N. albigula [Species]
N. angustapalata
N. anthonyi
N. bryanti
N. bunkeri
N. chrysomelas
N. cinerea
N. devia
N. floridana
N. fuscipes
N. goldmani

N. lepida
N. martinensis
N. mexicana
N. micropus
N. nelsoni
N. palatina
N. phenax
N. stephensi
N. varia
Neotomodon [Genus]
N. alstoni [Species]
Neotomys [Genus]
N. ebriosus [Species]
Nesomys [Genus]
N. rufus [Species]
Nesokia [Genus]
N. bunnii [Species]
N. indica
Nesoryzomys [Genus]
N. darwini [Species]
N. fernandinae
N. indefessus
N. swarthi
Neusticomys [Genus]
N. monticolus [Species]
N. mussoi
N. oyapocki
N. peruviensis
N. venezuelae
Niviventer [Genus]
N. andersoni [Species]
N. brahma
N. confucianus
N. coxingi
N. cremoriventer
N. culturatus
N. eha
N. excelsior
N. fulvescens
N. hinpoon
N. langbianis
N. lepturus
N. niviventer
N. rapit
N. tenaster
Notiomys [Genus]
N. edwardsii [Species]
Notomys [Genus]
N. alexis [Species]
N. amplus
N. aquilo
N. cervinus
N. fuscus
N. longicaudatus
N. macrotis
N. mitchellii
N. mordax
Nyctomys [Genus]
N. sumichrasti [Species]
Ochrotomys [Genus]
O. nuttalli [Species]
Oecomys [Genus]
O. bicolor [Species]
O. cleberi
O. concolor
O. flavicans
O. mamorae
O. paricola
O. phaeotis
O. rex
O. roberti
O. rutilus
O. speciosus
O. superans
O. trinitatis
Oenomys [Genus]
O. hypoxanthus [Species]
O. ornatus
Oligoryzomys [Genus]
O. andinus [Species]
O. arenalis
O. chacoensis
O. delticola
O. destructor
O. eliurus
O. flavescens
O. fulvescens
O. griseolus
O. longicaudatus
O. magellanicus
O. microtis
O. nigripes
O. vegetus
O. victus
Ondatra [Genus]
O. zibethicus [Species]
Onychomys [Genus]
O. arenicola [Species]
O. leucogaster
O. torridus
Oryzomys [Genus]
O. albigularis [Species]
O. alfaroi
O. auriventer
O. balneator
O. bolivaris
O. buccinatus
O. capito
O. chapmani
O. couesi
O. devius
O. dimidiatus
O. galapagoensis
O. gorgasi
O. hammondi
O. intectus
O. intermedius
O. keaysi
O. kelloggi
O. lamia
O. legatus
O. levipes
O. macconnelli
O. melanotis
O. nelsoni
O. nitidus
O. oniscus
O. palustris
O. polius
O. ratticeps
O. rhabdops
O. rostratus
O. saturatior
O. subflavus
O. talamancae
O. xantheolus
O. yunganus
Osgoodomys [Genus]
O. banderanus [Species]
Otomys [Genus]
O. anchietae [Species]
O. angoniensis
O. denti
O. irroratus
O. laminatus
O. maximus
O. occidentalis
O. saundersiae
O. sloggetti
O. tropicalis
O. typus
O. unisulcatus
Otonyctomys [Genus]
O. hatti [Species]
Ototylomys [Genus]
O. phyllotis [Species]
Oxymycterus [Genus]
O. akodontius [Species]
O. angularis
O. delator
O. hiska
O. hispidus
O. hucucha
O. iheringi
O. inca
O. nasutus
O. paramensis
O. roberti
O. rufus
Pachyuromys [Genus]
P. duprasi [Species]
Palawanomys [Genus]
P. furvus [Species]
Papagomys [Genus]
P. armandvillei [Species]
P. theodorverhoeveni
Parahydromys [Genus]
P. asper [Species]
Paraleptomys [Genus]
P. rufilatus [Species]

P. wilhelmina
Parotomys [Genus]
P. brantsii [Species]
P. littledalei
Paruromys [Genus]
P. dominator [Species]
P. ursinus
Paulamys [Genus]
P. naso [Species]
Pelomys [Genus]
P. campanae [Species]
P. fallax
P. hopkinsi
P. isseli
P. minor
Peromyscus [Genus]
P. attwateri [Species]
P. aztecus
P. boylii
P. bullatus
P. californicus
P. caniceps
P. crinitus
P. dickeyi
P. difficilis
P. eremicus
P. eva
P. furvus
P. gossypinus
P. grandis
P. gratus
P. guardia
P. guatemalensis
P. gymnotis
P. hooperi
P. interparietalis
P. leucopus
P. levipes
P. madrensis
P. maniculatus
P. mayensis
P. megalops
P. mekisturus
P. melanocarpus
P. melanophrys
P. melanotis
P. melanurus
P. merriami
P. mexicanus
P. nasutus
P. ochraventer
P. oreas
P. pectoralis
P. pembertoni
P. perfulvus
P. polionotus
P. polius
P. pseudocrinitus
P. sejugis
P. simulus
P. sitkensis
P. slevini
P. spicilegus
P. stephani
P. stirtoni
P. truei
P. winkelmanni
P. yucatanicus
P. zarhynchus
Petromyscus [Genus]
P. barbouri [Species]
P. collinus
P. monticularis
P. shortridgei
Phaenomys [Genus]
P. ferrugineus [Species]
Phaulomys [Genus]
P. andersoni [Species]
P. smithii
Phenacomys [Genus]
P. intermedius [Species]
P. ungava
Phloeomys [Genus]
P. cumingi [Species]
P. pallidus
Phyllotis [Genus]
P. amicus [Species]
P. andium
P. bonaeriensis
P. caprinus
P. darwini
P. definitus
P. gerbillus
P. haggardi
P. magister
P. osgoodi
P. osilae
P. wolffsohni
P. xanthopygus
Pithecheir [Genus]
P. melanurus [Species]
P. parvus
Phodopus [Genus]
P. campbelli [Species]
P. roborovskii
P. sungorus
Platacanthomys [Genus]
P. lasiurus [Species]
Podomys [Genus]
P. floridanus [Species]
Podoxymys [Genus]
P. roraimae [Species]
Pogonomelomys [Genus]
P. bruijni [Species]
P. mayeri
P. sevia
Pogonomys [Genus]
P. championi [Species]
P. loriae
P. macrourus
P. sylvestris
Praomys [Genus]
P. delectorum [Species]
P. hartwigi
P. jacksoni
P. minor
P. misonnei
P. morio
P. mutoni
P. rostratus
P. tullbergi
Prionomys [Genus]
P. batesi [Species]
Proedromys [Genus]
P. bedfordi [Species]
Prometheomys [Genus]
P. schaposchnikowi [Species]
Psammomys [Genus]
P. obesus [Species]
P. vexillaris
Pseudohydromys [Genus]
P. murinus [Species]
P. occidentalis
Pseudomys [Genus]
P. albocinereus [Species]
P. apodemoides
P. australis
P. bolami
P. chapmani
P. delicatulus
P. desertor
P. fieldi
P. fumeus
P. fuscus
P. glaucus
P. gouldii
P. gracilicaudatus
P. hermannsburgensis
P. higginsi
P. johnsoni
P. laborifex
P. nanus
P. novaehollandiae
P. occidentalis
P. oralis
P. patrius
P. pilligaensis
P. praeconis
P. shortridgei
Pseudoryzomys [Genus]
P. simplex [Species]
Punomys [Genus]
P. lemminus [Species]
Rattus [Genus]
R. adustus [Species]
R. annandalei
R. argentiventer
R. baluensis
R. bontanus
R. burrus

R. colletti
R. elaphinus
R. enganus
R. everetti
R. exulans
R. feliceus
R. foramineus
R. fuscipes
R. giluwensis
R. hainaldi
R. hoffmanni
R. hoogerwerfi
R. jobiensis
R. koopmani
R. korinchi
R. leucopus
R. losea
R. lugens
R. lutreolus
R. macleari
R. marmosurus
R. mindorensis
R. mollicomulus
R. montanus
R. mordax
R. morotaiensis
R. nativitatis
R. nitidus
R. norvegicus
R. novaeguineae
R. osgoodi
R. palmarum
R. pelurus
R. praetor
R. ranjiniae
R. rattus
R. sanila
R. sikkimensis
R. simalurensis
R. sordidus
R. steini
R. stoicus
R. tanezumi
R. tawitawiensis
R. timorensis
R. tiomanicus
R. tunneyi
R. turkestanicus
R. villosissimus
R. xanthurus
Reithrodon [Genus]
R. auritus [Species]
Reithrodontomys [Genus]
R. brevirostris [Species]
R. burti
R. chrysopsis
R. creper
R. darienensis
R. fulvescens
R. gracilis
R. hirsutus
R. humulis
R. megalotis
R. mexicanus
R. microdon
R. montanus
R. paradoxus
R. raviventris
R. rodriguezi
R. spectabilis
R. sumichrasti
R. tenuirostris
R. zacatecae
Rhabdomys [Genus]
R. pumilio [Species]
Rhagomys [Genus]
R. rufescens [Species]
Rheomys [Genus]
R. mexicanus [Species]
R. raptor
R. thomasi
R. underwoodi
Rhipidomys [Genus]
R. austrinus [Species]
R. caucensis
R. couesi
R. fulviventer
R. latimanus
R. leucodactylus
R. macconnelli
R. mastacalis
R. nitela
R. ochrogaster
R. scandens
R. venezuelae
R. venustus
R. wetzeli
Rhizomys [Genus]
R. pruinosus [Species]
R. sinensis
R. sumatrensis
Rhombomys [Genus]
R. opimus [Species]
Rhynchomys [Genus]
R. isarogensis [Species]
R. soricoides
Saccostomus [Genus]
S. campestris [Species]
S. mearnsi
Scapteromys [Genus]
S. tumidus [Species]
Scolomys [Genus]
S. melanops [Species]
S. ucayalensis
Scotinomys [Genus]
S. teguina [Species]
S. xerampelinus
Sekeetamys [Genus]
S. calurus [Species]
Sigmodon [Genus]
S. alleni [Species]
S. alstoni
S. arizonae
S. fulviventer
S. hispidus
S. inopinatus
S. leucotis
S. mascotensis
S. ochrognathus
Sigmodontomys [Genus]
S. alfari [Species]
S. aphrastus
Solomys [Genus]
S. ponceleti [Species]
S. salamonis
S. salebrosus
S. sapientis
S. spriggsarum
Spalax [Genus]
S. arenarius [Species]
S. giganteus
S. graecus
S. microphthalmus
S. zemni
Spelaeomys [Genus]
S. florensis [Species]
Srilankamys [Genus]
S. ohiensis [Species]
Stenocephalemys [Genus]
S. albocaudata [Species]
S. griseicauda
Steatomys [Genus]
S. caurinus [Species]
S. cuppedius
S. jacksoni
S. krebsii
S. parvus
S. pratensis
Stenomys [Genus]
S. ceramicus [Species]
S. niobe
S. richardsoni
S. vandeuseni
S. verecundus
Stochomys [Genus]
S. longicaudatus [Species]
Sundamys [Genus]
S. infraluteus [Species]
S. maxi
S. muelleri
Synaptomys [Genus]
S. borealis [Species]
S. cooperi
Tachyoryctes [Genus]
T. ankoliae [Species]
T. annectens
T. audax
T. daemon
T. macrocephalus
T. naivashae

T. rex
T. ruandae
T. ruddi
T. spalacinus
T. splendens
Taeromys [Genus]
T. arcuatus [Species]
T. callitrichus
T. celebensis
T. hamatus
T. punicans
T. taerae
Tarsomys [Genus]
T. apoensis [Species]
T. echinatus
Tateomys [Genus]
T. macrocercus [Species]
T. rhinogradoides
Tatera [Genus]
T. afra [Species]
T. boehmi
T. brantsii
T. guineae
T. inclusa
T. indica
T. kempi
T. leucogaster
T. nigricauda
T. phillipsi
T. robusta
T. valida
Taterillus [Genus]
T. arenarius [Species]
T. congicus
T. emini
T. gracilis
T. harringtoni
T. lacustris
T. petteri
T. pygargus
Tscherskia [Genus]
T. triton [Species]
Thallomys [Genus]
T. loringi [Species]
T. nigricauda
T. paedulcus
T. shortridgei
Thalpomys [Genus]
T. cerradensis [Species]
T. lasiotis
Thamnomys [Genus]
T. kempi [Species]
T. venustus
Thomasomys [Genus]
T. aureus [Species]
T. baeops
T. bombycinus
T. cinereiventer
T. cinereus
T. daphne
T. eleusis
T. gracilis
T. hylophilus
T. incanus
T. ischyurus
T. kalinowskii
T. ladewi
T. laniger
T. monochromos
T. niveipes
T. notatus
T. oreas
T. paramorum
T. pyrrhonotus
T. rhoadsi
T. rosalinda
T. silvestris
T. taczanowskii
T. vestitus
Tokudaia [Genus]
T. muenninki [Species]
T. osimensis
Tryphomys [Genus]
T. adustus [Species]
Tylomys [Genus]
T. bullaris [Species]
T. fulviventer
T. mirae
T. nudicaudus
T. panamensis
T. tumbalensis
T. watsoni
Typhlomys [Genus]
T. chapensis [Species]
T. cinereus
Uranomys [Genus]
U. ruddi [Species]
Uromys [Genus]
U. anak [Species]
U. caudimaculatus
U. hadrourus
U. imperator
U. neobritanicus
U. porculus
U. rex
Vandeleuria [Genus]
V. nolthenii [Species]
V. oleracea
Vernaya [Genus]
V. fulva [Species]
Volemys [Genus]
V. clarkei [Species]
V. kikuchii
V. millicens
V. musseri
Wiedomys [Genus]
W. pyrrhorhinos [Species]
Wilfredomys [Genus]
W. oenax [Species]
W. pictipes
Xenomys [Genus]
X. nelsoni [Species]
Xenuromys [Genus]
X. barbatus [Species]
Xeromys [Genus]
X. myoides [Species]
Zelotomys [Genus]
Z. hildegardeae [Species]
Z. woosnami
Zygodontomys [Genus]
Z. brevicauda [Species]
Z. brunneus
Zyzomys [Genus]
Z. argurus [Species]
Z. maini
Z. palatilis
Z. pedunculatus
Z. woodwardi

Anomaluridae [Family]
Anomalurus [Genus]
A. beecrofti [Species]
A. derbianus
A. pelii
A. pusillus
Idiurus [Genus]
I. macrotis [Species]
I. zenkeri
Zenkerella [Genus]
Z. insignis [Species]

Pedetidae [Family]
Pedetes [Genus]
P. capensis [Species]

Ctenodactylidae [Family]
Ctenodactylus [Genus]
C. gundi [Species]
C. vali
Felovia [Genus]
F. vae [Species]
Massoutiera [Genus]
M. mzabi [Species]
Pectinator [Genus]
P. spekei [Species]

Myoxidae [Family]
Dryomys [Genus]
D. laniger [Species]
D. nitedula
D. sichuanensis
Eliomys [Genus]
E. melanurus [Species]
E. quercinus
Glirulus [Genus]
G. japonicus [Species]
Graphiurus [Genus]
G. christyi [Species]
G. hueti
G. lorraineus
G. monardi
G. ocularis

G. parvus
G. rupicola
Muscardinus [Genus]
M. avellanarius [Species]
Myomimus [Genus]
M. personatus [Species]
M. roachi
M. setzeri
Myoxus [Genus]
M. glis [Species]
Selevinia [Genus]
S. betpakdalaensis [Species]

Petromuridae [Family]
Petromus [Genus]
P. typicus [Species]

Thryonomyidae [Family]
Thryonomys [Genus]
T. gregorianus [Species]
T. swinderianus

Bathyergidae [Family]
Bathyergus [Genus]
B. janetta [Species]
B. suillus
Cryptomys [Genus]
C. bocagei [Species]
C. damarensis
C. foxi
C. hottentotus
C. mechowi
C. ochraceocinereus
C. zechi
Georychus [Genus]
G. capensis [Species]
Heliophobius [Genus]
H. argenteocinereus
Heterocephalus [Genus]
H. glaber [Species]

Hystricidae [Family]
Atherurus [Genus]
A. africanus [Species]
A. macrourus
Hystrix [Genus]
H. africaeaustralis [Species]
H. brachyura
H. crassispinis
H. cristata
H. indica
H. javanica
H. pumila
H. sumatrae
Trichys [Genus]
T. fasciculata [Species]

Erethizontidae [Family]
Coendou [Genus]
C. bicolor [Species]
C. koopmani
C. prehensilis
C. rothschildi
Echinoprocta [Genus]
E. rufescens [Species]
Erethizon [Genus]
E. dorsatum [Species]
Sphiggurus [Genus]
S. insidiosus [Species]
S. mexicanus
S. pallidus
S. spinosus
S. vestitus
S. villosus

Chinchillidae [Family]
Chinchilla [Genus]
C. brevicaudata [Species]
C. lanigera
Lagidium [Genus]
L. peruanum [Species]
L. viscacia
L. wolffsohni
Lagostomus [Genus]
L. maximus [Species]

Dinomyidae [Family]
Dinomys [Genus]
D. branickii [Species]

Caviidae [Family]
Cavia [Genus]
C. aperea [Species]
C. fulgida
C. magna
C. porcellus
C. tschudii
Dolichotis [Genus]
D. patagonum [Species]
D. salinicola
Galea [Genus]
G. flavidens [Species]
G. spixii
Kerodon [Genus]
K. rupestris [Species]
Microcavia [Genus]
M. australis [Species]
M. niata
M. shiptoni

Hydrochaeridae [Family]
Hydrochaeris [Genus]
H. hydrochaeris [Species]

Dasyproctidae [Family]
Dasyprocta [Genus]
D. azarae [Species]
D. coibae
D. cristata
D. fuliginosa
D. guamara
D. kalinowskii
D. leporina
D. mexicana
D. prymnolopha
D. punctata
D. ruatanica
Myoprocta [Genus]
M. acouchy [Species]
M. exilis

Agoutidae [Family]
Agouti [Genus]
A. paca [Species]
A. taczanowskii

Ctenomyidae [Family]
Ctenomys [Genus]
C. argentinus [Species]
C. australis
C. azarae
C. boliviensis
C. bonettoi
C. brasiliensis
C. colburni
C. conoveri
C. dorsalis
C. emilianus
C. frater
C. fulvus
C. haigi
C. knighti
C. latro
C. leucodon
C. lewisi
C. magellanicus
C. maulinus
C. mendocinus
C. minutus
C. nattereri
C. occultus
C. opimus
C. pearsoni
C. perrensis
C. peruanus
C. pontifex
C. porteousi
C. saltarius
C. sericeus
C. sociabilis
C. steinbachi
C. talarum
C. torquatus
C. tuconax
C. tucumanus
C. validus

Octodontidae [Family]
Aconaemys [Genus]
A. fuscus [Species]
A. sagei
Octodon [Genus]
O. bridgesi [Species]
O. degus
O. lunatus

Octodontomys [Genus]
O. gliroides [Species]
Octomys [Genus]
O. mimax [Species]
Spalacopus [Genus]
S. cyanus [Species]
Tympanoctomys [Genus]
T. barrerae [Species]

Abrocomidae [Family]
Abrocoma [Genus]
A. bennetti [Species]
A. boliviensis
A. cinerea

Echimyidae [Family]
Boromys [Genus]
B. offella [Species]
B. torrei
Brotomys [Genus]
B. contractus [Species]
B. voratus
Carterodon [Genus]
C. sulcidens [Species]
Clyomys [Genus]
C. bishopi [Species]
C. laticeps
Chaetomys [Genus]
C. subspinosus [Species]
Dactylomys [Genus]
D. boliviensis [Species]
D. dactylinus
D. peruanus
Diplomys [Genus]
D. caniceps [Species]
D. labilis
D. rufodorsalis
Echimys [Genus]
E. blainvillei [Species]
E. braziliensis
E. chrysurus
E. dasythrix
E. grandis
E. lamarum
E. macrurus
E. nigrispinus
E. pictus
E. rhipidurus
E. saturnus
E. semivillosus
E. thomasi
E. unicolor
Euryzygomatomys [Genus]
E. spinosus [Species]
Heteropsomys [Genus]
H. antillensis [Species]
H. insulans
Hoplomys [Genus]
H. gymnurus [Species]
Isothrix [Genus]
I. bistriata [Species]
I. pagurus
Kannabateomys [Genus]
K. amblyonyx [Species]
Lonchothrix [Genus]
L. emiliae [Species]
Makalata [Genus]
M. armata [Species]
Mesomys [Genus]
M. didelphoides [Species]
M. hispidus
M. leniceps
M. obscurus
M. stimulax
Olallamys [Genus]
O. albicauda [Species]
O. edax
Proechimys [Genus]
P. albispinus [Species]
P. amphichoricus
P. bolivianus
P. brevicauda
P. canicollis
P. cayennensis
P. chrysaeolus
P. cuvieri
P. decumanus
P. dimidiatus
P. goeldii
P. gorgonae
P. guairae
P. gularis
P. hendeei
P. hoplomyoides
P. iheringi
P. longicaudatus
P. magdalenae
P. mincae
P. myosuros
P. oconnelli
P. oris
P. poliopus
P. quadruplicatus
P. semispinosus
P. setosus
P. simonsi
P. steerei
P. trinitatis
P. urichi
P. warreni
Puertoricomys [Genus]
P. corozalus [Species]
Thrichomys [Genus]
T. apereoides [Species]

Capromyidae [Family]
Capromys [Genus]
C. pilorides [Species]
Geocapromys [Genus]
G. brownii [Species]
G. thoracatus
Hexolobodon [Genus]
H. phenax [Species]
Isolobodon [Genus]
I. montanus [Species]
I. portoricensis
Mesocapromys [Genus]
M. angelcabrerai [Species]
M. auritus
M. nanus
M. sanfelipensis
Mysateles [Genus]
M. garridoi [Species]
M. gundlachi
M. melanurus
M. meridionalis
M. prehensilis
Plagiodontia [Genus]
P. aedium [Species]
P. araeum
P. ipnaeum
Rhizoplagiodontia [Genus]
R. lemkei [Species]

Heptaxodontidae [Family]
Amblyrhiza [Genus]
A. inundata [Species]
Clidomys [Genus]
C. osborni [Species]
C. parvus
Elasmodontomys [Genus]
E. obliquus [Species]
Quemisia [Genus]
Quemisia gravis [Species]

Myocastoridae [Family]
Myocastor [Genus]
M. coypus [Species]

Lagomorpha [Order]

Ochotonidae [Family]
Ochotona [Genus]
O. alpina [Species]
O. cansus
O. collaris
O. curzoniae
O. dauurica
O. erythrotis
O. forresti
O. gaoligongensis
O. gloveri
O. himalayana
O. hyperborea
O. iliensis
O. koslowi
O. ladacensis
O. macrotis
O. muliensis
O. nubrica
O. pallasi
O. princeps
O. pusilla
O. roylei

O. rufescens
O. rutila
O. thibetana
O. thomasi
Prolagus [Genus]
P. sardus [Species]

Leporidae [Family]
Brachylagus [Genus]
B. idahoensis [Species]
Bunolagus [Genus]
B. monticularis [Species]
Caprolagus [Genus]
C. hispidus [Species]
Lepus [Genus]
L. alleni [Species]
L. americanus
L. arcticus
L. brachyurus
L. californicus
L. callotis
L. capensis
L. castroviejoi
L. comus
L. coreanus
L. corsicanus
L. europaeus
L. fagani
L. flavigularis
L. granatensis
L. hainanus
L. insularis
L. mandshuricus
L. nigricollis
L. oiostolus
L. othus
L. pequensis
L. saxatilis
L. sinensis
L. starcki
L. timidus
L. tolai
L. townsendii
L. victoriae
L. yarkandensis
Nesolagus [Genus]
N. netscheri [Species]
Oryctolagus [Genus]
O. cuniculus [Species]
Pentalagus [Genus]
P. furnessi [Species]
Poelagus [Genus]
P. marjorita [Species]
Pronolagus [Genus]
P. crassicaudatus [Species]
P. randensis
P. rupestris
Romerolagus [Genus]
R. diazi [Species]
Sylvilagus [Genus]
S. aquaticus [Species]
S. audubonii
S. bachmani
S. brasiliensis
S. cunicularius
S. dicei
S. floridanus
S. graysoni
S. insonus
S. mansuetus
S. nuttallii
S. palustris
S. transitionalis

Macroscelidea [Order]

Macroscelididae [Family]
Elephantulus [Genus]
E. brachyrhynchus [Species]
E. edwardii
E. fuscipes
E. fuscus
E. intufi
E. myurus
E. revoili
E. rozeti
E. rufescens
E. rupestris
Macroscelides [Genus]
M. proboscideus [Species]
Petrodromus [Genus]
P. tetradactylus [Species]
Rhynchocyon [Genus]
R. chrysopygus [Species]
R. cirnei
R. petersi

A brief geologic history of animal life

A note about geologic time scales: A cursory look will reveal that the timing of various geological periods differs among textbooks. Is one right and the others wrong? Not necessarily. Scientists use different methods to estimate geological time—methods with a precision sometimes measured in tens of millions of years. There is, however, a general agreement on the magnitude and relative timing associated with modern time scales. The closer in geological time one comes to the present, the more accurate science can be—and sometimes the more disagreement there seems to be. The following account was compiled using the more widely accepted boundaries from a diverse selection of reputable scientific resources.

Geologic time scale

Era	Period	Epoch	Dates	Life forms
Proterozoic			2,500-544 mya*	First single-celled organisms, simple plants, and invertebrates (such as algae, amoebas, and jellyfish)
Paleozoic	Cambrian		544-490 mya	First crustaceans, mollusks, sponges, nautiloids, and annelids (worms)
	Ordovician		490-438 mya	Trilobites dominant. Also first fungi, jawless vertebrates, starfishes, sea scorpions, and urchins
	Silurian		438-408 mya	First terrestrial plants, sharks, and bony fishes
	Devonian		408-360 mya	First insects, arachnids (scorpions), and tetrapods
	Carboniferous	Mississippian	360-325 mya	Amphibians abundant. Also first spiders, land snails
		Pennsylvanian	325-286 mya	First reptiles and synapsids
	Permian		286-248 mya	Reptiles abundant. Extinction of trilobytes. Most modern insect orders
Mesozoic	Triassic		248-205 mya	Diversification of reptiles: turtles, crocodiles, therapsids (mammal-like reptiles), first dinosaurs, first flies
	Jurassic		205-145 mya	Insects abundant, dinosaurs dominant in later stage. First mammals, lizards, frogs, and birds
	Cretaceous		145-65 mya	First snakes and modern fish. Extinction of dinosaurs and ammonites, rise and fall of toothed birds
Cenozoic	Tertiary	Paleocene	65-55.5 mya	Diversification of mammals
		Eocene	55.5-33.7 mya	First horses, whales, monkeys, and leafminer insects
		Oligocene	33.7-23.8 mya	Diversification of birds. First anthropoids (higher primates)
		Miocene	23.8-5.6 mya	First hominids
		Pliocene	5.6-1.8 mya	First australopithecines
	Quaternary	Pleistocene	1.8 mya-8,000 ya	Mammoths, mastodons, and Neanderthals
		Holocene	8,000 ya-present	First modern humans

*Millions of years ago (mya)