George A. Feldhamer
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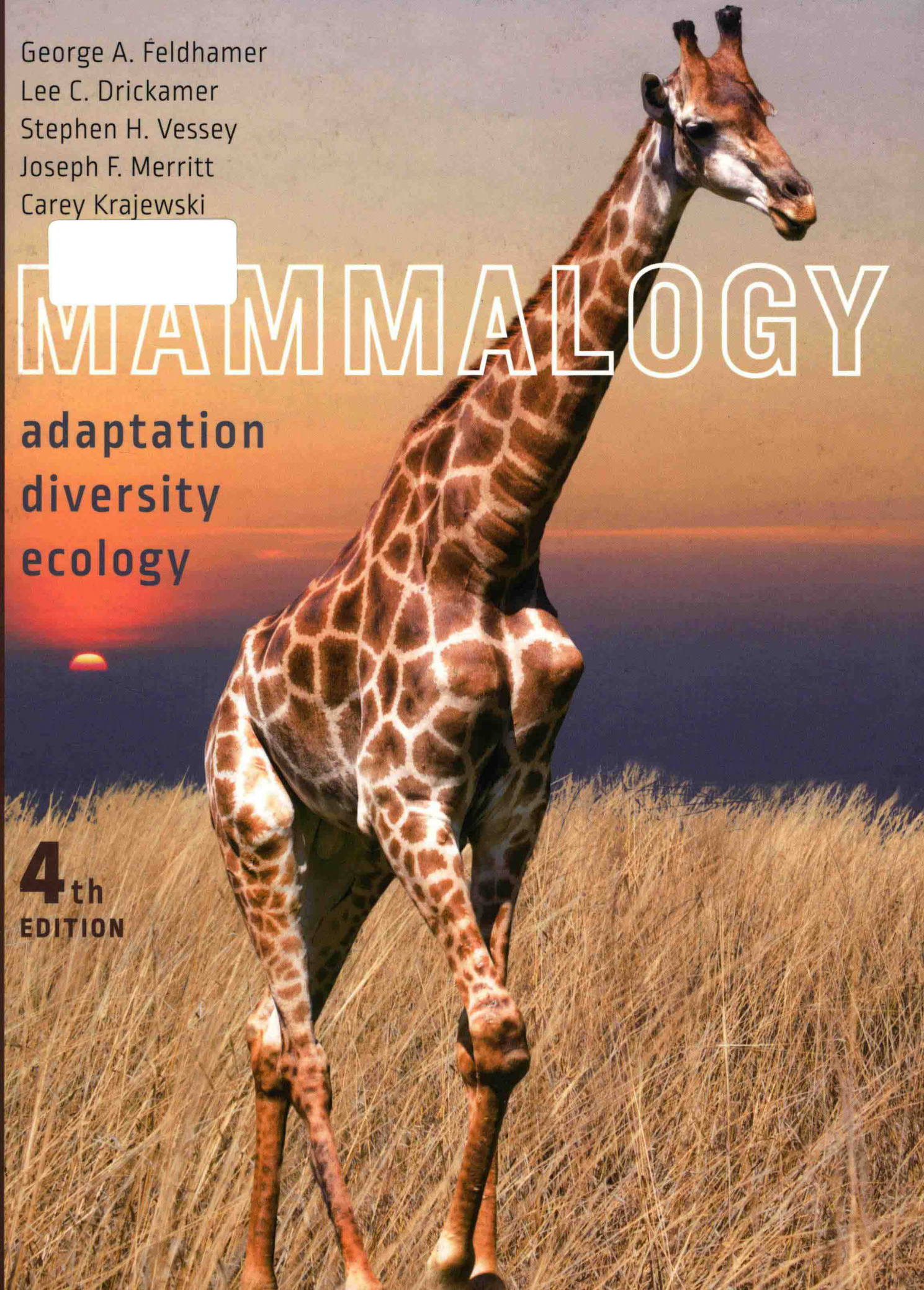
MAMMALOGY

adaptation
diversity
ecology



4th EDITION

MAMMALOGY

Adaptation, Diversity, Ecology

Fourth Edition

George A. Feldhamer

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MAMMALOGY

For Carla, Carrie, Andy, Jenny, and Lucy
– George

For my siblings, Lynn Drickamer, Kurt Drickamer, Margaret Drickamer, and Priscilla Atkins
– Lee

For Kristin, my highly significant other
– Steve

In memory of my parents, Robert E. Merritt and June A. Merritt
– Joe

To Birdie, Jenny, Robby, and Cody—inspiration every day
– Carey

About the Authors

George A. Feldhamer is Professor Emeritus of Zoology and former Director of the Environmental Studies Program at Southern Illinois University, Carbondale. His research has focused on mammalian populations, ecology, and management; biology of introduced deer; and threatened and endangered species of rodents and bats. He is a former associate editor for Forest Biology and Ecology for the *Journal of Forest Research* and a former associate editor of the *Wildlife Society Bulletin*. He is the senior editor of *Wild Mammals of North America: Biology, Management, and Conservation* (2003), coauthor of *Mammals of the National Parks* (2005), and *Deer: The Animal Answer Guide* (2012), all published by Johns Hopkins University Press, and coeditor of *Ecology, Behavior, and Conservation of the Golden Mouse: A Model Species for Research* (2007). He has had 35 years of experience teaching an upper-division mammalogy course. In 2011, he received the Joseph Grinnell Award from the American Society of Mammalogists "to honor individuals who have made outstanding and sustained contributions to education in mammalogy"

Lee C. Drickamer was Professor of Biology and Chair of the Department of Biological Sciences at Northern Arizona University, Professor of Biology at Williams College for 15 years, Professor of Zoology at Southern Illinois University, Carbondale, for 11 years, and is Regents' Professor Emeritus of Biological Science at Northern Arizona University. He is a past president of the Animal Behavior Society, past secretary-general of the International Council of Ethologists, past chair of the Division of Animal Behavior of what is now the Society for Integrative and Comparative Biology, and former editor of *Animal Behaviour*. His research emphases have included social factors affecting development and reproduction in house mice and swine, behavioral ecology of house mice and deer mice, social biology of primates, intrauterine position effects on behavior and reproduction of mice and swine, the consequences of mate selection for offspring viability in house mice, and prairie dog ecology and population biology.

Stephen H. Vessey is Professor Emeritus of Biological Sciences at Bowling Green State University. His research interests include the behavioral ecology of mammals, especially primates and rodents. He has been studying a population of white-footed mice in northwestern Ohio for more than 40 years. He is a former associate editor of the *Journal of Mammalogy* and is a Fellow of the Animal Behavior Society. He taught mammalogy and animal behavior at Bowling Green for 30 years and coauthored a textbook in animal behavior with Lee Drickamer. After retiring from Bowling Green in 2000, he served as Program Director and Deputy Division Director, Division of Integrative Biology and Neurosciences, National Science Foundation.

Joseph F. Merritt is Senior Mammalogist with the Illinois Natural History Survey, University of Illinois. He is the former Director of Powdermill Biological Station of the Carnegie Museum of Natural History and served as Distinguished Visiting Professor at the U.S. Air Force Academy in Colorado Springs, Colorado, during the academic year 2004–2005. Dr. Merritt is a physiological ecologist and functional morphologist specializing in adaptations of mammals to cold. He is the author of *Guide to the Mammals of Pennsylvania* (1987), published by the University of Pittsburgh Press, and editor of several technical monographs on specific taxa of mammals. His book *Biology of Small Mammals* was published by Johns Hopkins University Press in 2010. He is currently editor in chief of the *Journal of Mammalogy*. Dr. Merritt teaches mammalogy at the University of Colorado Mountain Research Station, courses in mammalian biology at Illinois State University, Normal, and courses in winter ecology at the Adirondack Ecological Center, SUNY College of Environmental Science and Forestry.

Carey Krajewski is Professor and Chair of Zoology at Southern Illinois University, Carbondale. His research in mammalogy has involved molecular studies of marsupial phylogeny, particularly the systematics of dasyuromorphians, as well as the evolution of gruoid birds. He was an associate editor for the *Journal of Mammalogy* and is currently associate editor of the *Journal of Mammalian Evolution* and of *Molecular Phylogenetics and Evolution*. From 1993 to 2010, he was an honorary research fellow in the Genetics Department at La Trobe University, Australia. He was named 2004 Outstanding Scholar in the College of Science at SIUC.

Preface

Research on all aspects of mammals continues at a rapid pace. Given this acceleration and the extent of new findings about mammals, it continues to be a challenge to produce a textbook that balances both breadth and depth of coverage for a one-semester upper-level undergraduate or graduate mammalogy course. In this fourth edition, we have retained the general format of previous editions with 30 chapters arranged in 5 parts. Part 1 (chapters 1 through 6) introduces the subject of mammalogy; provides a history of the discipline and an overview of current methods and molecular techniques important in systematics and population analyses; and presents the topics of mammalian phylogeny, evolution and dentition of mammals, and zoogeography. Part 2 (chapters 7 through 11) covers biological functions and the physical structure of mammals. Adaptive radiation in form and function among the 29 currently recognized mammalian orders is discussed in part 3 (chapters 12 through 21). Morphology, fossil records, conservation and economics, updated phylogeny and current classification, and a synopsis of all extant families are included for each order. Part 4 (chapters 22 through 27) focuses on new insights in behavior and ecology. Finally, in part 5 (chapters 28 through 30), we explore mammalian parasites and diseases, including zoonoses; domestication of mammals; and many current conservation issues. As in previous editions, all literature citations are collected at the end of the text to avoid redundancy. Technical terms throughout each chapter are in boldfaced type when they are first introduced, and those terms are defined in both the text and the glossary. Although there is continuity between sections and chapters of the text, instructors can select certain chapters based on individual interest, emphasis, or time constraints without sacrificing clarity and understanding.

Changes to the Fourth Edition

The major impetus for this edition of *Mammalogy: Adaptation, Diversity, Ecology* arose from significant changes in higher-level taxonomy of mammals. As noted in the introduction to part 3 (Adaptive Radiation and Diversity), the number of recognized mammalian species is rapidly approaching 6,000. This edition includes 2 new orders and 13 new families resulting from the considerable molecular and morphological work of the past decade. We have updated recent advances in anatomy and physiology, behavioral ecology, conservation, zoogeography, paleontology, and other areas of mammalogy. The fourth edition includes hundreds of new citations to recent literature, numerous new photos and figures, study questions designed to help generate critical thinking and discussion, and suggested readings. More specifically, part 1 includes a timely new chapter on mammalian phylogeny, with in-depth discussion of the relationships of extant orders as well as timing of mammalian radiations. Part 2 has updated information in all chapters. Taxonomic revisions, including new orders and families, as well as a variety of new species, are discussed in part 3. There, new fossil evidence and updated phylogenies that have recently become available for many orders are presented, as are advances in natural history for numerous families along with the current conservation status of threatened species. All chapters in part 4 have been updated. Part 5 includes discussion of current trends in Lyme disease and other zoonoses, as well as current material on domesticated species and conservation issues of various mammalian groups.

In terms of form and function, feeding and locomotion, mammals represent the most diverse class of vertebrates. Mammals are terrestrial, arboreal, freshwater, or marine; they burrow, run, glide, or fly; and they feed on meat, nectar, blood, pollen, leaves, or a variety of other things. They range in size from 2-gram white-toothed pygmy shrews and hog-nosed bats to 160-million-gram blue whales. We continue to explore the fascinating diversity and complexity of all aspects of mammals in this fourth edition. We hope this book does justice to past and present mammalogists on whose research and teaching efforts it is based. We also trust that it will continue to prove to be useful to students, the mammalogists of the future, as they explore and better appreciate the mysteries of mammals—those "fabulous furballs."

The five authors bring a combined total of nearly 200 years of field and laboratory research experience working with mammals in a variety of settings—as well as many decades of teaching—to the collaborative endeavor of this book. Each of us has also benefited from years of suggestions, ideas, and constructive criticism from many teachers, colleagues, students, and friends and from rewarding discussions with them.

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Brief Contents

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PART 1

Introduction

CHAPTER 1

The Study of Mammals

What Is Mammalogy?

Mammalogy is the study of the animals that constitute the Class Mammalia, a taxonomic group of vertebrates (Phylum Chordata, Subphylum Vertebrata) within the Kingdom Animalia. Humans (*Homo sapiens*) are mammals, as are many domesticated species of pets and livestock, as well as wildlife, such as deer and squirrels, with which we share our natural surroundings (figure 1.1). Many of the animals that have aroused public concern for their survival, such as elephants, whales, large cats, gorillas, and the giant panda, are mammals. Mammals share a number of features, including (1) the capacity for internal temperature control, often aided by a coat of fur; (2) the possession of mammary glands, which, in females, provide nourishment for the young during early development; and (3) with a few exceptions, the ability to give birth to live young. These and many other features of mammals are discussed in detail in chapter 5 and in parts 2 and 3.

Animal biology can be studied from a taxonomic perspective, that is, by concentrating on groups of organisms, such as mammals (mammalogy) or birds (ornithology). Or the functional perspective can be used, concentrating on processes, as in physiology or ecology. In this book, we combine both approaches. The disciplines of biochemistry, physiology, animal behavior, and ecology, among many others, all contribute to mammalogy. Our goal is to explore and integrate discoveries across disciplines to provide the most comprehensive and productive approach to the study of mammals.

Throughout the book, we weave together at least four major themes: evolution, methods for investigating mammals, diversity, and the interrelationships of form and function. A basic underlying theme for all of biology is evolution by natural selection. Beginning with chapters 5 and 6 we take up the thread of evolutionary thought, giving particular emphasis to both speciation and adaptations of mammals. Chapter 3 begins the second thread, scientific methods, and introduces how mammalogists formulate questions (hypotheses) for investigation and what methods they use to answer these questions. The third thread, which is covered in parts 2 and 4, involves how form, function, and behavior are

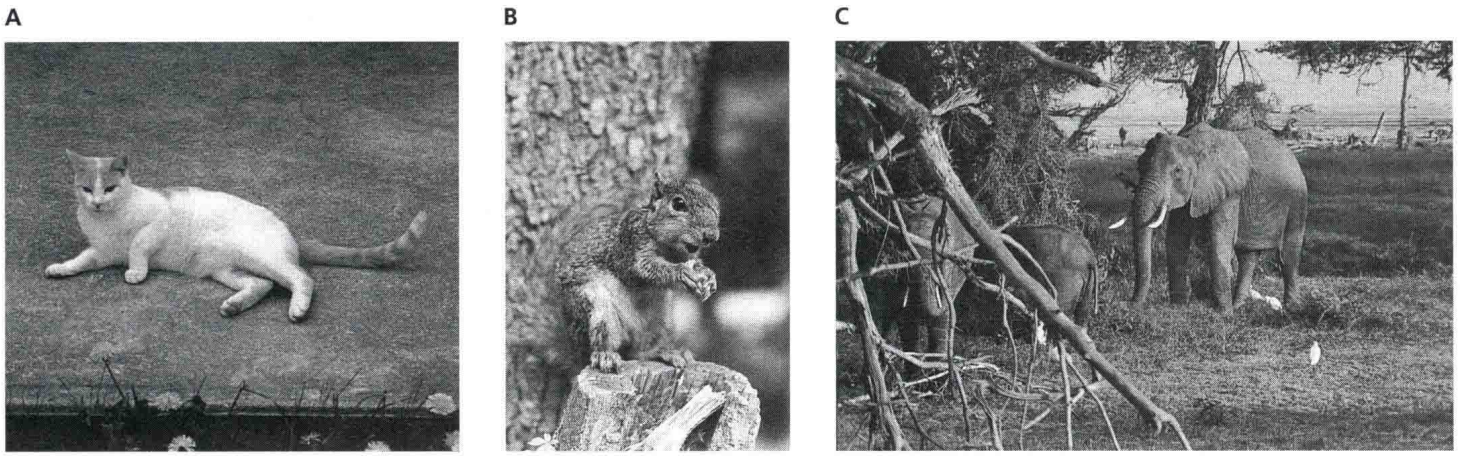

Figure 1.1 Mammals with which we share the world. In addition to our own species, mammals with which we share our world can be grouped roughly into (A) domestic pets and livestock, such as a house cat (*Felis catus*), (B) wildlife in our familiar environment, which we may see often or in other cases rarely, such as an Abert's squirrel (*Sciurus aberti*), and (C) wildlife from other lands, particularly endangered or threatened species, such as an African elephant (*Loxodonta africana*).

tightly interwoven and shaped by natural selection to provide solutions to the key problems of survival and reproduction in mammals. Our fourth thread, mammalian diversity, is emphasized in part 3, but examples offered throughout the text further underscore this theme.

Why Study Mammals?

Most of us have at least a passing interest in mammals, but we seldom stop to think why the formal study of this group is important. Mammalogy can be approached from a variety of directions and for diverse reasons (Wilson and Eisenberg 1990). Mammals were a resource for early humans; knowledge about them was important for hunting and trapping. Some mammals, such as the saber-toothed cats that coexisted with our ancestors, were potential predators on humans. Knowledge of their habits was important for survival. Indeed, there are still locations in the world where wild animals, including grizzly bears (*Ursus arctos*) in western North America and tigers (*Panthera tigris*) in India, may attack and kill humans. Mammals, both wild and domesticated, continue to be important to humans as food. People with a subsistence way of life may depend on capturing or killing free-ranging mammals. More industrialized cultures depend on domesticated livestock for food. In addition, humans have a long tradition of using mammals in numerous ways, including their hides, bones, fur, or blubber from whales and seals.

Humans keep many types of mammals as pets, ranging from cats, dogs, and mice to more exotic species, such as large cats, primates, and even skunks. Much of the practice of veterinary medicine, which developed originally to serve the needs of agriculture, is now devoted to the diagnosis and treatment of illnesses and injuries affecting our pets. Many species are hunted for sport in North America, including cottontail rabbits (*Sylvilagus floridanus*), white-tailed deer (*Odocoileus virginianus*), and elk (*Cervus elaphus*). Exotic forms of mammalian wildlife, including free-ranging populations of fallow deer (*Dama dama*), sika deer (*Cervus nippon*), and feral hogs (*Sus scrofa*), were introduced in several states, most notably Texas, to provide additional game species. Some exotics have become major pests after introduction because their interactions with native species were unforeseen. An example is the release of the Indian mongoose (*Herpestes javanicus*) on islands in the Caribbean Sea and the Hawaiian Islands. Mongooses were introduced to control rodents that had been brought to the islands by humans. Mongooses consume the eggs and young of many native bird species, however, as well as compete with native animals for resources.

Some mammals pose risks for humans and other animals because they serve as **reservoirs** or **vectors** for a variety of diseases and parasites (e.g., the black rat [*Rattus rattus*] is a vector for plague). Knowledge of the life cycles of parasites and the symptoms of various mammal-borne diseases is necessary for humans to avoid and treat these health hazards.

Some mammals can damage portions of our environment or negatively affect other animals. For instance, rats, mice, and occasionally other small mammals with which we share our living areas do great harm to both property and food stores. Some rodents exhibit explosive population growth and overrun large areas of planted cropland. A better understanding of the reproductive and population biology of such agricultural pests is necessary in order to develop means to control them. Moles and gophers may damage lawns, and beavers can cause flooding of forests and croplands. It is sometimes difficult to realize that these mammals are just carrying out their normal activities, which, unfortunately, often lead them into conflict with humans. Our anthropocentric (human-centered) perspective on life leads us to view many "normal" activities of nonhuman mammals as being in conflict with our goals.

Another currently important reason for studying mammals is conservation (see box). After driving many species into or close to extinction, some effort is being made to reverse the trend. Toward that goal, some biologists work to understand and protect the habitats of endangered or

Hot Topics in Mammalogy

During the past 20 years, several hot topics emerged in the field of mammalogy. Brief examples provide a flavor of current research in mammalogy.

1. *Molecular Techniques and Phylogeny.* New technology (see chapter 3) altered the landscape for several aspects of mammalogy, including phylogenetic analyses (see chapter 4). The surge of new papers using DNA-based molecular schemes for discerning taxonomic relationships and phylogeny continues to expand. Using DNA has ramifications for other aspects of mammalogy. Studies of behavior use information on parentage and familial relationships to assess social and reproductive biology. Conservation genetics involves information on which animals to breed and genetic diversity in populations. DNA-based techniques are employed in forensics, helping to determine the sources, for example, of poached ivory.
2. *Conservation and Climate Change Effects.* Sustained interest in conservation resulted in laws concerning endangered species, setting aside more and larger reserves for animals, and captive breeding programs. Now, in the second decade of the 21st century, the looming and, in some instances, measurable effects of climate change bring additional focus to and money for studies of mammalian conservation. Programs for training in conservation education and new research institutes are found in many countries; schools are awarding degrees in conservation biology. Individuals trained in specializations pertaining to preserving animal and plant life are in demand.
3. *Roles of Zoological Parks.* New habitat-based or enriched cage environments were developed in the last third of the 20th century. Zoos continue to expand their roles in several realms pertinent to modern mammalogy. One of these is education. Most zoos have programs for children and tours for people of all ages, introducing them to animals, their habitats, and where they are from. A more knowledgeable public will be more receptive to and understanding of the need for conservation measures. Zoos are involved in conservation issues. By learning about patterns of and requirements for successful reproduction, zoos are conducting breeding programs that enable both the maintenance of the species and possibilities for reintroduction to natural habitats.
4. *Marine Mammals.* Whaling decimated populations of many species by the middle of the 20th century (see chapter 18). Conservation measures resulted in population recovery for various species. Threats today come not from hunting but rather from human effects on their environment. Human activities include fishing nets that snare dolphins and porpoises, noises transmitted through water that disrupt navigation and communications systems, and despoiling the environment with chemicals, exhaust from ships, and toxic spills. The challenge now becomes how to clean up the results of our negative influences in order to preserve all marine life, particularly mammals.
5. *Disease—Bats, Tasmanian Devils.* In the past decade, there have been two major examples of diseases threatening the continued existence of certain mammals. More such threats will occur in coming years, and there is a growing need for specialists trained in mammalian diseases and epidemiology.

   One of these is white-nose syndrome infecting bats of several species; more than 6 million bats have died from this disease, primarily in the eastern United States. The white-nose syndrome is caused by a fungus (see chapter 14). It is spread by the bats and by humans who, in the course of visiting caves, become vectors, carrying the fungus to other locations. This is a major ongoing threat and one to which scientists are seeking answers.

   Tasmanian devils (*Sarcophilus harrisii*), on the island of the same name off the south coast of Australia, suffer from a parasitic cancer called devil facial tumor disease, which transmits from one animal to another via facial and other contact (see chapter 12). It produces large facial tumors that interfere with vision and other senses, as well as feeding, often resulting in starvation. The disease likely has killed between 20% and 40% of the devil population, primarily on the eastern half of Tasmania, though it continues to spread. Knowledge of diseases, their transmission, and molecular genetics is required to solve the problem.

threatened species. Others study social and reproductive biology under natural conditions or to establish captive breeding programs designed to eventually reintroduce species into their natural habitats. Good examples are current efforts involving black-footed ferrets (*Mustela nigripes*), wolves (*Canis lupus*), and wood bison (*Bison bison athabascae*).

In addition to examining the loss of species through extinction, conservation efforts in recent years have made a broad-based attempt to account for all living species of animals and plants. This effort has resulted in the discovery of previously unrecorded species; more discoveries continue to be made each year. For example, two new species of rodents (*Leptomys paulus* and *L. arfakensis*) from New Guinea, a new flying fox from the Philippines (*Desmalopex microleucopterus*), and two new uakaris in Brazil (*Cacajao ayresi* and *Cacajao hosomi*) were all described in the past decade (Boubli et al. 2008; Esselstyn et al. 2008; Musser et al. 2008). Some of these new species are new because they were observed for the first time, while others have resulted from splitting existing taxa based on new, more thorough information. The distinctions needed to differentiate these new taxa from those that were previously described involve traditional measures of morphology and modern molecular techniques based on DNA, which we learn about in chapter 4.

Because we are mammals, we can learn much about ourselves by studying similar processes that occur in other mammals. Some animals serve as models for various diseases or as subjects for developing or testing vaccines for eventual use on humans. We also maintain large colonies of some mammals in captivity to better study a whole variety of physiological, behavioral, and related medical phenomena. Work on particular species broadens and enhances our knowledge about such basic processes as developmental biology, immunology, endocrinology, and reproduction.

Resources for Mammalogists

A variety of resources is available to help us learn about mammals. Those who study mammals over many years