



Feldhamer • Drickamer • Vessey • Merritt

*Second Edition*

# MAMMALOLOGY

*Adaptation Diversity Ecology*

Adaptation, Diversity, Ecology  
**Mammalogy**

*Second Edition*

**George A. Feldhamer**

*Southern Illinois University  
at Carbondale*

**Lee C. Drickamer**

*Northern Arizona University*

**Stephen H. Vessey**

*Bowling Green State University*

**Joseph F. Merritt**

*Carnegie Museum of Natural History*



**Higher Education**

Boston Burr Ridge, IL Dubuque, IA Madison, WI New York San Francisco St. Louis  
Bangkok Bogotá Caracas Kuala Lumpur Lisbon London Madrid Mexico City  
Milan Montreal New Delhi Santiago Seoul Singapore Sydney Taipei Toronto

The McGraw-Hill Companies



**Higher Education**

**MAMMALOLOGY: ADAPTATION, DIVERSITY, AND ECOLOGY**  
**SECOND EDITION**

Published by McGraw-Hill, a business unit of The McGraw-Hill Companies, Inc., 1221 Avenue of the Americas, New York, NY 10020. Copyright © 2004, 1999 by The McGraw-Hill Companies, Inc. All rights reserved. No part of this publication may be reproduced or distributed in any form or by any means, or stored in a database or retrieval system, without the prior written consent of The McGraw-Hill Companies, Inc., including, but not limited to, in any network or other electronic storage or transmission, or broadcast for distance learning.

Some ancillaries, including electronic and print components, may not be available to customers outside the United States.



This book is printed on recycled, acid-free paper containing 10% postconsumer waste.

3 4 5 6 7 8 9 0 CCW/CCW 0 9 8 7 6 5

ISBN 0-07-290948-X

Publisher: *Margaret J. Kemp*  
Senior developmental editor: *Donna Nemmers*  
Marketing manager: *Heather K. Wagner*  
Project manager: *Joyce Watters*  
Senior production supervisor: *Laura Fuller*  
Senior coordinator of freelance design: *Michelle D. Whitaker*  
Cover/interior design: *Jamie E. O'Neal*  
Cover image: © *National Geographic Image Collection/Kenneth Garrett*  
Lead photo research coordinator: *Carrie K. Burger*  
Photo research: *Karen Pugliano*  
Compositor: *Precision Graphics*  
Typeface: *10/12 ACaslon Regular*  
Printer: *Courier Westford*

The credits section for this book begins on page 530 and is considered an extension of the copyright page.

**Library of Congress Cataloging-in-Publication Data**

Mammalogy : adaptation, diversity, ecology / [edited by] George A. Feldhamer . . . [et. al.]. — 2nd ed.  
p. cm.

Includes bibliographical references and index.

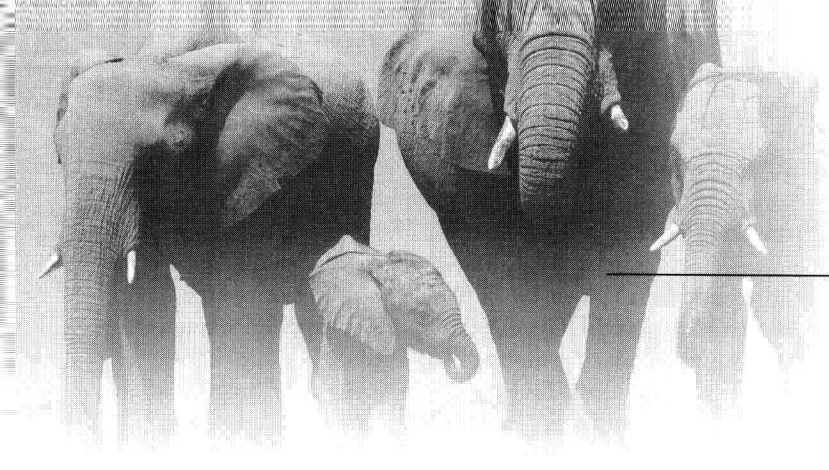
ISBN 0-07-290948-X (hard copy : alk. paper)

1. Mammalogy. I. Feldhamer, George A.

QL703M36 2004  
599—dc21

2003007410  
CIP





# Preface

---

As was the case throughout the twentieth century, research and resulting insight on all aspects of mammals continues at a rapid pace today. Balancing breadth and depth of coverage, we have maintained a textbook length tailored to a one-semester mammalogy course appropriate for upper-level undergraduates and graduate students with a basic background in vertebrate biology. In this second edition, we have retained the format of 29 chapters arranged in 5 parts. Part 1 (chapters 1 through 4) introduces the subject of mammalogy, history of the discipline, current methods and molecular techniques important in systematics and population analyses, and the evolution of mammals. Part 2 (chapters 5 through 9) covers biological functions and the physical structure of mammals. Adaptive radiation in form and structure among the currently recognized mammalian orders is covered in Part 3 (chapters 10 through 19). Morphology, fossil records, conservation and economics, and a brief synopsis of all extant families are included for each order. Part 4 focuses on behavior, ecology, and zoogeography (chapters 20 through 26). Finally, in Part 5 (chapters 27 through 29), we explore mammalian parasites and diseases, including zoonoses; domestication of mammals; and conservation issues. Literature cited within a chapter is 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 Second Edition

This edition of *Mammalogy: Adaptation, Diversity, Ecology* updates recent advances in mammalian anatomy and physiology, behavioral ecology, molecular genetics, systematics, conservation, zoogeography, paleontology, and many other complementary and interrelated areas of mammalogy since the first edition in 1999. The second edition includes hundreds of new citations to recent literature, many new photos and figures, study questions designed to help generate critical thinking and discussion, and suggested readings. More specifically, Part 1 includes added coverage and expanded explanations of molecular techniques as well as current thinking concerning mammalian evolution. Part 2 has additional

new information on locomotion, mosaic evolution, and dormancy, as well as expanded coverage on the immune system of mammals. Throughout Part 3, new fossil evidence and updated phylogenies are given for many orders, as are recent advances in natural history for numerous families along with the current conservation status of threatened species. Part 4 includes recent functional information on such topics as humpback whale songs, the nasal area of the star-nosed mole, and the role of the major histocompatibility locus. We also update material on the role of neuroendocrine factors in parental care of offspring, group size in social carnivores, and the role of path integration and the hippocampus in orientation and spatial navigation. Current trends in Lyme disease and other zoonoses are given in Part 5 along with updated material on domesticated species and conservation issues of various mammalian groups.

In terms of form and function, feeding and locomotion, the approximately 4600 species of mammals represent the most diverse class of vertebrates. Mammals are terrestrial, arboreal, or marine; they burrow, run, 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 explore the diversity and complexity of all aspects of mammals in this second edition of *Mammalogy: Adaptation, Diversity, Ecology*. We hope this book does justice to past and present mammalogists on whose research and teaching efforts it is largely based. We also trust that it will continue to prove useful to students, the mammalogists of the future, as they better appreciate and explore the mysteries of mammals—those “fabulous furballs.”

## Acknowledgments

The four authors of this text bring a combined total of around 140 years of field and laboratory experience with mammals in a variety of settings to the collaborative endeavor of this book. The benefits of this collaboration, including the experience and insights gained from writing the first edition, are reflected in this revised text. Also, we have each gained through the years from the suggestions, ideas, discussions, and constructive criticism of many teachers, colleagues, students, and friends. Many individuals reviewed parts of the manuscript or the entire text of the original edition. Their input as well is reflected in this second edition.



## Second Edition Reviewers

Anthony D. Barnosky, *University of California, Berkeley*  
 Bruce E. Coblentz, *Oregon State University*  
 John D. Harder, *Ohio State University*  
 Lynda A. Randa, *College of DuPage*  
 Thomas McK. Sproat, *Northern Kentucky University*  
 Michael D. Stuart, *University of North Carolina  
at Asheville*  
 Christopher J. Yahnke, *University of Wisconsin-  
Stevens Point*  
 John A. Yunker, *Governors State University*

## First Edition Reviewers

David M. Armstrong, *University of Colorado at Boulder*  
 Richard Buchholz, *Northeast Louisiana University*  
 Jack A. Cranford, *Virginia Polytechnic Institute and State  
University*  
 Jim R. Goetze, *Laredo Community College*  
 Dalton R. Gossett, *Louisiana State University*  
 Kay E. Holekamp, *Michigan State University*  
 Carey Krajewski, *Southern Illinois University*  
 Thomas H. Kunz, *Boston University*  
 Peter L. Meserve, *Northern Illinois University*  
 Christopher J. Norment, *SUNY College at Brockport*  
 Larry S. Roberts, *University of Miami*  
 Robert K. Rose, *Old Dominion University*  
 Michael D. Stuart, *University of North Carolina  
at Asheville*  
 John A. Vucetich, *Michigan Technological University*  
 Wm. David Webster, *University of North Carolina  
at Wilmington*  
 John O. Whitaker, Jr., *Indiana State University*  
 Bruce A. Wunder, *Colorado State University*

The authors are also grateful for the assistance of the McGraw-Hill staff who guided them through the revision of this second edition: Marge Kemp, Publisher; Donna Nemmers, Senior Developmental Editor; Joyce Watters, Project Manager; Carrie Burger, Lead Photo Research Coordinator; and Michelle Whitaker, Coordinator of Freelance Design. We also thank Science Librarian Kathy Fahey and her staff at Southern Illinois University at Carbondale for their help throughout both editions. The invaluable assistance of Lisa Russell of the Environmental Studies Program at SIUC in all phases of the second edition is gratefully acknowledged.

## About the Authors

**George A. Feldhamer** is Professor of Zoology as well as Coordinator of the Environmental Studies Program at Southern Illinois University at Carbondale. His research has focused exclusively on mammalian populations, ecology, and management; biology of introduced cervids; and threatened and endangered species. He is an 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 the 2003 *Wild Mammals of North America: Biology, Management, and Conservation* published by Johns Hopkins University Press. He is curator of the mammal collection at SIUC and has 25 years of experience teaching an upper-division mammalogy course. In 2000, he was named Outstanding Teacher in the College of Science at SIUC.

**Lee C. Drickamer** was Professor of Biology at Williams College for 15 years, Professor of Zoology at Southern Illinois University at Carbondale for 11 years, and is currently Professor of Biology and Chair of the Department of Biological Sciences at Northern Arizona University. He is a past president of the Animal Behavior Society, past secretary-general of the International Council of Ethnologists, 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 30 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. Since 2000, he has served as Program Director and Deputy Division Director, Division of Integrative Biology and Neuroscience, National Science Foundation.

**Joseph F. Merritt** is Director of Powdermill Biological Station, the field station of the Carnegie Museum of Natural History. He is a physiological ecologist specializing in adaptations of small mammals to cold. He is the author of *Guide to Mammals of Pennsylvania*, published by the University of Pittsburgh Press, and editor of several technical monographs on specific taxa of mammals. He has served on the Editorial Committee of the American Society of Mammalogists since 1990 and is currently the editor for Special Publications of the *Journal of Mammalogy*. He teaches mammalogy at the University of Pittsburgh's Pymatuning Laboratory of Ecology and teaches courses in mammalian ecology at Antioch New England Graduate School and at the Adirondack Ecological Center, SUNY College of Environmental Science and Forestry.

# Brief Contents

---



|   |           |  |     |
|---|-----------|--|-----|
| <i>Preface</i>  | <i>ix</i> | Chapter 17 Rodentia and Lagomorpha                             | 280 |
| <b>PART 1</b>   |           | Chapter 18 Proboscidea, Hyracoidea, and Sirenia                | 300 |
| <i>Introduction</i>   |           | Chapter 19 Perissodactyla and Artiodactyla                     | 312 |
| Chapter 1 The Study of Mammalogy                                    | 2         |  |     |
| Chapter 2 History of Mammalogy                                      | 7         |  |     |
| Chapter 3 Methods and Techniques for Studying Mammals               | 20        |  |     |
| Chapter 4 Evolution and Dental Characteristics                      | 40        |  |     |
| <b>PART 2</b>   |           | <b>PART 4</b>  |     |
| <i>Structure and Function</i>                                       |           | <i>Behavior, Ecology, and Biogeography</i>                     |     |
| Chapter 5 Integument, Support, and Movement                         | 59        | Chapter 20 Communication, Aggression, and Spatial Relations    | 331 |
| Chapter 6 Foods and Feeding   | 79        | Chapter 21 Sexual Selection, Parental Care, and Mating Systems | 344 |
| Chapter 7 The Nervous and Endocrine Systems, and Biological Rhythms | 102       | Chapter 22 Social Behavior                                     | 357 |
| Chapter 8 Environmental Adaptations                                 | 113       | Chapter 23 Dispersal, Habitat Selection, and Migration         | 369 |
| Chapter 9 Reproduction  | 146       | Chapter 24 Populations and Life History                        | 382 |
|   |           | Chapter 25 Community Ecology                                   | 399 |
|   |           | Chapter 26 Zoogeography  | 416 |
| <b>PART 3</b>   |           | <b>PART 5</b>  |     |
| <i>Adaptive Radiation and Diversity</i>                             |           | <i>Special Topics</i>  |     |
| Chapter 10 Monotremes and Marsupials                                | 168       | Chapter 27 Parasites and Diseases                              | 433 |
| Chapter 11 Insectivora, Macroscelidea, Scandentia, and Dermoptera   | 188       | Chapter 28 Domestication and Domesticated Mammals              | 448 |
| Chapter 12 Chiroptera   | 199       | Chapter 29 Conservation  | 459 |
| Chapter 13 Primates   | 219       |  |     |
| Chapter 14 Xenarthra, Pholidota, and Tubulidentata                  | 238       | <i>Glossary</i>  | 475 |
| Chapter 15 Carnivora  | 247       | <i>References</i>  | 492 |
| Chapter 16 Cetacea  | 261       | <i>Credits</i>   | 530 |
|   |           | <i>Index</i>   | 532 |



# Contents

---

## *Preface*

## **PART 1**

### *Introduction*

|  |           |
|--|-----------|
| <b>Chapter 1 The Study of Mammalogy</b>                          | <b>2</b>  |
| What is Mammalogy?   | 2         |
| Why Study Mammals?   | 2         |
| Resources for Mammalogists                                       | 4         |
| Organization of the Book   | 5         |
| Summary  | 6         |
| Discussion Questions   | 6         |
| Suggested Readings   | 6         |
| <b>Chapter 2 History of Mammalogy</b>                            | <b>7</b>  |
| First Interest in Mammals  | 8         |
| Seventeenth- and Eighteenth-Century                              |           |
| Natural History  | 9         |
| Nineteenth-Century Mammalogy                                     | 10        |
| Emergence of Mammalogy as a Science                              | 16        |
| Summary  | 18        |
| Discussion Questions   | 19        |
| Suggested Readings   | 19        |
| <b>Chapter 3 Methods and Techniques<br/>for Studying Mammals</b> | <b>20</b> |
| Field Methods  | 20        |
| Laboratory Methods   | 26        |
| Morphometrics  | 26        |
| Summary  | 38        |
| Discussion Questions   | 39        |
| Suggested Readings   | 39        |
| <b>Chapter 4 Evolution and Dental<br/>Characteristics</b>        | <b>40</b> |
| Synapsid Lineage   | 40        |
| Pelycosaurs and Therapsids                                       | 42        |
| The First Mammals  | 46        |
| Cenozoic Mammals and Mammalian Radiation                         | 49        |
| Summary of Anatomical Trends in Organization from                |           |
| Mammal-Like Amniotes to Mammals                                  | 50        |
| Characteristics of Modern Mammals                                | 52        |
| Dentition  | 53        |
| Summary  | 56        |
| Discussion Questions   | 57        |
| Suggested Readings   | 57        |

*ix*

## **PART 2**

### *Structure and Function*

|  |            |
|--|------------|
| <b>Chapter 5 Integument, Support,<br/>and Movement</b>                             | <b>59</b>  |
| Integument   | 59         |
| Basic Skeletal Patterns  | 66         |
| Muscles of Mammals   | 69         |
| Modes of Locomotion  | 69         |
| Summary  | 77         |
| Discussion Questions   | 77         |
| Suggested Readings   | 78         |
| <b>Chapter 6 Foods and Feeding</b>   | <b>79</b>  |
| Modes of Feeding   | 79         |
| Foraging Strategies  | 96         |
| Summary  | 99         |
| Discussion Questions   | 100        |
| Suggested Readings   | 101        |
| <b>Chapter 7 The Nervous and Endocrine<br/>Systems, and Biological<br/>Rhythms</b> | <b>102</b> |
| Control Systems  | 102        |
| Nervous System   | 102        |
| Endocrine System   | 105        |
| Immune System  | 107        |
| Biological Rhythms   | 108        |
| Summary  | 111        |
| Discussion Questions   | 112        |
| Suggested Readings   | 112        |
| <b>Chapter 8 Environmental Adaptations</b>   | <b>113</b> |
| Heat Transfer Between a Mammal<br>and the Environment                              | 114        |
| Temperature Regulation   | 114        |
| Adaptations to Cold  | 115        |
| Avoidance and Resistance   | 116        |
| Adaptations to Heat  | 131        |
| Summary  | 143        |
| Discussion Questions   | 144        |
| Suggested Readings   | 144        |

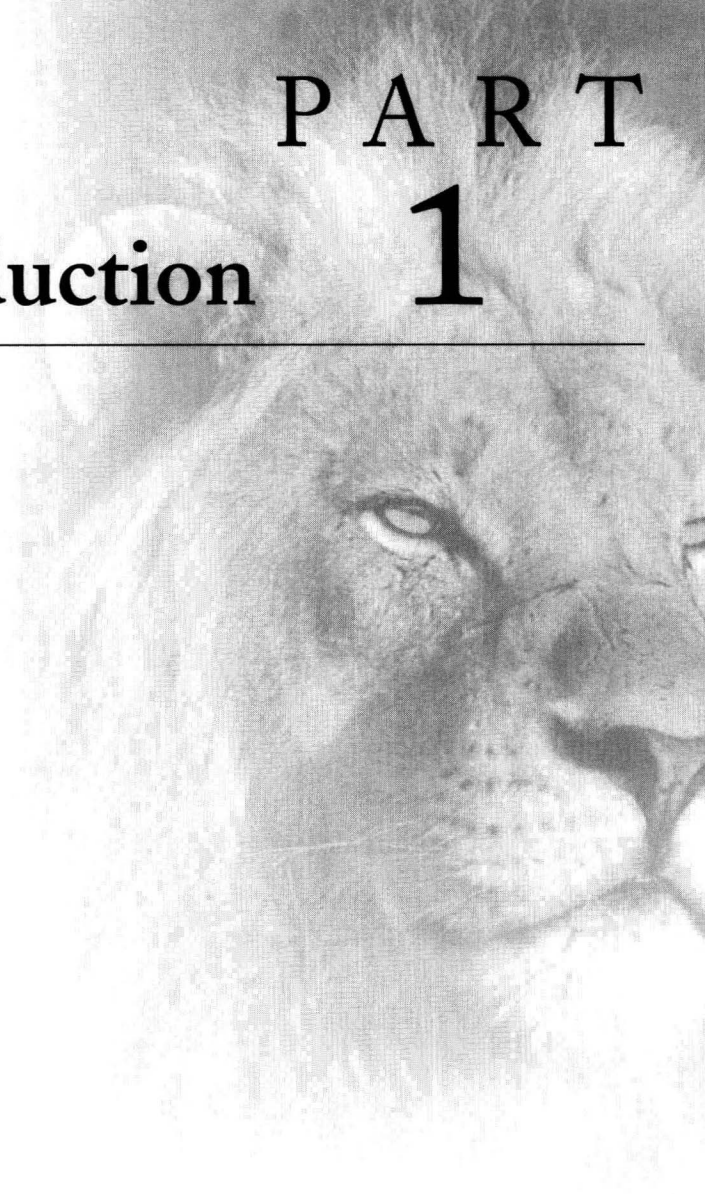


|  |   |   |   |                                |
|--|---|---|---|--------------------------------|
| <b>Chapter 9</b>                               | <b>Reproduction</b>   | <b>146</b>  | Tubulidentata   | 245                            |
| The Reproductive Systems                       | 147   | Summary   | 246   |                                |
| Gestation and Parturition                      | 156   | Discussion Questions                              | 246   |                                |
| Reproductive Variations                        | 157   | Suggested Readings                                | 246   |                                |
| Parturition                                    | 159   |   |   |                                |
| Lactation                                      | 160   | <b>Chapter 15</b>                                 | <b>Carnivora</b>  | <b>247</b>                     |
| Summary  | 162   | Morphology  | 249   |                                |
| Discussion Questions                           | 162   | Fossil History                                    | 250   |                                |
| Suggested Readings                             | 163   | Economics and Conservation                        | 251   |                                |
|  |   | Suborders and Families                            | 251   |                                |
|  |   | Summary   | 260   |                                |
|  |   | Discussion Questions                              | 260   |                                |
|  |   | Suggested Readings                                | 260   |                                |
| <b>PART 3</b>                                  |   |   |   |                                |
| <b><i>Adaptive Radiation and Diversity</i></b> |   |   |   |                                |
| <b>Chapter 10</b>                              | <b>Monotremes and Marsupials</b>                              | <b>168</b>  | <b>Chapter 16</b>                                       | <b>Cetacea</b>                 |
| Monotremata                                    | 168   | Morphology  | 261   |                                |
| Marsupials                                     | 172   | Fossil History                                    | 268   |                                |
| Summary  | 186   | Economics and Conservation                        | 270   |                                |
| Discussion Questions                           | 187   | Suborders and Families                            | 272   |                                |
| Suggested Readings                             | 187   | Summary   | 278   |                                |
|  |   | Discussion Questions                              | 278   |                                |
|  |   | Suggested Readings                                | 279   |                                |
| <b>Chapter 11</b>                              | <b>Insectivora, Macroscelidea, Scandentia, and Dermoptera</b> | <b>188</b>  | <b>Chapter 17</b>                                       | <b>Rodentia and Lagomorpha</b> |
| Insectivora                                    | 188   | Rodentia  | 280   |                                |
| Macroscelidea                                  | 195   | Lagomorpha  | 296   |                                |
| Scandentia                                     | 196   | Summary   | 298   |                                |
| Dermoptera                                     | 197   | Discussion Questions                              | 299   |                                |
| Summary  | 198   | Suggested Readings                                | 299   |                                |
| Discussion Questions                           | 198   |   |   |                                |
| Suggested Readings                             | 198   | <b>Chapter 18</b>                                 | <b>Proboscidea, Hyracoidea, and Sirenia</b>             | <b>300</b>                     |
|  |   | Proboscidea                                       | 300   |                                |
| <b>Chapter 12</b>                              | <b>Chiroptera</b>   | <b>199</b>  | Hyracoidea  | 305                            |
| Morphology                                     | 200   | Sirenia   | 307   |                                |
| Fossil History                                 | 206   | Summary   | 311   |                                |
| Economics and Conservation                     | 206   | Discussion Questions                              | 311   |                                |
| Suborders and Families                         | 207   | Suggested Readings                                | 311   |                                |
| Summary  | 217   |   |   |                                |
| Discussion Questions                           | 218   | <b>Chapter 19</b>                                 | <b>Perissodactyla and Artiodactyla</b>                  | <b>312</b>                     |
| Suggested Readings                             | 218   | Perissodactyla                                    | 312   |                                |
|  |   | Artiodactyla                                      | 317   |                                |
| <b>Chapter 13</b>                              | <b>Primates</b>   | <b>219</b>  | Summary   | 328                            |
| Ordinal Characteristics                        | 220   | Discussion Questions                              | 328   |                                |
| Primate Evolution                              | 220   | Suggested Readings                                | 329   |                                |
| Morphology                                     | 220   |   |   |                                |
| Fossil History                                 | 220   | <b>PART 4</b>                                     |   |                                |
| Economics and Conservation                     | 223   | <b><i>Behavior, Ecology, and Biogeography</i></b> |   |                                |
| Strepsirhine Primates                          | 224   |   |   |                                |
| Haplorhine Primates                            | 230   | <b>Chapter 20</b>                                 | <b>Communication, Aggression, and Spatial Relations</b> | <b>331</b>                     |
| Summary  | 237   | Communication                                     | 331   |                                |
| Discussion Questions                           | 237   | Aggression and Competition                        | 339   |                                |
| Suggested Readings                             | 237   | Spatial Relations                                 | 339   |                                |
| <b>Chapter 14</b>                              | <b>Xenarthra, Pholidota, and Tubulidentata</b>                | <b>238</b>  |   |                                |
| Xenarthra                                      | 238   |   |   |                                |
| Pholidota                                      | 243   |   |   |                                |

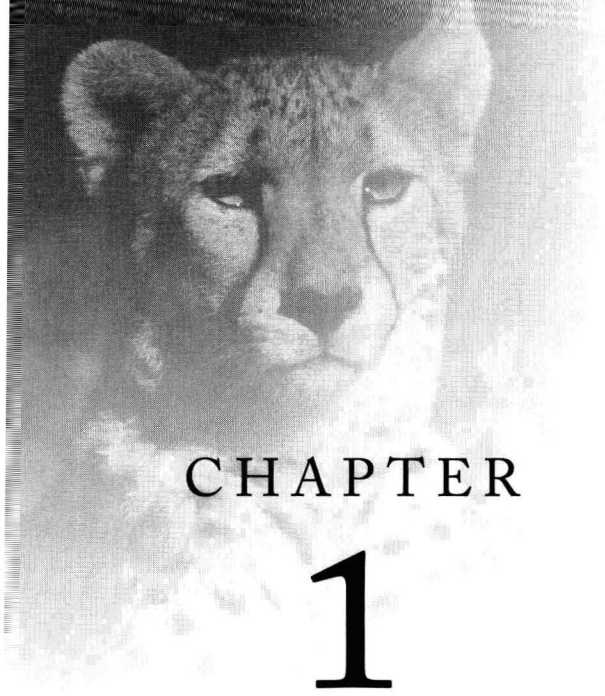
|   |            |  |            |
|---|------------|--|------------|
| Summary   | 342        | Historical Zoogeography of Mammals                           | 419        |
| Discussion Questions  | 343        | Ecological Zoogeography of Mammals                           | 424        |
| Suggested Readings  | 343        | Summary  | 430        |
| <b>Chapter 21 Sexual Selection, Parental Care,<br/>and Mating Systems</b> | <b>344</b> | Discussion Questions   | 431        |
| Anisogamy and the Bateman Gradient  | 344        | Suggested Readings   | 431        |
| Sex Ratio   | 345        | <b>PART 5</b>  |            |
| Sexual Selection  | 346        | <b><i>Special Topics</i></b>                                 |            |
| Parental Investment   | 349        | <b>Chapter 27 Parasites and Diseases</b>                     | <b>433</b> |
| Parent-Offspring Conflict   | 352        | Parasite Collection  | 434        |
| Mating Systems  | 352        | Effects of Parasites on Host Populations                     | 434        |
| Summary   | 355        | Coevolution of Parasites and Mammalian Hosts                 | 435        |
| Discussion Questions  | 355        | Mammalian Parasites and Diseases                             | 436        |
| Suggested Readings  | 356        | Vector-Borne Zoonoses  | 440        |
| <b>Chapter 22 Social Behavior</b>   | <b>357</b> | Nonvector Zoonoses   | 444        |
| Examples of Cooperative Social Behavior                                   | 357        | Summary  | 446        |
| Why Mammals Live in Groups  | 359        | Discussion Questions   | 447        |
| How Social Behavior Evolves   | 361        | Suggested Readings   | 447        |
| Summary   | 368        | <b>Chapter 28 Domestication<br/>and Domesticated Mammals</b> | <b>448</b> |
| Discussion Questions  | 368        | Why Domesticate Mammals?                                     | 448        |
| Suggested Readings  | 368        | How Domestication Began                                      | 449        |
| <b>Chapter 23 Dispersal, Habitat Selection,<br/>and Migration</b>         | <b>369</b> | Mammals That Have Been Domesticated                          | 450        |
| Dispersal from the Place of Birth   | 369        | Morphological Effects<br>of Domestication                    | 456        |
| Habitat Selection   | 372        | Domestication: Human Artifact or Evolutionary<br>Process?    | 456        |
| Migration   | 375        | Current Initiatives  | 457        |
| Homing  | 377        | Summary  | 457        |
| Summary   | 380        | Discussion Questions   | 458        |
| Discussion Questions  | 381        | Suggested Readings   | 458        |
| Suggested Readings  | 381        | <b>Chapter 29 Conservation</b>                               | <b>459</b> |
| <b>Chapter 24 Populations and Life History</b>                            | <b>382</b> | Nature of the Problem  | 459        |
| Population Processes  | 382        | Solutions to Conservation Problems                           | 468        |
| Life History Traits   | 385        | Case Studies   | 471        |
| Population Growth and Regulation  | 388        | Summary  | 473        |
| Summary   | 397        | Discussion Questions   | 474        |
| Discussion Questions  | 398        | Suggested Readings   | 474        |
| Suggested Readings  | 398        | <b>Glossary</b>  | <b>475</b> |
| <b>Chapter 25 Community Ecology</b>                                       | <b>399</b> | <b>References</b>  | <b>492</b> |
| The Ecological Niche  | 399        | <b>Credits</b>   | <b>530</b> |
| Species Interactions and<br>Community Structure                           | 400        | <b>Index</b>   | <b>532</b> |
| Community Function  | 408        |  |            |
| Community Patterns  | 410        |  |            |
| Summary   | 414        |  |            |
| Discussion Questions  | 415        |  |            |
| Suggested Readings  | 415        |  |            |
| <b>Chapter 26 Zoogeography</b>  | <b>416</b> |  |            |
| What is Zoogeography?   | 416        |  |            |
| Faunal Regions  | 417        |  |            |

# PART 1 Introduction

---







## CHAPTER

# 1

What is Mammalogy?

Why Study Mammals?

Resources for Mammalogists

Organization of the Book

# The Study of Mammalogy

## 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 whom we share our natural surroundings (figure 1.1). Many of the species of animals that have aroused public concern for their survival, such as elephants, whales, large cats, gorillas, and the giant panda, are mammals.

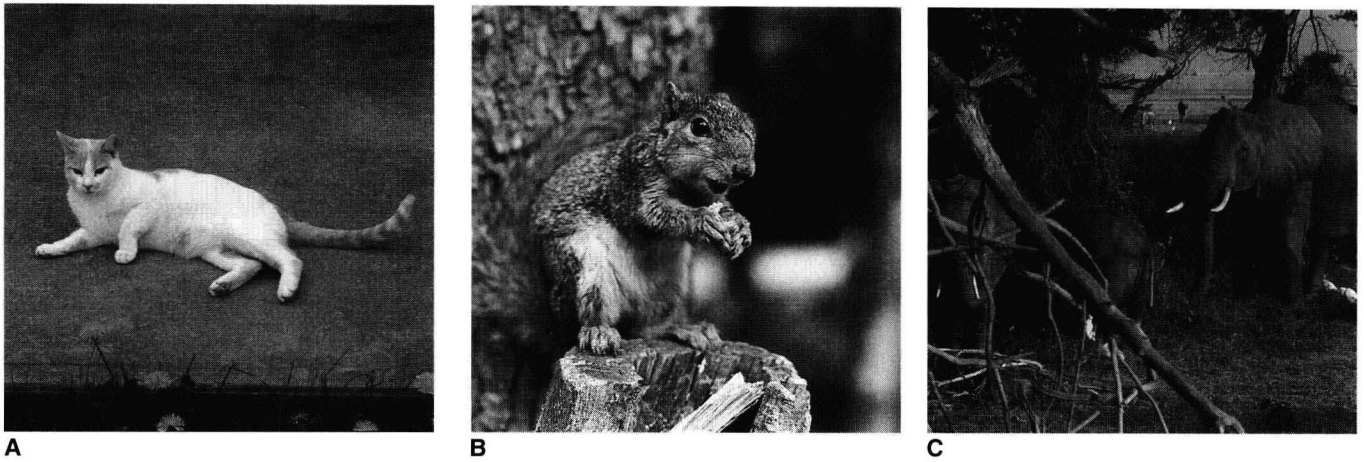
Mammals share a number of common features, including (1) the capacity for internal temperature control, often aided by a coat of fur; (2) the possession of mammary glands, which, in females, provide nourishment for the young during early development; and (3) with a few exceptions, the ability to give birth to live young. These and many other features of mammals are discussed in detail in chapter 4 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 and 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 from all these 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 chapter 4, 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, which deals with 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 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 mammalogy 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 if humans were to successfully hunt or trap them. Some mammals, such as the saber-toothed cats that coexisted with early humans, were potential predators on humans. Knowledge of their



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

habits was important for survival. Indeed, there are still locations throughout 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 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 hides, bones, fur, or blubber from whales and seals.

Mammals serve the needs of humans as pets and for recreational hunting. 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 mammalian pets. Many species are hunted for sport in North America, including the cottontail rabbit (*Sylvilagus floridanus*), the 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*), have been introduced in several states, most notably Texas, to provide additional game species. Some exotics have become major pests after introduction for sport or trade because their interactions with native species were unforeseen. An example is the release of the Indian mongoose (*Herpestes javanicus*) on many islands in the Caribbean Sea and on the Hawaiian Islands. Mongooses were introduced to control rodents that had, in turn, been brought to the islands by humans. Mongooses consume the eggs and young of many native bird species, however, as well as compete with other native animals.

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*] or black-tailed prairie dog [*Cynomys ludovicianus*] are vectors 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 mammals. Rats, mice, and occasionally other small mammals with whom we share our living areas do great harm to both our 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 can lead to means for controlling them. Moles or gophers may damage our 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 of 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. After driving many species into or close to extinction, some effort is being made to reverse the trend. Toward that goal, some people work to understand and protect the habitats of endangered or 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 the black-footed ferret (*Mustela nigripes*) and red wolf (*Canis rufus*).

In addition to examining the loss of species through extinction, a further result of conservation efforts in recent years is 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. For example, two new species of rodents, *Andalgalomys roigi* from Argentina

and *Tapecomys primus* from Bolivia, have both been described in the past several years (Mares and Braun 1996; Anderson and Yates 2000). The distinctions needed to differentiate these new taxa from those that were previously described has involved traditional measures of morphology and modern molecular techniques based on DNA.

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 develop personal libraries of pertinent materials, including general reference works and guidebooks containing keys for identifying mammals and providing basic information on the habits of particular species.

A great deal of literature is available on all aspects of mammals. Some volumes encompass worldwide coverage, such as *Walker's Mammals of the World* (Nowak 1991); Macdonald's (1984) *Encyclopedia of Mammals*; and Wilson and Reeder's (1993) *Mammal Species of the World*. Other books provide coverage of a particular continent or faunal region, such as Hall and Kelson's *The Mammals of North America* (1959), Hall's second edition of the same work (1981, 2001), and Burt and Grossenheider's *A Field Guide to the Mammals* (1980), covering North America; *Field Guide to the Mammals of Southern Africa* (Stuart and Stuart 1988), *Mammals of Australia* (Strahan 1995), *The Mammals of the Palearctic Region* (Corbet 1988), and *Wild Mammals of North America* (Chapman and Feldhamer 1982). In the United States, many books cover the mammals of various regions, for example, *Wild Mammals of New England* (Godin 1977), *Mammals of the Intermountain West* (Zaveloff 1988), *Mammals of the Great Lakes Region* (Kurta 1995), and *Guide to the Mammals of the Plains States* (Jones et al. 1985), as well as of practically every state, for example, *Mammals of Wyoming* (Clark and Stromberg 1987), *Mammals of Indiana* (Mumford and Whitaker 1982), *Mammals of Illinois* (Hoffmeister 1989), and *Guide to the Mammals of Pennsylvania* (Merritt 1987). Other works are specialized treatises on particular taxonomic groups (e.g., *The Natural History of Badgers* by Neal [1986]) or even monographs on particular species (e.g., *White-Tailed Deer Ecology and Management*, edited by Halls [1984]). There are books on practically every mammalian order, on particular families, and on many individual species.

A variety of journals also are devoted strictly to mammals, such as *Journal of Mammalogy*, *Acta Theriologica*, *Mammalia*,

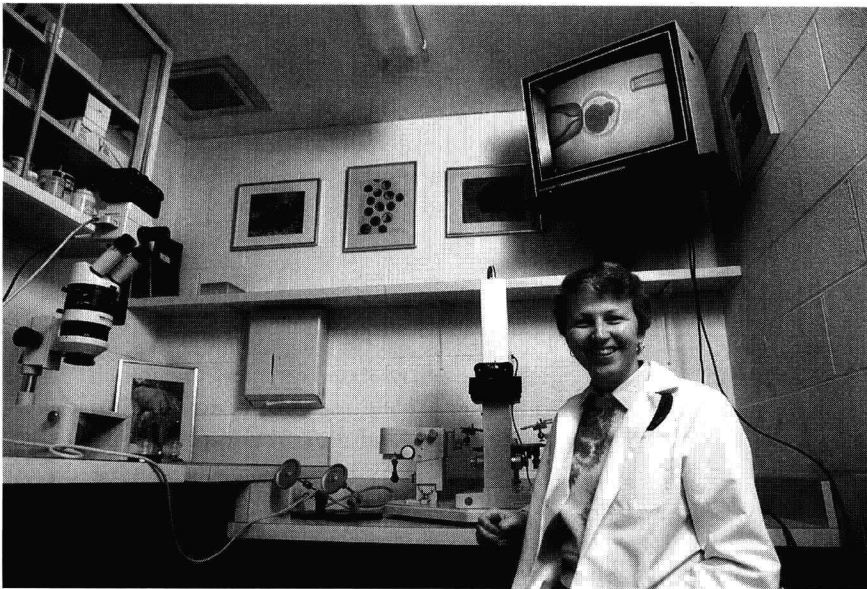
*Mammal Review*, and others published by national or international professional societies devoted to the study of mammals. In addition, a number of professional organizations promote the study of mammals through national and international meetings and publications as well as by mentoring younger scientists interested in the discipline. Most notable among these organizations is the American Society of Mammalogists, founded in 1919 (see Birney and Choate 1994).

Mammalogists rely on good university or college libraries for extensive collections of books and journals containing information on mammals. The *Zoological Record*, which began in 1848 and is issued annually, is the best overall source for literature on mammals. It provides information by species, subject, author, and geographic area. Computerized bibliographic databases are very useful for locating literature on a particular subject or a specific mammalian species, or works by a particular author. A note of caution is in order; most computerized bibliographic databases are limited to information going back only 15 to 20 years. Works published earlier than that are not recorded. Because mammalogy has a history of significant work dating back more than a century, additional sources beyond databases should be consulted. One method uses reference lists in books or papers to compile a retrospective list of articles that encompasses a broad time period.

Mammals are studied as both living organisms and preserved specimens. Living mammals are studied in various situations, including in the wild in their natural habitats. Observing mammals directly through such means as trapping or radiotelemetry can provide particular insights and may involve travel to exotic places or simply being "out in the field." Other types of research are conducted in a captive setting, usually a laboratory facility, zoological park, or aquarium. Some species are either rare enough in the wild or are small, nocturnal, or secretive enough to necessitate the use of a zoological park or laboratory setting to conduct research. Many people who visit zoos are unaware that they also function as places of scientific study. In some exhibit buildings or enclosed areas not open to the public, species conservation and related investigations are taking place (figure 1.2). Today, a number of zoos have separate facilities for the study of species that may be endangered or threatened. An excellent example is the Smithsonian Institution (National Zoological Park) facility at Front Royal, Virginia, which was formerly a major horse-breeding station for the U.S. Army cavalry. Investigations of domestic animals, both livestock and pets, also are carried out under more controlled conditions in a variety of laboratory research settings and on farms.

The field of mammalogy is fortunate that, beginning several centuries ago, museum collections of preserved mammals were started, and public and private menageries, the forerunners of the modern zoological parks, came into existence. For a short but thorough summary of this topic, with particular emphasis on North America, consult Wilson and Eisenberg (1990). Today, a large network of museums and related collections of mammals provides study skins, whole mounts, skeletal remains, and, in some instances, preserved





**Figure 1.2 Research at zoos.** Exhibit areas of many zoological parks that are not open to the public are important in terms of the studies taking place there on breeding and social biology. Often these areas involve breeding programs of endangered species, such as that shown here in a behind-the-scenes view from the Cincinnati Zoo.

soft anatomy and tissues for genetic studies (Hafner et al. 1997). These collections also include large numbers of fossils discovered by paleontologists. Without such materials, we would not be able to discern very much about the evolutionary history of mammals. Although we generally see such museums in their role as educational institutions, they also contain vast storage and work areas where professionals curate and study the preserved materials (figure 1.3). In several countries (e.g., Canada), computerized databases exist of all of the preserved and fossil materials from most museums, permitting investigators throughout the country to access the location of and information about particular specimens. A global network of this sort may be developed in the coming decades.

## Organization of the Book

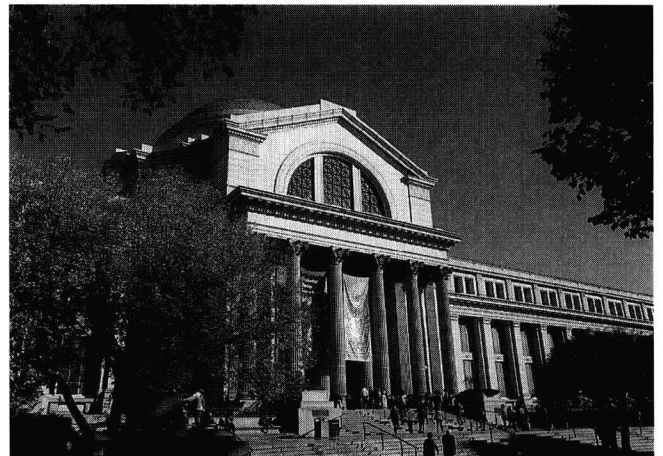
This book is divided into five parts. In the first part, after these introductory remarks, we examine the history of mammalogy (chapter 2). Chapter 3 explores how mammalogists proceed with their investigations; what questions they ask, and how they answer them. Chapter 4 deals with the evolution of mammals and the diagnostic characteristics that define them.

Part 2 integrates the morphological features of mammals with their physiological functions and behavior. This material and the examples provide a foundation for structure and function, and illustrate variation among mammals, including specialized adaptations that serve as solutions to particular problems.

Part 3 is a taxonomic examination of biodiversity among the 26 orders of mammals, emphasizing traits that characterize each mammalian family. Methods for discerning relationships among mammals at various levels of taxonomic classification are covered, including such recent developments as the use of protein allozymes and DNA.

Part 4 examines the interactions of mammals from behavioral and ecological perspectives. Vaughan (1986) commented that behavior and related topics were slow in developing. In earlier textbooks by Cockrum (1962) and Gunderson (1976), as well as earlier editions of Vaughan's text, we find scant coverage of behavior and only modest coverage of ecology. As is true for ornithology and herpetology, a shift in emphasis has taken place in the last quarter century: Behavior and ecology are now receiving considerably more attention. An examination of recent issues of the *Journal of Mammalogy* further illustrates our point. Fifty percent or more of the papers deal with these topics. Some

earlier books on mammals, including the text by Davis and Golley (1963) and the volume on natural history by Bourlière (1970), provided substantial coverage of ecology and behavior. In part 4, we build on the foundations of classical mammalogy and combine description, systematics, form, and function to examine the ecology and behavior of mammals.



**Figure 1.3 National Museum of Natural History, Washington, D. C.** Museums are important repositories for large collections of preserved and fossilized specimens of mammals and other animals. The more familiar function of such facilities, serving to educate and entertain the public, may also be viewed as an important reason for the study of mammals.

The final section (part 5) covers several specialized topics. Animal diseases and parasites (chapter 27) are important from both biological and practical perspectives. Domestication of mammals (chapter 28) has long been a part of human life. Recently, emphasis on management of animals in zoological parks and on game farms and ranches worldwide has

been renewed. Conservation biology (chapter 29) takes on renewed importance each time we read about the threat to an endangered species. This last chapter attempts to apply what we have learned throughout the book to the issues of habitat conservation, reproductive biology, and related species preservation efforts.

## Summary

Mammals are one of the classes of vertebrates or animals with backbones. All mammals share a series of common characteristics, including internal control of body temperature (often aided by an insulating layer of fur), mammary glands, and (with a few exceptions) live birth of young. Mammals are studied for a variety of reasons, including their use for food and other products; as subjects of recreational hunting; as pets; as pests that cause damage; their conservation; their role in disease and related health considerations; because we are mammals ourselves; and for aesthetic interest.

Our study of mammals

1. Examines the history of the discipline, the methods used by mammalogists, and the evolution and characteristics of mammals
2. Explores the details of relationships between structure and function in the morphological and physiological systems of mammals
3. Reviews the taxonomic subdivisions of mammals

4. Explores the behavior and ecology of mammals
5. Provides special chapters on diseases, parasites, domesticated mammals and those kept on game ranches, and conservation.

Our approach weaves four major themes together: the process of evolution by natural selection as it has shaped mammals, in terms of both adaptation and speciation; how mammalogists ask and go about answering questions; the interrelationships of morphology, physiology, and behavior; and the diversity of mammals.

A variety of helpful resources are available for students and professionals interested in mammalogy. These include places to study mammals, such as zoological parks, aquaria, laboratories, and the natural setting. Excellent collections of preserved material from mammals are located in museums. Finally, modern libraries, with their collections of books, journals, and computerized databases, contain vast quantities of readily accessible information.

## Discussion Questions

1. Make a list of all of the mammals (use common names for now) that you have encountered in the past month. Note also where you saw them and any key features you used to distinguish them first as mammals and then as individual species.
2. After reading the section on reasons for studying mammals, compile your own list of reasons for investigating this group of animals. You can use these reasons as a starting point and provide some more detailed purposes, or you can start from scratch to come up with some reasons for the study of mammals and see how your list compares with the one provided. For each reason on your list, provide a brief specific example of how that rationale for the study of mammals has already affected you.
3. At your library, locate the computer terminals that access bibliographic databases. Select four topics related to mammalogy. Search these topics and the several permutations of those topics that occur to you as you peruse the search output. This exercise should familiarize you with the use of such databases and can provide references for topics that may become part of a required paper in the course you are taking.

## Suggested Readings

Bourlière, F. 1970. *The natural history of mammals*. Alfred A. Knopf, New York.  
 Macdonald, D. (ed.). 1984. *The encyclopedia of mammals*. Facts on File Publications, New York.

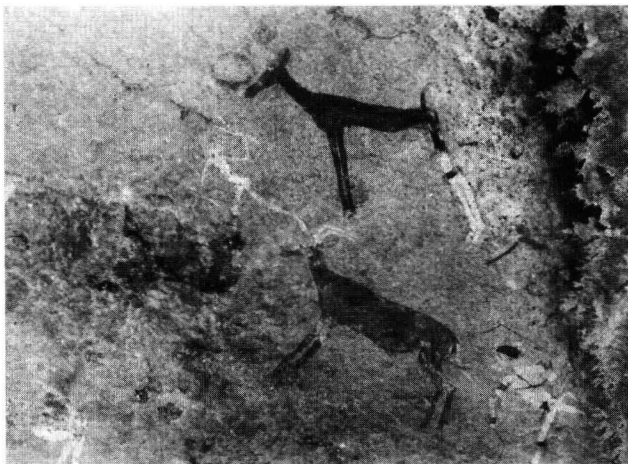
Wilson, D. E. and J. F. Eisenberg. 1990. *Origin and applications of mammalogy in North America*. Pp. 1–35 *in* *Current mammalogy*, vol. 2 (H. H. Genoways, ed.). Plenum, New York.

# History of Mammalogy

Early in human evolution, our ancestors became aware of other mammals with whom they shared habitat. In some cases, this knowledge about mammals served to determine possible prey that could be food. In other instances, information about potential predators was necessary for humans to avoid becoming food for larger carnivores. Other mammals have always been competitors with humans for food and shelter.

Early recorded indications of human knowledge about mammals come from cave paintings and petroglyphs (figure 2.1). Other evidence comes from sites where humans either drove herds of mammals over cliffs to their death or forced them through a narrow passage to be trapped and clubbed or otherwise killed. Prior knowledge of the behavior and movement patterns of mammals was crucial to the development of an effective hunting strategy. Some relationships between early humans and mammals were even closer. Dogs were domesticated from wolves (*Canis lupus*), and sheep (*Ovis aries*), goats (*Capra hircus*), and cattle (*Bos taurus*) were domesticated from wild ungulates (chapter 28). Religious icons, such as small statues (figure 2.2), indicate that humans ascribed certain mystical powers to the animals with whom they shared their world. Throughout much of human history, many mammalian species have also been used to convey people and goods. It has only been within the last several hundred years that other major modes of transportation have replaced mammals. Even today in many locations around the world, mammals are a major means of transport.

In the sections that follow, we trace the development of mammalogy from the days of classical Greece and Rome through the period of exploration and the dawn of natural history, and we end with a brief examination of the discipline of mammalogy today.



**Figure 2.1 Cave painting of a mammal.** Early humans daily dealt with other living mammals in their environment. The large ungulate mammal represented here in a cave painting from Alpera, Spain, was likely hunted by the people who painted it. The animal was eaten for food, and its bones, fur, and other products were also put to good use as tools and clothing.

## CHAPTER 2

### First Interest in Mammals Seventeenth- and Eighteenth- Century Natural History

Naturalists

Concepts and Ideas

### Nineteenth-Century Mammalogy

Explorations and Expeditions

Museums

Zoos

New Theories and Approaches

Early Written Works on Mammals

### Emergence of Mammalogy as a Science





**Figure 2.2 Early mammalian carving.** The mammal shown in this statue from a Meso-American archeological site is a cat, and is represented because it shared the environment with the people who carved it. The fact that it is depicted in this small carving suggests that it also may have been the subject of some form of religious importance or it may have served as a clan totem.

Mammalogy and the study of mammals are important to humans for at least three reasons. First, as humans, we are mammals, and thus we share similar physiological, behavioral, social, and ecological traits. Gaining knowledge about nonhuman mammals aids in understanding ourselves and human evolution. Second, some species of mammals, perhaps a disproportionately high number relative to other vertebrates, are endangered in our world today. If we are to conduct effective programs to preserve these species, we need an enhanced understanding of mammals. Third, mammals have been most useful to scientists in the search for general principles of evolution, ecology, and behavior. This last point is covered in greater detail in part 4.

## First Interest in Mammals

From the days when most humans were hunters and gatherers through the beginnings of agriculture about 9000 to 10,000 years ago, a body of knowledge about mammals developed and was passed from generation to generation. With the advent of written language, some of this knowledge was recorded in glyphs, replacing or augmenting earlier depictions in art and oral stories. Particularly important in these early times was knowledge about mammals as food sources and work animals. Mammals were first domesticated in the Middle East and Asia. These early rudiments of formal interest in mammals, including scholarly writings, were later fostered in Egypt, Greece, and Rome as part of a growing body of information about the natural world.

Interest in mammals involved both curiosity about living forms and attention to various fossils that were discovered, collected, and passed among what were then called natural philosophers, a group that included Hippocrates (460–377 BC) and Aristotle (384–322 BC). Although Aristotle did not actually generate a classification scheme for living organisms, he did group animal forms as he saw them (Singer 1959). The category he labeled as having red blood and viviparous reproduction (mammals) included three major groups: (1) viviparous quadrupeds, subdivided into the ruminants with cutting teeth in the lower jaw only and having cloven hoofs (e.g., sheep, oxen), the solid-hoofed animals (e.g., horses), and other viviparous quadrupeds; (2) cetaceans (whales and their relatives); and (3) humans.

Fossilized bones and teeth were discovered from time to time in the ancient world. These remains often raised questions about the origin of these animals and their relationships to existing animal life. Even early in the history of mammalogy as a science, fossils were important in attempts to understand mammals, their history, and their distribution around the globe (Miller and Gidley 1934).

Fossil remains of mammals remain today an important topic for study, including determining relationships between living and past forms. A fossil discovery in Wyoming, an insectivore, may turn out to be the smallest mammal ever known (Bloch et al. 1998). Even though body size does not fossilize, it is possible to use relationships between tooth size (or leg bone size) and body mass to predict the fossil organism's mass. Such a calculation relies on a range of living organisms on which we can measure both the teeth and the body mass. Only by continued work in the study of fossils, a field called paleontology, can we eventually piece together the evolutionary histories of mammals, both extinct and extant.

Aristotle and Pliny the Elder (AD 23–79) made extensive records of what they observed and heard about various mammals. Although these writings are primarily anecdotal, they are interesting, as the following quote from Pliny illustrates:

*In the mountains of Mauretania it is said that the herds of elephants move at the new moon down to a river by the name of Amilo, ceremoniously cleanse themselves there by spraying one another with water, and after having thus paid their respect to the heavenly light return to the forests bearing their weary calves with them. It is also said that when they are to be transported overseas, they refuse to go onboard until the master of the ship has given them a promise under oath to convey them home again. Further, they are so modest that they never mate except in secluded spots, while adultery never occurs amongst them. Towards weaker animals they show compassion, so that an elephant when passing through a flock of sheep will with his trunk lift out of the way those he meets, for fear of trampling on them. (Nordenskiöld 1928:55)*

Other early natural historians, such as the Roman anatomist Galen (AD 130–201), performed dissections, thereby generating new knowledge about the structure and function of different organ systems of animals, including