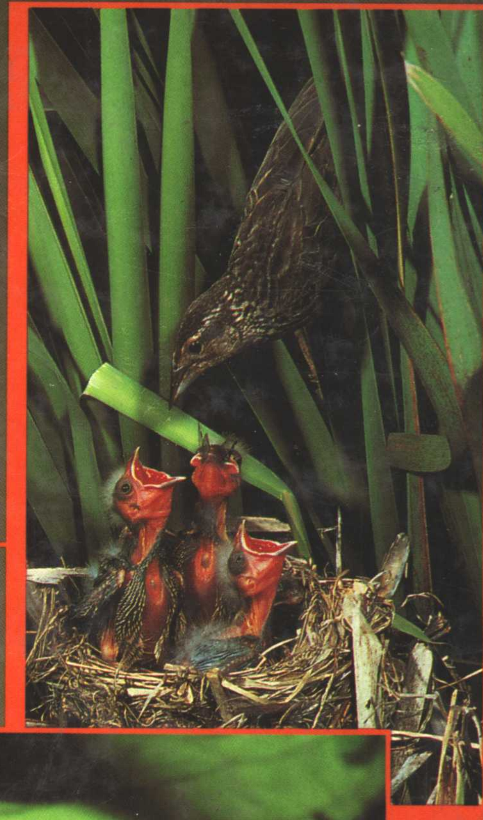
Vertebrate Life

THIRD EDITION



F. Harvey Pough
John B. Heiser
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John B. Heiser
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Cornell University

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COVER PHOTOGRAPHS

Front, top to bottom: A female red-winged blackbird (*Agelaius phoeniceus*) feeding its young; see Chapter 18. (Photograph by Michael Hopiak, courtesy of the Cornell Laboratory of Ornithology.) □ The aposematic pattern of a Costa Rican dart-poison frog (*Dendrobates pumilio*); see page 410. (Photograph by Frank J. Joyce.) □ Grooming is an important social behavior of baboons (*Papio cyanocephala*); see page 810. (Photograph by Carol Saunders.)

Back, top to bottom: The abundance and diversity of fishes active during the day on a coral reef in the Red Sea; see page 323. (Photograph by John B. Heiser.) □ The bright feathers on the head of the Costa Rican royal flycatcher (*Onychorhynchus coronatus*) are probably displayed during social interactions; see Chapter 18. (Photograph by Frank J. Joyce.) □ Combat between male impala (*Aepyceros melampus*); see page 803. (Photograph by Joy Belsky.) □ Warning display of the Central American rattlesnake (*Crotalus durissus*); see page 542. (Photograph by Frank J. Joyce.)

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Preface

The third edition of *Vertebrate Life* incorporates major changes that reflect the extraordinary activity in vertebrate biology during the past decade. The most pervasive changes have resulted from the widespread adoption of phylogenetic systematics (cladistics) as the basis for determining the phylogenetic relationships of organisms. The stress that this system of classification places on the importance of monophyletic groupings has ramifications in broad areas of biology. As an objective (although frequently controversial) classification that, in particular, reflects information about the sequence of changes during evolution, cladistics provides an evolutionary framework in which ideas from other biological specialties can be accommodated. As a result, studies of behavior, physiology, and ecology are increasingly being placed in an explicitly evolutionary context, and this common ground has fostered increased interaction among those specialties.

We have adopted a cladistic classification as the basis for organizing the third edition of *Vertebrate Life*, and have included cladograms illustrating the postulated relationships of the different lineages of vertebrates. In doing so, we have tried to reconcile the views of various authorities, and pointed out major areas of disagreement. The cladograms include synopses of the character states on which they are based and citations of the primary sources used. This information will facilitate exploration of different views, and will help faculty and students to modify the phylogenies presented here as new interpretations are published.

As a result of the cladistic perspective of this edition, we have reorganized the large quantity of information about morphology and physiology that was distributed among chapters in earlier editions. Chapter 3 presents a comprehensive review of vertebrate morphology and its evolutionary changes, including new material about embryonic development. Chapter 4 presents a parallel treatment of the general aspects of vertebrate physiology and homeostasis. Topics unique to particular groups are highlighted in the chapters treating those groups.

Another important conceptual change in this edition is the inclusion of a large quantity of material about ecology, behavior, and ecological physiology in response to requests from colleagues who teach courses that cover only living vertebrates. Chapters 16 and 23 present descriptions of the biology of ectotherms and endotherms, respectively, that focus on organismal function in the broadest sense and integrate information about ecology, behavior, and physiology to present a view of the way vertebrates interact with their environments. Chapter 22 summarizes information about the social behavior of mammals in a similarly broad context. We hope that students will find that these treatments illustrate the fascination the authors find in the study of vertebrate biology.

Literature citations have been brought up-to-date, with many references from 1987 and 1988. As before, we have chosen citations on the basis of their helpfulness to students attempting to enter the literature of the subject; review articles are cited where possible, and recent references are used because students can trace earlier work through them.

The task of reviewing all of vertebrate biology is nearly overwhelming, and would have been impossible without the hours of time that colleagues spent helping us. The list is now so long that we have added an acknowledgments section. We are exceedingly grateful to all of them.

Acknowledgments

Writing a book with a scope as broad as this one requires the assistance of many people. We are grateful to the following colleagues for their generous responses to our requests for information and their comments and suggestions: Michael Benton, Bruce Brewer, Sara Cairns, Cynthia Carey, Robert Carroll, Charles Cole, Martin Feder, Robert Full, Malcolm Gordon, James Hopson, Raymond Huey, Kenneth Kennedy, Tom Kemp, George Lauder, Rachel Levin, Deedra McClearn, Amy McCune, Peter Nathanielsz, A. L. Panchen, Karen Reiss, John Reiss, Carol Saunders, Alan Savitzky, Ellen Smith, Margaret Stewart, Stanley Temple, Keith Thomson, Laurie Vitt, David Winkler, and Richard Zweifel.

Dean G. Dillery (Albion College) and James C. Ha (Colorado State University) reviewed the second edition of *Vertebrate Life* and made many suggestions for improvements. William E. Bemis (University of Massachusetts at Amherst), Virginia Hayssen (Smith College), David G. Huckaby (California State University, Long Beach), and Leslie K. Johnson (The University of Iowa) reviewed the entire manuscript of the third edition. Their suggestions have shaped nearly every aspect of this book, and we cannot sufficiently express our gratitude for their efforts.

The illustrations in the third edition have benefitted greatly from the kindness of many colleagues who provided photographs and line drawings: George A. Bartholomew, Albert F. Bennett, Joy Belsky, Philip Bogdonoff, Edward B. Brothers, R. Bruce Bury, Sara J. Cairns, Robert L. Carroll, Mark A. Chappell, Charles J. Cole, Jack A. Cranford, David M. Dennis, Alan A. Detrich, Lang Elliott, Sharon B. Emerson, John W. Goerg, Peter E. Hillman, Daniel H. Janzen, Farish A. Jenkins, Jr., Cynthia L. Jensen, Frank J. Joyce, Jeffrey W. Lang, Rachel N. Levin, Amy R. McCune, Gail R. Michener, Kenneth A. Nagy, Frederick J. O. Nuss, Charles R. Peterson, Michael A. Recht, Karen Z. Reiss, David Robertshaw, Gerhard Roth, Carol D. Saunders, Robert D. Stevenson, Margaret M. Stewart, Janet M. Storey, Kenneth B. Storey, Theodore L. Taigen, David B. Wake, Marvalee H. Wake, Richard J. Wassersug, and David Winkler.

Lucile Macera painstakingly typed the entire manuscript onto computer disks, Linda Berman meticulously prepared the indices, and Margaret Pough handled ably the final checking of page proofs. Nearly all of the illustrations retained from earlier editions were redrawn and many new illustrations added. We are grateful to the artists: Frances Zweifel, Matthew Zweifel, Mary Dersch, and Network Graphics for their patience and painstaking care. Finally, the production supervisor at Macmillan, Dora Rizzuto, has earned our gratitude for the aplomb with which she has coordinated the activities of three authors and four artists in an enterprise that increased in complexity by the number of people involved.

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Contents

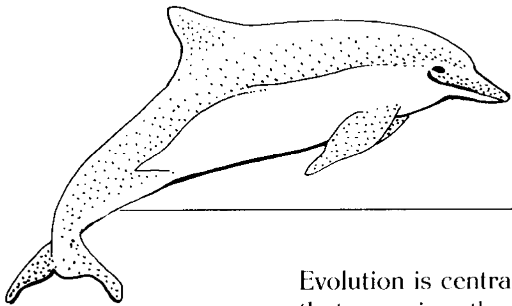
PART ONE

Vertebrate Diversity, Function, and Evolution

The 50,000 living species of vertebrates inhabit nearly every part of the Earth, and other kinds of vertebrates that are now extinct lived in habitats that no longer exist. Increasing knowledge of the diversity of vertebrates was one of the products of European exploration and expansion that began in the fifteenth and sixteenth centuries. In the middle of the eighteenth century the Swedish naturalist Carolus Linnaeus developed a binomial classification to catalog the varieties of animals and plants. The Linnean system remains the basis for naming living organisms today.

A century later Charles Darwin explained the diversity of plants and animals as the product of natural selection and evolution, and in the early twentieth century Darwin's work was coupled with the burgeoning information about mechanisms of genetic inheritance. This combination of genetics and evolutionary biology is known as the New Synthesis or Neo-Darwinism, and continues to be the basis for understanding the mechanics of evolution. Recent work has broadened our view of evolutionary mechanisms by suggesting, on one hand, that some major events in evolution may be the result of chance rather than selection, and, on the other hand, that natural selection can sometimes extend beyond individuals to related individuals, populations, or even to entire species. Methods of classifying animals also have changed their emphasis during the twentieth century, and classification, which began as a way of trying to organize the diversity of organisms, has become a way of generating testable hypotheses about evolution.

Vertebrate biology and the fossil record of vertebrates have been at the center of these changes in our view of life. Comparative studies of the anatomy, embryology, and physiology of living vertebrates have often supplemented the fossil record. These studies reveal that evolution acts by changing existing structures. All vertebrates have basic characteristics in common that are the products of their common ancestry, and progressive modifications of these characters can trace the progress of evolution. Thus, an understanding of vertebrate form and function is basic to understanding the evolution of vertebrates and the ecology and behavior of living species.



Evolution is central to vertebrate biology because it provides a principle that organizes the diversity that we see among living vertebrates and helps to fit extinct forms into the context of living species. Classification, initially a process of attaching names to organisms, has become a method of understanding evolution. Current views of evolution stress natural selection operating at the level of individuals as a predominant mechanism that produces change over time. Additional mechanisms may involve selection that operates at higher and lower levels of biological organization and chance events. The processes and events of evolution are intimately linked to the changes that have occurred on Earth during the history of vertebrates. These changes have resulted from the movements of continents and the effects of those movements on climates and geography. In this chapter we present an overview of the scene, the participants, and the rules governing the events that have shaped the biology of vertebrates.

The Diversity, Evolution, and Classification of Vertebrates

1

The Vertebrate Story

Mention "animal" and most people will think of a vertebrate. Vertebrates are often abundant and conspicuous parts of people's experience of the natural world. Vertebrates are also very diverse: The 50,000 living species of vertebrates range in size from fishes that weigh as little as 0.1 gram when they are fully mature to whales that weigh nearly 100,000 kilograms. Vertebrates live in virtually all the habitats on earth: Bizarre fishes, some with mouths so large they can swallow prey longer than their own bodies, cruise through the depths of the sea, sometimes luring prey to them with glowing lights. Some 15 kilometers above the fishes, migrating birds fly over the crest of the Himalayas, the highest mountains on Earth. Birds can live at these high altitudes where mammals are incapacitated by lack of oxygen because the lungs of birds have a pattern of airflow that is different from that of mammals and bird lungs are more effective than mammalian lungs at extracting oxygen from the air.

The behaviors of vertebrates are as diverse and complex as their body forms. Vertebrate life is energetically expensive, and vertebrates get the energy they need from food they eat. Carnivores eat the flesh of other animals and show a wide range of methods of capturing prey: Some predators search the environment to find prey, whereas others wait in one place for prey to come to them. Some carnivores pursue their prey at high speeds, others pull prey into their mouths by suction. In some cases the foraging behaviors that vertebrates use appear to be exactly the ones that maximize the amount of energy they obtain for the time they spend hunting; in other cases vertebrates can appear to be remarkably inept predators. Many vertebrates swallow their prey intact, sometimes while it is alive and struggling, but other vertebrates have very specific methods of dispatching prey: Venomous snakes inject complex mixtures of toxins, and cats (of all sizes from house cats to tigers) kill their prey with a distinctive bite on the neck. Herbivores eat plants: Plants do not run away when an animal approaches, but they are hard to digest and they frequently contain toxic compounds. Herbivorous vertebrates show an array of specializations to deal with the difficulties of eating plants: these specializations include elaborately sculptured teeth and digestive tracts that provide sites in which symbiotic microorganisms digest compounds that are impervious to the digestive systems of vertebrates.

Reproduction is a critical factor in the evolutionary success of an organism and vertebrates show an astonishing range of behaviors associated with mating and reproduction. In general males court females and females care for the young, but these roles are reversed in many species of vertebrates. The forms of reproduction employed by vertebrates range from laying eggs to producing living young. These variations range across almost all kinds of vertebrates—many fishes and amphibians produce live young and a few mammals lay eggs. In fact, only birds show no variation in their reproductive mode; all birds lay eggs. At the time of birth or hatching some vertebrates are entirely self-sufficient and never see their parents, whereas other vertebrates (including humans) have extended periods of obligatory parental care. Extensive parental care is found in seemingly unlikely groups of vertebrates—fishes that incubate eggs in their mouths, frogs that incubate eggs in their stomachs, and birds that feed their nestlings a fluid called crop milk that is very similar in composition to mammalian milk.

The diversity of living vertebrates is fascinating, but the species now living are only a small proportion of the species of vertebrates that have existed. For each living species there may be as many as ten extinct species, and some of these have no counterparts among living forms. The dinosaurs, for example, that dominated the Earth for 180 million years are so entirely different from any living animals that it is hard to reconstruct the lives they led. Even mammals were once more diverse than they are now: the Pleistocene saw giants of many kinds—ground sloths as big as modern rhinoceroses and raccoons and rodents as large as bears. Humans are closely related to the great apes (especially to chimpanzees and gorillas) and much of the biology of humans is best understood in the context of our vertebrate heritage. In the modern world the fate of other species of vertebrates is very much affected, for good or ill, by human decisions, and our responsibilities to other vertebrates cannot be ignored.

The story of vertebrates is fascinating: Where they originated, how they evolved, what they do, and how they work provides endless intriguing details. In preparation to tell this story we must introduce some basic information: What the different kinds of vertebrates are called and how they are classified, how evolution works, and what the world within which the story of vertebrates unfolded was like. In this chapter we provide an overview of the vertebrates and the processes of evolution and environmental change that have shaped them.

The Different Kinds of Vertebrates

Describing and classifying the variety of vertebrates, living and extinct, has become more complicated recently than it used to be as a result of a change in the criteria used for recognizing natural groups of organisms. Most of us have grown used to classifying vertebrates as jawless fishes, cartilaginous fishes, bony fishes, amphibians, reptiles, birds, or mammals. Those names are familiar; each conjures up an image of a particular kind of animal. When someone said "reptile" we thought of turtles, alligators, crocodiles, lizards, and snakes. The term "reptile" communicated information about particular animals, and the same was true of the terms "jawless fishes" or "birds."

The animals that we recognized by those names still exist, of course, but some go by different names and are grouped differently now. The reason for the change is an increased emphasis on the proposition that *groups* of animals can be identified only if they share a common evolutionary lineage. Basically the old method of classification (which can be called evolutionary systematics) lumped together animals that had very different evolutionary histories and produced groups that contained unrelated evolutionary lineages. The class Reptilia is the major example of the consequences of this sort of lumping, because the evolutionary lineages that gave rise to the living turtles and crocodilians separated about the same time as the divergence of mammals from both of those groups. That is, crocodilians are no more closely related to turtles than they are to mammals, and it makes no sense to place turtles and crocodilians in one class (Reptilia) and mammals in a class of their own (Mammalia). Similarly, crocodilians and birds are quite closely related, whereas snakes and lizards are only distantly related to cro-