Animal Behavior

ELEVENTH EDITION

Dustin R. Rubenstein • John Alcock

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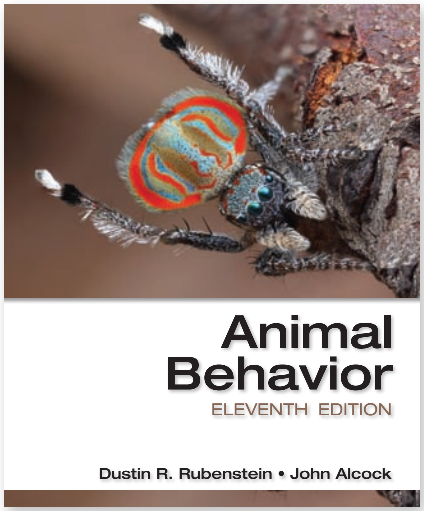
Columbia University   Arizona State University

SINAUER ASSOCIATES

NEW YORK   OXFORD
OXFORD UNIVERSITY PRESS



About the Cover

This male peacock spider (*Maratus elephans*) from Tamworth, NSW, Australia, unfurls from underneath his abdomen what looks like the tail of a male peacock. He also raises his legs as if to dance, something you can watch by following the QR code on the back cover. (Photograph by Michael Doe.)

Animal Behavior, Eleventh Edition

Oxford University Press is a department of the University of Oxford. It furthers the University's objective of excellence in research, scholarship, and education by publishing worldwide. Oxford is a registered trade mark of Oxford University Press in the UK and certain other countries.

Published in the United States of America by Oxford University Press
198 Madison Avenue, New York, NY 10016, United States of America

Sinauer Associates is an imprint of Oxford University Press.

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Address editorial correspondence to:
Sinauer Associates
23 Plumtree Road
Sunderland, MA 01375 USA
publish@sinauer.com

Address orders, sales, license, permissions, and translation inquiries to:
Oxford University Press USA
2001 Evans Road
Cary, NC 27513 USA
Orders: 1-800-445-9714

Library of Congress Cataloging-in-Publication Data

Names: Alcock, John, 1942- author. | Rubenstein, Dustin R., author.
Title: Animal behavior / Dustin R. Rubenstein, Columbia University, John Alcock, Arizona State University.
Description: Eleventh edition. | Sunderland, Massachusetts: Oxford University Press, [2019] | Revised edition of: Animal behavior: an evolutionary approach / John Alcock. 10th ed. c2013. | Includes bibliographical references.
Identifiers: LCCN 2018004580| ISBN 9781605355481 (paperback) | ISBN 9781605357706 (ebook)
Subjects: LCSH: Animal behavior--Evolution.
Classification: LCC QL751 .A58 2019 | DDC 591.5--dc23
LC record available at https://lccn.loc.gov/2018004580

9 8 7 6 5 4 3 2 1
Printed in the United States of America

To my parents,
who inspired in me a love of nature
and animal behavior at an early age.
DRR

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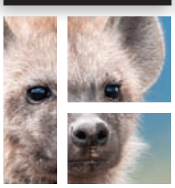

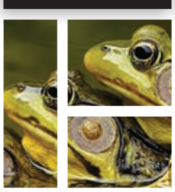

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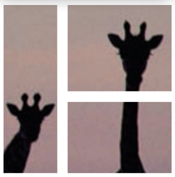

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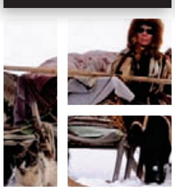

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Preface

For more than 40 years, *Animal Behavior* has been the leading textbook for introducing undergraduate students to the topic of animal behavior. John Alcock authored the first edition of this book in 1975, and after 9 subsequent versions, this eleventh edition brings on a new lead author, Dustin Rubenstein. The eleventh edition maintains its narrative tone as well as its focus on both evolutionary and mechanistic approaches to understanding how and why animals as different as insects and humans behave the way they do. In an effort to keep up with the rapidly evolving field of animal behavior, this new version also brings a more integrative approach to studying behavior, emphasizing the growing body of research linking behavior to the brain, genes, and hormones, as well as to the surrounding ecological and social environments. Topics like epigenetics and collective behaviors are highlighted for the first time. Additionally, the book covers the growing number of comparative phylogenetic studies in animal behavior that make use of ever-larger molecular phylogenies to generate and test new ideas in the evolution of animal behaviors. Ultimately, the book retains its primary goal of giving students a window into the various level of analysis that researchers use to explain why all living things—including humans—behave, often in complex ways.

New to the Eleventh Edition

In addition to a new lead author, the eleventh edition features several new approaches and features that support both student learning and instructor teaching. After extensive research concluded that most users prefer the classic organizational structure from early editions, rather than the changes that were made in the tenth edition, the book returns to its classic organizational structure, with proximate mechanisms introduced early in the book and before an extended discussion of the ultimate factors underlying behavior. Yet, each chapter attempts to highlight both proximate and ultimate explanations throughout, illustrating the integrative nature of the field today. This edition also includes a refined organizational structure within each chapter that makes material more accessible to students and instructors alike. Figures and photos throughout the book have been updated and revised as well, providing a fresher look that, along with the addition of error bars on most graphical figures, makes it easier for students to learn how to interpret data. The addition of new pedagogical features also makes it easier for students to learn complex concepts and apply behavioral and evolutionary thinking to thought-provoking questions and problems. Found in every chapter, these new boxes and tables emphasize hypothesis testing, data interpretation, and problem solving. Finally, since most students are drawn to animal behavior out of a fascination with something they have seen on TV or in nature, in each chapter we use QR codes offset in the margins to give students rapid access to high-definition video and audio clips of the behaviors discussed in the text.

Focus on Integration

This book provides a comparative and integrative overview of animal behavior, linking a diversity of behaviors and their adaptive functions to the brain, genes, and hormones, as well as to the surrounding ecological and social environments. Just as so many modern studies in animal behavior are taking advantage of new neurobiological or molecular approaches, this book introduces these and other cutting-edge techniques to its readers, all while maintaining a focus on the theoretical aspects of the field in an explicit hypothesis-testing framework. Ultimately, the book highlights both the evolutionary and mechanistic approaches to studying animal behavior, as well as the interdisciplinary approaches that emphasize the neural, genetic, and physiological mechanisms underlying adaptive behaviors. Because this new edition of the book is more integrative than previous versions, we have dropped the book's subtitle, *An Evolutionary Approach*, and now simply call it *Animal Behavior*. The concept of evolution by natural selection remains our guide as we expand in new and exciting directions.

In addition to the focus on integrative approaches, this edition features an update of specific topics such as how new technologies are revolutionizing the way we study animal movements and the genetic architecture of behavior, as well as new and expanded coverage of animal social behavior, animal communication, and human behavior, in addition to other topics. New empirical examples have been added to each chapter, some of which extend classic examples in new and exciting directions.

New Pedagogical Approach

Built upon the foundation of rich content and discussion topics from previous editions, we've applied more modern pedagogical tools and added new features in the eleventh edition. Found in every chapter, these new boxes and tables emphasize hypothesis testing, data interpretation, and problem solving. These features are designed to engage students, both inside and outside of the classroom, and aid instructors in developing their courses and delivering their lectures. New features include:

- **INTEGRATIVE APPROACHES:** Focusing attention on cutting-edge tools in the study of animal behavior, these boxes cover tools for studying birdsong, animal coloration, behavioral genetics, hormones, and how to conduct ethical studies of humans, among other topics.
- **HYPOTHESES TABLES:** In brief summaries, alternative or non-mutually exclusive hypotheses for specific animal behaviors are presented side-by-side.
- **EXPLORING BEHAVIOR BY INTERPRETING DATA:** In these boxes, we explore a concept in data analysis, such as analyzing spectrograms to show how song learning in birds can be adopted by other species, or drawing conclusions and generating new hypotheses from empirical data figures.

- **DARWINIAN PUZZLES:** Adapted from this popular feature in the tenth edition, these boxes deal specifically with unresolved "puzzles" in behavioral research, such as why females in some species have what looks like a penis but males don't.

In most boxes, students are challenged to "Think Outside the Box" by answering a series of thought-provoking questions related to the content and figures inside the box. These have been designed to foster in-class discussion between instructors and students. This feature complements Discussion Questions, which have now been consolidated online for easier student and instructor access.

QR Codes/Direct Web Links for Audio and Video Clips

Students taking a course on animal behavior want to see and hear animals behaving, and in this edition, we've integrated that directly into the text in an easily accessible manner. Using QR codes (and short URLs), students can immediately access audio and video directly related to the text in real-time, without having to wade through a large collection of resources on a companion website.

ABOUT THE TECHNOLOGY. On many iPhones and some Android phones, QR codes no longer require a QR reader app. (Any iPhone running iOS 11 or newer can read QR codes directly.) Simply open the camera, hold the phone over the QR code, and the audio/video link will appear. Other smartphones may require that you download a mobile app. For those who don't want to scan the QR codes, short URLs are provided for each individual audio and video clip (e.g., ab11e.sinauer.com/a2.1).

ABOUT THE AUDIO AND VIDEO LINKS. Most of the audio and video links in the book are provided by researchers whose examples appear in the text, or by the Macaulay Library at the Cornell Lab of Ornithology, drawing from their extensive collection of nearly 7,000,000 pictures, videos, and animal sounds.

Author Biographies

Dustin Rubenstein, an Associate Professor of Ecology, Evolution, and Environmental Biology at Columbia University, has studied animal behavior in birds, reptiles, mammals, insects, and crustaceans for nearly 20 years throughout Africa, Asia, Central and South America, and the Caribbean. As a leading expert in animal social behavior and evolution, his research has been published in top journals like *Science*, *Nature*, and *PNAS*, and he is co-editor of the book *Comparative Social Evolution*, published in 2017. In recognition of his research accomplishments, he has received young investigator awards from the Animal Behavior Society, the American Ornithologists' Union, the Society for Behavioral Neuroendocrinology, and the University of Michigan, and been made a Fellow of the American Ornithological Society. He was also recognized by the National Academy of Sciences as both a Kavli Fellow for his research accomplishments and an Education Fellow in the Sciences for his innovations in STEM teaching.

Throughout his education and training at Dartmouth College, Cornell University, and the University of California, Berkeley, Rubenstein has used *Animal Behavior* in his courses since its fifth edition. He seems to have learned a thing or two, having met his wife in his undergraduate animal behavior class. From his own work using stable isotopes to study avian migration, to studying stress hormones and breeding behavior in birds and lizards, to examining the genetic and epigenetic bases of reproductive behavior in insects and birds, Rubenstein approaches the study of animal behavior in an integrative and interdisciplinary manner. Over the past few years, he has helped lead a series of workshops and symposia about the integrative study of behavior, a topic of great emphasis in this new edition. His goal in taking over this classic textbook was to highlight the modern approach to animal behavior, while maintaining the book's timeless writing style and structure. Rubenstein thanks his wife Kate and two children, Renna and Ian, for their patience and support over the past few years of book writing. Many mentors helped teach and train Dustin in animal behavior over the years, but none were more important than his father, Daniel Rubenstein, a fellow behavioral biologist who has inspired him since his earliest days, together observing spiders in the backyard or zebras in Africa.

John Alcock retired in 2009 after having had an academic life full of rewards, such as trips to Australia on sabbaticals and during leaves of absence. His research focused on insect reproductive behavior and the many puzzles it provides for behavioral biologists, both in his home state of Arizona as well as in Costa Rica and Australia. Although retired, he continues to study insects, especially in Virginia, where he lives on the family farm in the spring and summer months. Alcock has written a number of natural history books for a general audience, such as *Sonoran Desert Spring* and his most recent effort along these lines, *After the Wildfire*. This book describes the account of the environmental recovery that occurred in the ten years that followed an intense wildfire in the mountains about an hour to the north of his home in Tempe, Arizona. Now 75, Alcock enjoys being a grandfather, thanks to a son Nick and his wife Sara who have produced two grandchildren for him (and others). His other son Joe and his wife Satkirin are both doctors, and Joe is deeply interested in evolutionary medicine. This version of the textbook that Alcock first wrote long, long ago has been revised by Dustin Rubenstein, a good choice to carry the book forward as the readers of this text will shortly learn.

Acknowledgements

For over four decades, this book has greatly benefitted from the generosity of many colleagues who have contributed reviews, photographs, videos, and other means of support. We are especially grateful to the reviewers for this eleventh edition, whose suggestions improved the structure, content, and tone of many of the chapters. The reviewers for this edition include:

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We are also indebted to our wonderful colleagues at Sinauer Associates. Without their dedication, patience, and careful oversight (and occasional prodding), this book—as well as the ten previous editions—would never have made it to print. The team that worked on this edition included:

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Rachel Meyers, Acquisitions Editor
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Beth Roberge Friedrichs, Production Specialist
Joanne Delphia, Book Designer
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Elizabeth Pierson, Copy Editor

Media and Supplements

to accompany *Animal Behavior*, Eleventh Edition

eBook

(ISBN 9-781-60535-770-6)
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For the Student

Companion Website (oup.com/us/rubenstein11e)

The *Animal Behavior*, Eleventh Edition, Companion Website includes a variety of study and review aids—all available at no cost to the student. The site includes the following:

- Chapter Summaries give the student a thorough review of each chapter's content.
- Audio and Video Links provide a set of online sites and resources relevant to each chapter.
- The Glossary provides definitions for all textbook bolded terms.

Student Lab Manual

This electronic lab manual walks students through the scientific process to improve their fluency with hypothesis development, observing and quantifying animal behavior, statistical analysis, and data presentation.

For the Instructor

Ancillary Resource Center (oup-arc.com)

The Ancillary Resource Center provides instructors using *Animal Behavior* with a wealth of resources for use in course planning, lecture development, and assessment. Contents include:

TEXTBOOK FIGURES AND TABLES

All the figures and tables from the textbook are provided in JPEG format, reformatted for optimal readability, with complex figures provided in both whole and split formats.

POWERPOINT RESOURCES

This presentation includes all of the figures and tables from the chapter, with titles on each slide and complete captions in the Notes field.

INSTRUCTOR'S MANUAL AND TEST BANK

These resources facilitate the preparation of lectures, quizzes, and exams. Contents include:

- Answers to the discussion questions in the textbook
- A list of films and documentaries about animal behavior, for use in the classroom
- A test bank, consisting of a range of multiple-choice and short answer questions drawn from textbook content, along with writing assignments to engage students in deeper thinking.

Learning the Skills of Research: Animal Behavior Exercises in the Laboratory and Field

Edited by Elizabeth M. Jakob and Margaret Hodge

Students learn best about the process of science by carrying out projects from start to finish. Animal behavior laboratory classes are particularly well suited for independent student research, as high-quality projects can be conducted with simple materials and in a variety of environments. The exercises in this electronic lab manual are geared to helping students learn about all stages of the scientific process: hypothesis development, observing and quantifying animal behavior, statistical analysis, and data presentation. Additional exercises allow the students to practice these skills, with topics ranging from habitat selection in isopods to human navigation. The manuals provide both student and instructor documentation. Data sheets and other supplementary material are offered in editable formats that instructors can modify as desired.

To learn more about any of these resources, or to get access, please contact your OUP representative.

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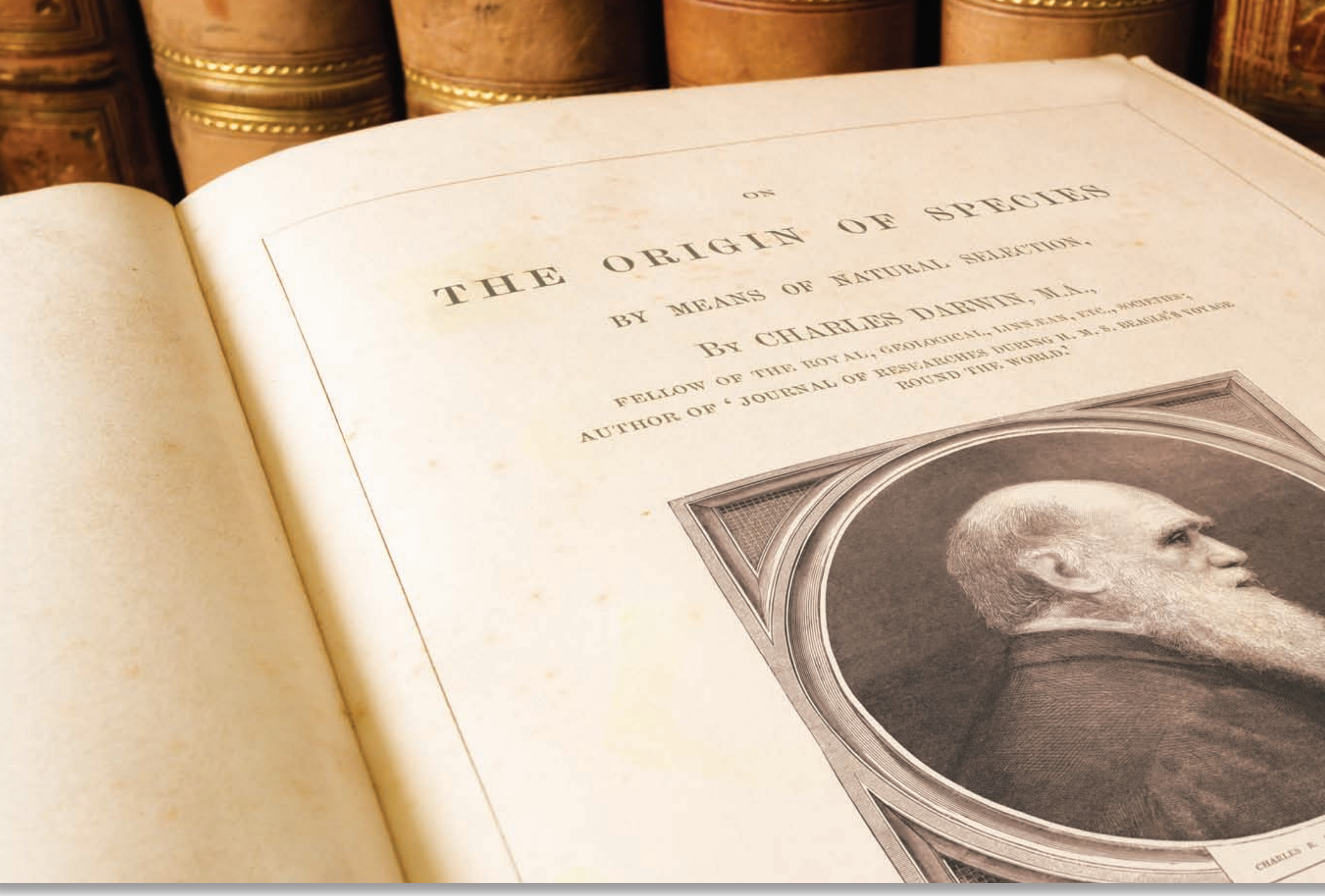
ON
THE ORIGIN OF SPECIES
BY MEANS OF NATURAL SELECTION,
BY CHARLES DARWIN, M.A.,
FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE
ROUND THE WORLD.'

CHAPTER

1

An Introduction to Animal Behavior

If you've ever been stung by a honey bee (*Apis mellifera*), you know that animals can behave in ways that seem illogical to humans. After all, just a few minutes after stinging you, that female honey bee will die. Why would an individual kill itself to temporarily hurt you? Although we will not fully answer this question until Chapter 12, the solution lies deep in the portion of the stinging bee's genetic code that it shares with its hive mates. As you will see in this chapter, behavioral theory gives us a framework within which to understand this and other seemingly paradoxical behaviors. As a student of animal behavior, you will use this book to begin exploring the natural world and examine how and why the diversity of animals that live in it behave in the ways they do.

Chapter 1 opening photograph by duncan1890/E+/Getty Images.

The discipline of animal behavior is vibrant and growing rapidly, thanks to thousands of behavioral biologists who are exploring everything from the genetics of bird song to why women find men with robust chins attractive. A major reason why the field is so active and broad ranging has to do with a book published more than 150 years ago, Charles Darwin's *On the Origin of Species* (Darwin 1859). In this book, Darwin (**FIGURE 1.1**) introduced the concept of **natural selection**, which argues that living species are the product of an unguided, unconscious process of reproductive competition among their ancestors. Natural selection theory provides the guiding principle for studying animal behavior, as well as most of biology more generally. Knowing that animal behavior, like every other aspect of living things, has a history guided by natural selection is hugely important. An understanding of evolutionary theory gives us a scientific starting point when we set out to determine why animals do the things they do—and why they have the genetic, developmental, sensory, neuronal, physiological, and hormonal mechanisms that make these behavioral abilities possible. To truly understand why a bee will kill itself to sting you, you must approach the study of animal behavior from an evolutionary perspective, from the perspective of Darwin himself. As the evolutionary biologist Theodosius Dobzhansky once said, "Nothing in biology makes sense except in the light of evolution" (Dobzhansky 1973). We hope to convince you that Dobzhansky was right when it comes to animal behavior as well. If we succeed, you will come to understand the appeal of the evolutionary approach to animal behavior, as it helps scientists identify interesting subjects worthy of explanation, steers them toward hypotheses suitable for testing, and ultimately produces robust conclusions about the validity of certain hypotheses.

Darwin's influence continues strongly to this day, which is why this book was titled *Animal Behavior: An Evolutionary Approach* for its first ten editions. Over the editions, we have explored the assortment of behaviors that animals exhibit and discuss not only how and why they evolved, but why they evolved in one species and not another, or in one sex and not the other. In this eleventh edition, we extend the evolutionary approach emphasized by the subtitle in the book's prior editions and take a more integrative approach. The concept of evolution by natural selection remains our guide, but we will also weave into our discussion topics such as epigenetics, development, and ecology, as well as tools such as game theory and molecular genetics. Indeed, as you will see in the following chapters, the study of animal behavior has itself evolved since Darwin made his observations about natural selection more than 150 years ago. In fact, the study of animal behavior has changed considerably since the first edition of this book was published more than 40 years ago. Therefore, in this edition, we go beyond an evolutionary approach to the study of animal behavior. We also consider an ecological approach. A mechanistic approach. A developmental approach. In short, we take an integrative approach to the study of animal behavior (Rubenstein and Hofmann 2015, Hofmann et al. 2016), discussing how the interaction among genes, development, and the environment shapes the evolution of animal behaviors. This means that students of animal behavior today may need to use the material learned in a biochemistry or molecular biology class just as much as they do the material learned in an ecology class. We illustrate the ways, for example, that genomics and neurobiology are changing how we study animal behavior in a manner that Darwin could not have imagined. And we demonstrate how new phylogenetic comparative methods are enabling us to use data collected from dozens to thousands of species to test existing, as well as generate novel, hypotheses.

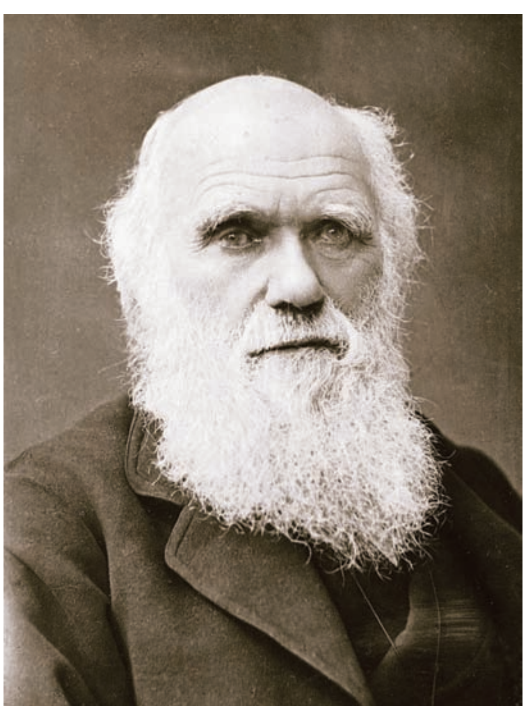

FIGURE 1.1 Charles Darwin. Taken in 1881 by Herbert Rose Barraud (1845–1896), this is thought to be the last photograph of Darwin before his death. The original is in The Huntington Library in San Marino, California.

But first we introduce you to the fascinating field of animal behavior in this chapter. We begin with a detailed discussion of how natural selection governs the evolution of behavior. We introduce adaptationist thinking and the gene's eye view of behavioral trait evolution. We discuss the cost–benefit approach to behavioral biology, as well as the critical role that hypothesis testing plays in the scientific method. Ultimately, we argue that an integrative approach to studying animal behavior is essential for understanding how and why behaviors evolve, a topic we will explore in greater detail in Chapter 2 and then throughout the rest of the book.

Natural Selection and the Evolution of Behavior

When biologists ask questions about the behavior of animals, they are guided by Darwin's theory of evolution by natural selection. Darwin was puzzled by the fact that living organisms could increase their numbers geometrically, but that most didn't. Even in bacteria, which can reproduce rapidly and efficiently, some individuals replicate more than others. So which individuals reproduce more, and why? As Darwin came to realize after a lifetime of observing animals in their natural habitat, if in the past some individuals left more descendants than others, then these reproductively successful individuals would inevitably gradually reshape their species in their image. The logic of natural selection is such that evolutionary change is inevitable if just three conditions are met:

1. *Variation*, with members of a population differing in a particular characteristic
2. *Differential reproductive success*, with some individuals with particular characteristics having more offspring than others
3. *Heredity*, with parents able to pass on those characteristics to their offspring

If there is variation within a species (and there almost always is), if some of that variation is heritable and passed from parents to offspring, and if some of those individuals consistently reproduce more successfully than others, then the increased abundance of living descendants of the more successful types will gradually change the species. Over time, the "old" population—it is important to remember that natural selection acts on populations of individuals—evolves into one whose members possess the characteristics (or **traits**) that were associated with successful reproduction in the past. How successful an individual is at passing on its heritable traits to the next generation is referred to as **fitness**. As you will see throughout this book, fitness—which depends on both survival and reproduction—forms the foundation for understanding which traits are likely to evolve via natural selection and become more or less common in a population. After all, to reproduce and pass one's traits on to one's offspring, an individual has to survive long enough to breed.

Darwin not only laid out the logic of his theory clearly, he also provided abundant evidence that heritable variation in traits is common within species, and that high rates of mortality are also the rule. Indeed, the conditions necessary and sufficient for evolutionary change by natural selection to occur are present in all living things, a point that Darwin demonstrated by showing that people could cause dogs and pigeons to evolve by selectively breeding those individuals with traits that the breeders wanted in future generations of their domesticated animals. And although it was a heretical concept in Darwin's Victorian England, we now know that people, like all other organisms, also evolve by natural selection. For example, the ability of many humans to continue to digest lactose, the dominant sugar in milk, after childhood appeared around the time our ancestors domesticated livestock and has been hypothesized to have been strongly favored by natural selection because it allowed some individuals to survive on a milk diet.

We call the traits associated with successful survival and reproduction, and on which natural selection acts, **adaptations**. Figuring out exactly how a putative adaptation contributes to the **reproductive success** of individuals is perhaps the central goal for most behavioral biologists, some of whom are happy to be known as "adaptationists." Certainly Darwin would have agreed with the way adaptationists think about evolution, especially with respect to the hereditary foundation of evolutionary theory. Although Darwin himself knew nothing about **genes**, regions of DNA that encode traits, we now can reconfigure his argument to deal with selection at the level of the gene. Just as adaptations that increase the reproductive success of individuals will spread through populations over time, so too will the hereditary basis for these attributes. Because genes can be present in populations in different forms known as **alleles**, those alleles that contribute to traits linked to individual reproductive success will become more common over time, whereas those associated with reproductive failure will eventually disappear from the population and perhaps even the genome. In evolutionary biology, we refer to traits as **phenotypes** (aspects of an individual that arise from an interaction of the individual's genes with its environment), and to the set of alleles underlying the development of those traits as **genotypes**. The genetic basis of most complex phenotypes—including most behaviors—is rarely known in full, and when it is, it is typically only in model organisms. (Although as you will see in subsequent chapters, this is changing and scientists are now capable of identifying the hereditary basis of a trait in almost any organism.) Linking phenotypes to genotypes is not only an essential part of modern molecular and evolutionary biology, but with the powerful new tools and approaches from these disciplines being applied to non-model organisms in their natural habitats, it is also becoming crucial to behavioral biology as well.

It is critical to recognize three points about this so-called gene-centered, or gene's eye, view of evolution by natural selection:

1. Only genes replicate themselves; organisms do not. Instead, organisms—or groups of organisms—are vehicles within which replicators (genes) travel, a point we will discuss further in Chapter 12 (Dawkins 1989). Adaptive evolution therefore occurs through the differential survival of competing genes, which increases the frequency of those alleles whose phenotypic effects promote their own propagation.

2. Evolution is not natural selection. Evolution is gene frequency change within a population. Natural selection is one of several causes of evolution, as are mutation, migration, and genetic drift.

3. Natural selection is not guided by anything or anyone. Selection is not "trying" to do anything. Instead, it is the individuals that reproduce more that cause a population or species to evolve over time, a process that Darwin called **descent with modification**.

Notice also that the only kinds of heritable traits that will become more common in a species are those that promote individual reproductive success, which do not necessarily benefit the species as a whole. Although "for the good of the species" arguments were often made by biologists not so long ago, it is entirely possible for adaptations (and particular alleles) to spread through populations even if they do nothing to perpetuate the species (see Chapter 12). Indeed, traits and alleles that are harmful to group survival in the long run can still be favored by natural selection. Yet as we will discuss later in this book, there are also special cases when selection acts on traits that do benefit others, even seemingly at the expense of the individuals that possess those traits.

The Cost–Benefit Approach to Behavioral Biology

To help establish why a particular behavior has evolved, behavioral biologists must propose a **hypothesis**, or an explanation based on limited evidence. Of course, for most behaviors there may be multiple potential explanations, which requires posing multiple hypotheses. When only one of a series of competing hypotheses could explain a given behavior, we call these **alternative hypotheses**. In contrast, when multiple hypotheses could apply to a given behavior, we refer to them as **non-mutually exclusive hypotheses**. Throughout this book, we highlight hypotheses in blue in the text, and also define them in the page margins. When there are multiple hypotheses to explain a behavior, we group them together in a margin box and note whether they are alternative or non-mutually exclusive hypotheses.

Once a hypothesis has been generated, researchers can use it to make a **prediction**, or expectation that should follow if the hypothesis is true. Predictions allow for the discrimination among competing hypotheses. Generating, falsifying, and then generating new hypotheses and predictions is a natural part of the **scientific method**.

When behavioral biologists set out to test hypotheses and predictions related to a potentially adaptive behavior, they often consider the costs and benefits of that behavior; they take a cost–benefit approach to the study of animal behavior. When they speak of costs, behavioral biologists are talking about **fitness costs**, the negative effects of a trait on the number of surviving offspring produced by an individual or a reduction in the number of copies of its alleles that it contributes to the next generation. When they speak of **fitness benefits**, they are referring to the positive effects of a trait on reproductive (and genetic) success. Fitness costs and benefits are the units that behavioral biologists use to study adaptations and the process of evolution by natural selection. Most behavioral biologists study traits that they assume are adaptations, an assumption that they make in order to test specific hypotheses about the possible **adaptive value**, or the contribution to fitness, of the characteristic of interest. Recall that an adaptation is a heritable trait that has spread or is spreading by natural selection, and has replaced or is replacing any alternative traits in the population or species. Such an attribute has a better ratio of fitness benefits to costs than the alternative forms of this trait that have occurred in the species. Thus, studying why a behavioral adaptation has evolved depends on measuring the potential reproductive costs and benefits to the individual adopting that behavior.

Since fitness is an abstract term, behavioral biologists often have to settle for an indicator or correlate of reproductive success when they attempt to measure fitness. In the chapters that follow, the terms *fitness*, *reproductive success*, and *genetic success* are often used more or less interchangeably when referring to such indicators as offspring survival, the number of young that survive to fledging, the number of mates inseminated, or even more indirectly, the quantity of food ingested per unit of time, the ability to acquire a breeding territory, and so on. These proxies give us a currency with which to measure fitness costs and benefits and ultimately to test hypotheses underlying the evolution of a range of animal behaviors.

Using natural selection theory and the cost–benefit approach helps us identify why behaviors evolve, including seeming anomalies that require explanation such as why traits that appear to reduce rather than raise an individual's reproductive success persist or even spread through a population. As we discussed at the outset, a honey bee sting is a good example of a behavioral trait that at first seems counterintuitive, or even maladaptive for the individual doing the stinging. (In Chapter 12

FIGURE 1.2 A male lion (*Panthera leo*) carrying a young lion cub that he has killed. Because infanticide by males occurs in several different species under similar social circumstances, the behavior is likely to be adaptive. (Photograph © Laura Romin and Larry Dalton/Alamy Stock Photo.)

we will explore why animals perform self-sacrificial acts such as this.) Throughout the book, we will refer to these challenges to evolutionary theory as **Darwinian puzzles**. Biologists deal with these puzzles by developing possible hypotheses based on natural selection theory for how the trait might actually help individuals reproduce and pass on their genes. As an illustration of this approach, we describe in **BOX 1.1** an example of a behavior that has long puzzled behavioral biologists: infanticide (**FIGURE 1.2**).

The Levels of Analysis

Now that we have discussed how traits—including behavioral ones—evolve via natural selection, let's consider what a behavioral trait is and how we study it. Although "behavior" seems like it should be an easy term to define, it actually means different things to different people, particularly those in different fields. You would think that behavioral biologists could at least agree on what a behavior is, but they don't. Daniel Levitis and colleagues posed a seemingly simple question—"What is animal behavior?"—to nearly 175 behavioral biologists at a series of scientific society meetings, and much to their surprise, there was no consensus on how behavioral biologists define animal behavior. Levitis and colleagues suggested defining behavior as the internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes (Levitis et al. 2009). This definition focuses largely on intrinsic factors. What if we gave you a different definition, something like this: behavior describes the way an individual acts or interacts with others or the environment? This definition has nothing to do with the internal processes of an individual. Instead, this definition emphasizes interactions between individuals or between an individual and its environment. Why do these definitions of behavior differ so much?

Part of the reason why behavioral biologists define behavior so differently is that animal behavior is a wide and varied discipline that has itself evolved over time. The field of animal behavior has inherited traditions from ethology and the

BOX 1.1 DARWINIAN PUZZLE

Natural selection and infanticide in primates

Hanuman langurs (*Semnopithecus entellus*) are monkeys that live in groups of several females and their offspring, accompanied by one or a few adult males (**FIGURE A**). In the course of a long-term research project in India, male Hanuman langurs were seen attacking and sometimes even killing the very young infants of females in their own group. The puzzle here is obvious: how can it be adaptive for a male langur to harm the offspring of females in his group, particularly since attacking males are sometimes injured by mothers defending their babies (**FIGURE B**)? Some primatologists have argued that the infanticidal behavior of these males was not adaptive but was instead the aberrant aggressive response by males to the overpopulation and crowding that occurred when langurs came together to be fed by Indian villagers. According to these observers, overcrowding caused abnormal aggressive behavior, and infanticide was simply a maladaptive result (Curtin and Dolhinow 1978).

(Continued)

(A)

FIGURE A Hanuman langur females and offspring. Males fight to monopolize sexual access to the females in groups such as this one. (Photograph © Heini Wehrle/AGE Fotostock.)

(B)

FIGURE B Male langurs commit infanticide. (Left) A nursing baby langur that has been paralyzed by a male langur's bite to the spine (note the open wound). This infant was attacked repeatedly over a period of weeks, losing an eye and finally its life at age 18 months. (Right) An infant-killing male langur flees from an aggressive protective female belonging to the band he is attempting to join. (Left, photograph by Carola Borries; right, photograph by Volker Sommer, from Sommer 1987.)