ANIMAL BEHAVIOR

TWELFTH EDITION

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Dustin R. Rubenstein
Columbia University

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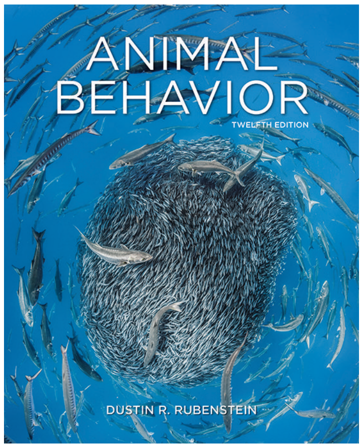

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About the cover

European barracuda (*Sphyraena sphyraena*) and Bluefish (*Pomatomus saltatrix*) circling a baitball of Atlantic horse mackerel (*Trachurus trachurus*) Formigas Islets, Azores.

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

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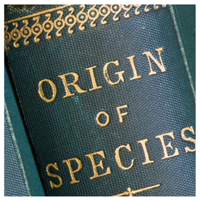

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Foreword

I wrote the first edition of this book almost 50 years ago because I was unhappy with the current textbooks on animal behavior, all of which failed to focus on questions about the adaptive value of behavior in favor of "how questions" largely aimed at understanding the underlying mechanisms of behavior. As we shall see, "why questions" (those about adaptive value) took advantage of advances in evolutionary theory made by people like George Williams (who explained what natural selection really was) and William Hamilton (who devoted his efforts to the theory of kin selection and how individuals could increase copies of their genes by helping their relatives reproduce). Many others had a role to play in these advances of theory, but Williams and Hamilton were important pioneers whose work was (I thought) ignored in the textbooks then available.

In the years since the first edition appeared, my focus and that of the current author, Dustin Rubenstein, have continued to remain on the adaptive value of animal behavior with some significant changes. First and foremost, the integration of why and how questions is highly significant. As it turns out, work on how the underlying mechanisms of behavior are themselves adaptations is very relevant to why the behaviors whose development they control are also adaptations. Second, with the integration of how and why came the application of new tools and techniques to the study of animal behavior that helped propel the field forward. For example, research began with the microsatellite (genetic) studies of male parentage in birds, a key question since male birds often copulate with several females. Figuring who had fathered which chick was essential to determining which male had actually reaped the reproductive benefit of a copulation with a given female. Since then we have many more genetic methods of establishing not just parentage or relatedness, but also molecular and neurobiological (brain) mechanisms of adaptive value to individuals. For example, behavioral biologists can now study the genes and neural circuits that underlie different behaviors in animals as diverse as honey bees and field mice in both the wild and the lab, enabling these researchers to understand how behavioral adaptations evolve.

Studies of fitness in free-living animals were in their infancy when the first edition of this book was published. Yet, some of those same research projects continue to this day. Indeed, from birds to primates to pinnipeds, there have been major studies of the reproductive success of individuals followed for their entire lifetimes, so that these datasets are remarkably complete. The results of these studies can be and have been used to determine the average lifetime reproductive success of two or more variants within a population such as typical aggressive males and female mimicking males, which occur in any number of species including a deer in Europe that has been studied for decades.

A final key change involves the existence of robust phylogenetic (evolutionary relationship) information about groups of related species, as for example among bees. If one only has a few cases from which to draw inferences, one may mistakenly conclude that the similarities among some of the species are due to shared ecological pressures and thus they are independently evolved to these pressures when in actuality they are the product of shared evolutionary relationships carried from one species to its relative. To avoid errors of this sort, it is wise to have complete or nearly complete phylogenies on hand and this we have tried to do. And along with these molecular phylogenies, we also have access to a wealth of behavioral and life history data from thousands of animal species, enabling broad-scale comparative studies in almost every taxonomic group on earth.

Over the past 12 editions, there have been many modifications of the material contained within this book, but the central goal of this text has remained the same—to present the results of research on the hypotheses that entertain all behavioral biologists no matter what their interests, but especially if they are concerned with the adaptive value of behavioral traits. It's hard to imagine where the field of animal behavior will be in another 50 years. For the moment, the book is in the capable hands of Dustin Rubenstein who knows how and why questions and their value for each other in shaping the research that follows. My hope is that this book will continue to live on in order to excite inquisitive students about the world around them and to train future generations of behavioral biologists.

John Alcock

Preface

For nearly 50 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 (see Foreword), and after 10 subsequent versions, Dustin Rubenstein has now taken over for this, the Twelfth Edition. This 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 that 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. Additionally, the book covers the growing number of comparative phylogenetic studies in animal behavior that make use of ever-larger molecular phylogenies and trait datasets 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 levels of analysis that researchers use to explain why all living things—including humans—perform complex behaviors.

New to the Twelfth Edition

The Twelfth Edition expands upon many of the new features introduced in the past edition, when Dustin Rubenstein joined as an author. In addition to the Enhanced e-book, this edition introduces several new approaches and features that support both student learning and instructor teaching, including the following:

- Improved pedagogical features, including Chapter Goals, Learning Objectives, Synthesis sections, and expanded boxes.
- An Enhanced e-book with exclusive content, including integrated audio and video clips, interactive figures, and in-line self-assessment questions that correspond to the new Learning Objectives.
- Focus on new integrative tools, including CRISPR to edit genomes in model and non-model organisms alike, and optogenetics to manipulate cells in living organisms.
- Highlighting cutting-edge and current research, including how the Covid-19 pandemic affected the behavior of animals.

Expanded 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.

Accessible Color Content

Every opportunity has been taken to ensure that the content herein is fully accessible to those who have difficulty perceiving color. Exceptions are cases where the colors provided are expressly required because of the purpose of the illustration.

Author Biography

Dustin Rubenstein, a Professor of Ecology, Evolution, and Environmental Biology at Columbia University, has studied animal behavior in birds, reptiles, mammals, insects, and crustaceans for nearly 25 years throughout Africa, Asia, Central and South America, Australia, and the Caribbean. As a leading expert in animal social behavior and evolution, his research has been published in top journals like *Science* and *Nature*, 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 Association for the Advancement of Science and 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 innovation 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 explore avian migration, to studying stress hormones and breeding behavior in birds and lizards, to examining the factors that shape the evolution of complex societies in birds, insects, and shrimp, to probing 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. Rubenstein thanks his wife Kate and two children, Renna and Ian, for their patience and support over the past few years of book writing, particularly during the Covid-19 pandemic. Many mentors helped teach and train Rubenstein in animal behavior over the years, but none were more important than his own 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.

Acknowledgments

For nearly five decades, this book has greatly benefitted from the generosity of many colleagues from all over the world who have contributed suggestions, reviews, photographs, videos, and other means of support. I would like to thank Stefanie Siller, who was instrumental in developing the new Chapter Goals and Learning Objectives. I am especially grateful to the reviewers for this Twelfth Edition, whose ideas improved many of the chapters. The reviewers for this edition include the following people:

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Writing this book during the Covid-19 pandemic was challenging, to say the least. I thank my colleagues from Oxford University Press for their professionalism, patience, and perseverance. This book would not have been possible without the great team that included the following people:

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For the Instructor

(Available at oup.com/he/rubenstein12e)

Instructors using *Animal Behavior,* Twelfth Edition, have access to a wide variety of resources to aid in course planning, lecture development, and student assessment.

Content includes the following:

- **Learning the Skills of Research: Animal Behavior Exercises in the Laboratory and Field**, edited by Elizabeth M. Jakob and Margaret Hodge. This electronic lab manual includes exercises geared to helping students learn about all stages of the scientific process, from hypothesis development and observing and quantifying animal behavior to statistical analysis and data presentation. Additional exercises allow students to practice these skills. Student and instructor documentation is provided, with data sheets and other supplementary material.
- **PowerPoint Presentations**—All of the figures and tables from each chapter, with figure numbers and titles on each slide, complete captions in the notes field, and alt-text embedded for accessibility. All of the artwork has been reformatted and optimized for exceptional image quality when projected in class.
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- **Test Bank**—Revised and updated for the Twelfth Edition, the Test Bank consists of a broad range of questions covering key facts and concepts in each chapter. Both multiple-choice and short-answer questions are provided. All questions are ranked according to Bloom's Taxonomy and aligned to new Learning Objectives. Available in multiple formats, including MS Word and Common Cartridge (for import into learning management systems).
- **Thinking Outside the Box**—Answers to questions posed in in-text features.
- **Chapter Summaries**
- **Additional Resources**—Suggested media resources that can be used to enhance the content of the text.

Enhanced E-Book for the Student

(ISBN 9780197559086)

Ideal for self-study, the *Animal Behavior*, Twelfth Edition, Enhanced e-book delivers the full suite of digital resources in a format independent from any courseware or learning management system platform, making *Animal Behavior*'s online resources more accessible for students.

The Enhanced e-book is available via RedShelf, VitalSource, and other leading higher education e-book vendors and includes the following student resources:

- *Learning Objectives* outline the important takeaways of every major section. NEW for this edition.
- *Interactive Figures* enable students to break down and explore in detail key figures of the text. NEW for this edition.
- *Self-Assessment Quizzes* following each major section allow students to gauge their understanding of key concepts before proceeding. NEW for this edition.
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- *Flashcards* help students master the hundreds of new terms introduced in the textbook.

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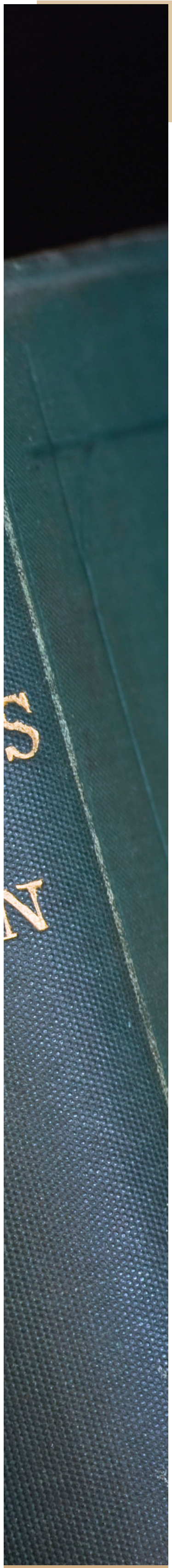
1.1 Natural Selection and the Evolution of Behavior
The Cost–Benefit Approach
The Levels of Analysis
The Integrative Study of Animal Behavior

1.2 Approaches to Studying Behavior
Examining the Adaptive Basis of Behavior
Inferring the Evolutionary History of Behavior



1

An Introduction to Animal Behavior

- Identify the central role of natural selection in guiding the evolution of behavior.
- Recognize the importance of using an integrative approach to consider how proximate and ultimate levels of analysis can be used to study behavior.
- Describe how researchers use the scientific method to develop and test hypotheses in order to explain how and why a behavior evolved.

Anyone who has been stung by a honey bee (*Apis mellifera*) will know that animals can behave in ways that seem illogical to humans. After all, just a few minutes after stinging, that female honey bee will die. Why would an individual kill itself to temporarily hurt someone? 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 we will see in this chapter, behavioral theory gives us a framework within which to understand this and other seemingly paradoxical behaviors. As students of animal behavior, we 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 that they do.

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 animals choose the mates that they do, to how animals evade predators or why they form groups. 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

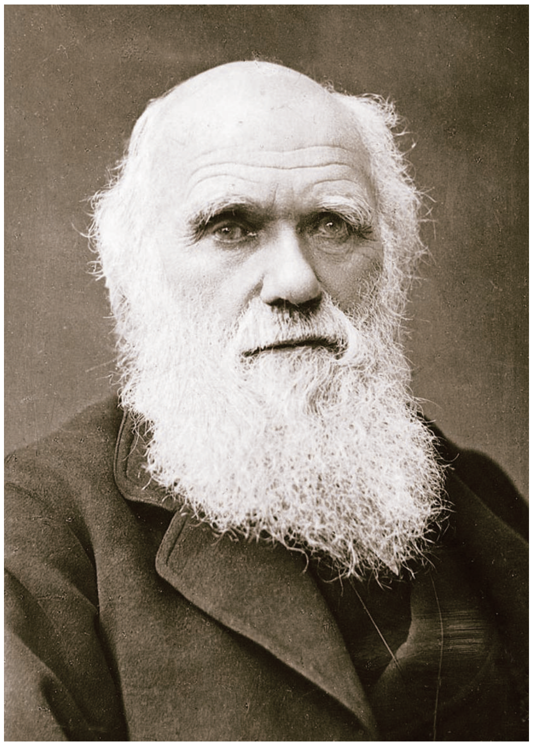


FIGURE 1.1 **Charles Darwin.** Taken in 1881 by Herbert Rose Barraud (1845–1896), this is thought to be the last photograph of Darwin before his death. The original is in The Huntington Library in San Marino, California.

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 organisms, has a history shaped 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 what 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 a human being, we 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). Each of the chapters in this book will demonstrate that Dobzhansky was right when it comes to animal behavior as well. We will illustrate the appeal of the evolutionary approach to studying 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 on the field of animal behavior continues strongly to this day, which is why this book was long titled *Animal Behavior: An Evolutionary Approach*. Over the editions, this book has explored the assortment of behaviors that animals exhibit and discussed 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. Yet, we will see in the following chapters how 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 nearly 50 years ago. Therefore, in this edition, we go beyond an evolutionary approach to the study of animal behavior by also considering an ecological approach, a mechanistic approach, and 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. The concept of evolution by natural selection remains our guide, but we will also weave into our discussion topics such as epigenetics, brain development, and ecology, as well as conceptual and modeling tools, such as optimization and game theory, and fine-grained molecular genetics and neurophysiological approaches. This means that students of animal behavior today may need to use the material learned in a biochemistry or molecular biology class, or even a mathematics, computer science, or economics class, just as much as they do the material learned in an ecology or evolution 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.

But first, this chapter will introduce the fascinating field of animal behavior. 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 that we will explore in greater detail in Chapter 2 and then throughout the rest of the book, which is now titled simply *Animal Behavior* to better reflect the broad and varied field of study.

1.1 Natural Selection and the Evolution of Behavior

LEARNING OBJECTIVES

- Identify the conditions required to produce evolutionary change through natural selection and examine these conditions using the gene's eye view.
- Review how researchers use the scientific method to test hypotheses and predictions related to a potentially adaptive behavior in order to consider its fitness costs and benefits, evaluate its adaptive value, and identify why it evolved.
- Consider how proximate and ultimate levels of analysis can be used to provide an integrative understanding of the development, mechanism, adaptive value, and evolutionary history of a 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 is one cause of evolution that acts on individuals within populations—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 we 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 upon 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 (or genetic) 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 often only in model organisms. Yet, as we 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, including free-living ones that exhibit a range of interesting behaviors. 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 that 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 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 more than one potential explanation, 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 use the scientific method to test hypotheses and predictions related to a potentially adaptive behavior, they often consider the costs and benefits of that behavior. That is, 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. In addition, behavioral biologists often assume that natural selection has maximized the differences between an attribute's benefits and costs. 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 researchers 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 and should not be maintained by natural selection since the actor perishes. In fact, it could even be considered maladaptive for the individual doing the stinging. In Chapter 12, 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, **BOX 1.1** describes an example of a behavior that has long puzzled behavioral biologists: **infanticide** (**FIGURE 1.2**).

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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.

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. One 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 et al. 2009). The researchers 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. This definition focuses largely on intrinsic factors. But what if we used 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 observation of animals in the wild, as well as those from experimental psychology where experiments are generally conducted in the lab under controlled conditions. As we said at the outset, animal behavior is becoming increasingly integrative and continues to evolve as a discipline to this day. Some scientists tend to take a more mechanistic or developmental approach, as the first definition implied. Still other scientists take an adaptive or evolutionary approach, as the second definition suggested. Indeed, these **ultimate causes** of behavior provide us with a perspective on the adaptive value and the evolutionary history of a trait of interest. However, there is much more to behavioral research than studies of adaptation and evolutionary history. As the behavioral biologist Nikolaas Tinbergen pointed out long ago, biologists also need to study how a behavior develops over the lifetime of an individual and how an animal's physiological systems make behaving possible if they are to really understand the evolution of a behavior (Tinbergen 1963). Because the mechanisms that underlie development and neurophysiology act within the life span of individuals, they are considered to be immediate and mechanistic, or what behavioral biologists call **proximate causes** of behavior. Ultimately, every behavioral trait is the result of both proximate and ultimate factors; the self-sacrificing behavior of the honey bee, the infanticidal behavior of the langur, and so forth—all are driven by immediate underlying mechanisms acting within the bodies of bees, monkeys, and every other animal, including humans.

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).

Behavioral biologist Sarah Hrdy used natural selection theory to try to solve the puzzle of infanticide in a different way, namely by asking whether the killer males were behaving in a reproductively advantageous manner (Hrdy 1977). She reasoned that by committing infanticide, the males might cause the baby-less females to resume ovulating, which otherwise does not happen for several years in females that retain and nurse their infants. Once females began ovulating, the males could then mate with them. Hrdy tried to explain how infanticide might have spread through Hanuman langur populations in the past as a reproduction-enhancing tactic for individual males.

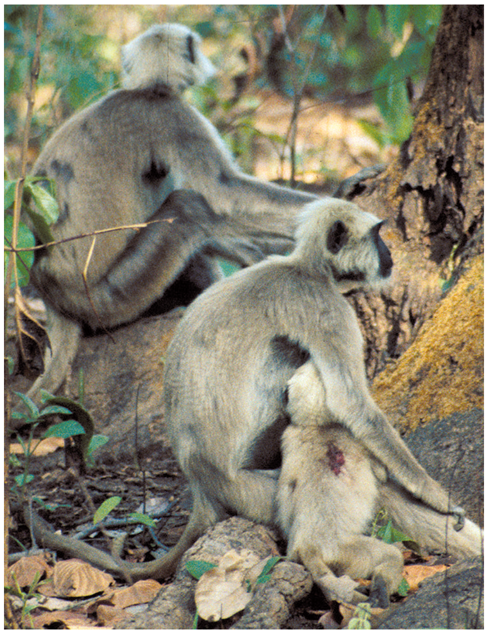
(*Continued*)

(A)

© Heini Wehrle/AGE Fotostock

Hanuman langur females and offspring. Males fight to monopolize sexual access to the females in groups such as this one.

(B)



Courtesy of Carola Borries

Courtesy of Volker Sommer, from V. Sommer 1987. *Primates* 28: 163–197

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.

BOX 1.1 DARWINIAN PUZZLE *(continued)*

This **infanticide hypothesis** leads to several expectations, of which the most important is the prediction that males will not kill their own progeny, but will instead focus their attacks on the offspring of other males. This prediction in turn generates the expectation that infanticide will be linked to the arrival of a new male or males into a group of females, with the associated ejection of the father or fathers of any baby langurs in the group. In cases of male turnover in groups, the new males could father offspring more quickly if they first killed the existing infants. Females that lose their infants do resume ovulating, which enables the new males in the group to father replacement offspring. Since these predictions have been shown to be correct for this species (Borries et al. 1999) as well as for some other primates (Beehner and Bergman 2008, Lyon et al. 2011) and for various carnivores, horses, rodents, and even a bat (Knörnschild et al. 2011), we can conclude that infanticide in Hanuman langurs is indeed an adaptation, the product of natural selection.

infanticide hypothesis Infanticide is a reproduction-enhancing tactic practiced by males.

Thinking Outside the Box

Given what we just read about the gene's eye view of evolution by natural selection, can the infanticide hypothesis be rephrased using this terminology? In other words, consider infanticide from a gene's perspective and discuss why it could be a beneficial behavior from the perspective of a gene that underlies that behavior. Would a gene for infanticidal behavior be more or less likely to be passed on than a gene that does not promote the killing of young? ■

To paint a complete picture of how and why an animal behaves, we need to explore and integrate both the proximate and the ultimate causes of the behavior, which are referred to as the **levels of analysis**. The two levels of analysis are clearly complementary, but one focuses on the underlying mechanistic and developmental features that give rise to behavioral variation, while the other deals with the role of evolutionary history in influencing behavioral variation and the fitness consequences of that behavioral variation. These two levels can be further subdivided into what are typically called **Tinbergen's four questions**, because in the 1960s, Niko Tinbergen argued that to best understand a behavior, one must conduct both a proximate and an ultimate analysis (**TABLE 1.1**). Within the proximate level of analysis fall questions relating to development (such as understanding how behaviors change ontogenetically over the course of an animal's lifetime) and to mechanism (such as determining the physiological, neurobiological, hormonal, or genetic

TABLE 1.1 Levels of analysis in the study of animal behavior

Proximate Level	Ultimate Level
Development How genetic-developmental mechanisms influence the assembly of an animal and its internal components	**Evolutionary History** The evolutionary history of a behavioral trait as affected by descent with modification from ancestral species
Mechanism How neuronal-hormonal mechanisms that develop in an animal during its lifetime control what an animal can do behaviorally	**Adaptive Function** The adaptive value of a behavioral trait as affected by the process of evolution by natural selection

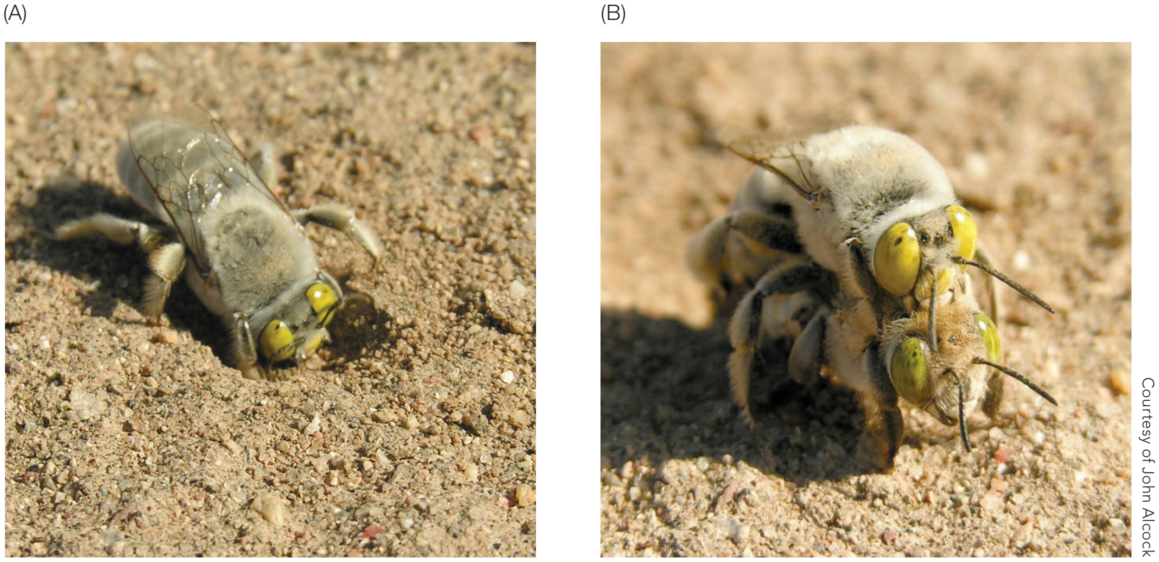
Source: After N. Tinbergen 1963. *Z Tierpsychol* 20: 410–433; K. E. Holekamp and P. W. Sherman. 1989. *Am Sci* 77: 232–239.

correlates of behavior). Within the ultimate level of analysis fall questions relating to evolutionary history (such as understanding how a shared ancestry influences variation in behavior) and adaptive function (such as determining how behavior affects survival and reproduction—fitness).

The Integrative Study of Animal Behavior

Tinbergen's four questions are linked to one another because behaviors that have spread through a species due to their positive effects on fitness must have underlying proximate mechanisms that can be inherited. Let's illustrate the power of Tinbergen's integrative approach by examining the namesake behavior of the digger bee *Centris pallida*. Digger bees live in the deserts of the American Southwest and get their name because males dig holes in the desert floor (**FIGURE 1.3A**). Why do males do this? John Alcock showed that males dig because they are searching for females that have completed their development in underground chambers that their mothers built and provisioned with food for their female (and male) larval offspring (Alcock et al. 1976). In other words, males dig to find a mate, and when a male reaches a female emerging from her chamber, he will immediately climb onto her and attempt to breed (**FIGURE 1.3B**). A male digger bee can find emerging females efficiently because this skill is adaptive, which is to say that it evolved and is now maintained by natural selection and passed on from parent to son.

But how does a male digger bee know where to dig to find a mate that is buried a centimeter or more beneath the desert floor? As Tinbergen first pointed out, because the immediate mechanisms of behavior have an evolutionary basis, the proximate and ultimate causes of behavior are related, and both are required for a full explanation of any behavioral trait (Alcock and Sherman 1994). Alcock hypothesized that digging males could somehow smell females that had burrowed up close to the surface (Alcock et al. 1976). This ability to smell hidden females—a proximate mechanism underlying the digging behavior—enabled males to reproduce more successfully than rivals without the same capacity. The ability to smell a mate might be related to specific genes, and identifying these genes or studying their expression and evolution might be useful. These genes have proximate effects when they, in conjunction with the cellular environment in which they operate and the ecological



Courtesy of John Alcock

FIGURE 1.3 A digger bee, *Centris pallida*, searching for a mate. (A) A male digging in the ground in search of a female. (B) A male copulating with a female that he had discovered before she emerged from the ground.

environment in which the bee lives, cause the bee to develop in a particular manner. The proximate developmental mechanisms within the egg, larva, prepupa, and pupa of digger bees have follow-on consequences, as they influence the production of the sensory and motor mechanisms with which adult male digger bees are endowed. The scent-detecting sensory cells in the bee's antennae, in concert with olfactory neural networks in the bee's nervous system, make it possible for males to find preemergent females in the desert soil. As a result, males are ready to dig up and pounce on sexually receptive females when they come out of their emergence tunnels.

There is also a history to the behavior, with adaptive changes such as extreme sensitivity to odors linked to buried females, layered onto traits that already had evolved previously in the history of the digger bee species. We can go even further and not only ask questions about how digging behavior varies among males and differentially influences their ability to reproduce, but also ask how this variation is proximately related to a male's age or developmental state. For example, are older, more experienced male bees better at finding females than younger, less experienced ones? We can go back even further and wonder how such a small animal is able to dig so vigorously through the hard-packed desert soil. Since males of many bee species mate after finding receptive females at flowers, do digger bees have unique morphological adaptations, such as stronger leg muscles or specially shaped legs, that allow them to dig into the earth in search of mates instead of finding them elsewhere? Finally, we may wonder whether digger bees are unique, or if all bees that nest in the ground in deserts behave this way and have the same suite of morphological adaptations and even the same set of underlying genes. Ultimately, we can ask a range of questions across both levels of analysis to gain a richer and more integrated understanding of both how and why male digger bees dig into the desert floor, just as Tinbergen envisioned. And as we go forward in this book, we will endeavor to do just that when we introduce a new type of behavior. We will illustrate this integrative approach to studying animal behavior in Chapter 2, where we explore the proximate and ultimate explanations for bird song.

1.2 Approaches to Studying Behavior

LEARNING OBJECTIVES

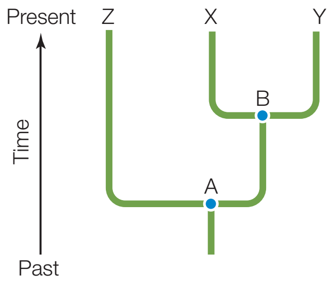
- Compare the various applications for using an observational, experimental, or comparative approach in the study of animal behavior.
- Using the example of mobbing in black-headed gulls, review the evidence collected by each approach to support the proposed adaptive hypothesis for the behavior.
- Consider the use of the comparative approach for understanding cases of convergent and divergent evolution.

To ask questions at different levels of analysis, behavioral biologists can use several complimentary approaches. The most basic approach is simply to watch animals behaving in nature or in the lab. Using this **observational approach**, behavioral biologists can define and record the behaviors of organisms, and then relate them to features of the animals' social or ecological environment, or to their internal or developmental state. In addition, hypotheses can be tested judiciously by observing an animal behave under one set of conditions and comparing it to what happens under another set of conditions. Observational approaches are inherently correlational, meaning one has to be very careful about drawing conclusions in relation to what is cause and what is effect. Instead of observing a relationship between a behavior and the environment and coming up with an explanation, a researcher might instead use an **experimental approach** where they can manipulate features of the animal or its environment to more directly establish a causal relationship among traits. Controlled experiments can be done in the lab, but also in the field if designed carefully to account for all of the natural variation. Finally, some behavioral biologists may want to generate ideas that move beyond a single species by using a **comparative approach** for inferring the adaptive basis of a behavior utilizing multiple different species to look for general patterns of why behaviors evolved. A comparative approach provides information about the **evolutionary history** of a potentially adaptive trait by identifying the characteristics that extinct or ancestral species may have had and how those traits gave rise to the ones that we see in the extant species today. This approach requires a resolved **phylogeny**, or evolutionary tree, that describes the historical relationships among species (**BOX 1.2**). The comparative approach can also be used to ask if there were **evolutionary constraints**, or restrictions, limitations, or biases to the outcome of adaptive evolution, on the appearance of a trait.

BOX 1.2 INTEGRATIVE APPROACHES

Phylogenies and the comparative method

The **FIGURE** in this box is a phylogenetic tree that represents the evolutionary history of three extant animal species (X, Y, and Z) and their links to two ancestral species (A and B). To create a phylogeny of this sort, it is necessary to determine which of the three extant species are more closely related and thus which are descended from the more recent common ancestor. Phylogenies can be drawn on the basis of anatomical, physiological, or even behavioral comparisons among species, but most often, molecular comparisons are used. The molecule DNA is very useful for this purpose because it contains so many "characters" on which such comparisons can be based, namely the specific sequences of nucleotide bases that are linked together to form an immensely long chain. Each of the two strands of that chain has a base sequence that can now be read by an automated DNA-sequencing instrument. Therefore, one can compare a cluster of species by extracting a specific segment of DNA from either the nuclei or mitochondria in cells from each species and identifying the base sequences of that particular segment.



For the purposes of illustration, here are three made-up DNA base sequences that constitute part of a particular gene found in all three hypothetical extant species of animals:

Position	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Species X	A	T	T	G	C	A	T	A	T	G	T	T	A	A	A
Species Y	A	T	T	G	C	A	T	A	T	G	G	T	A	A	A
Species Z	G	T	T	G	T	A	C	A	T	G	T	T	A	A	T

These data can be used to conclude that species X and Y are more closely related to each other than either is to species Z. The basis for this conclusion is that the base sequences of species X and Y are nearly identical (differing by a single change in position 11 of the chain), whereas species Z differs from species X and Y by four and five base changes, respectively. The shared genetic similarity between species X and Y can be explained in terms of their evolutionary history, which must have featured a recent common ancestor (species B in the phylogenetic tree). Species B must have split so recently into the two lineages leading to extant species X and Y that there has not been sufficient time for more than one mutation to become incorporated in this segment of DNA. The lesser, but still substantial, similarities among all three species can be explained in terms of their more ancient common ancestor, species A. The interval between the time when species A split into two lineages and the present has been long enough for several genetic changes to accumulate in the different lineages, with the result that species Z differs considerably from both species X and species Y.

Throughout this book, we will see and discuss several phylogenies that vary in size from a handful of taxa to a few thousand species. We will use these evolutionary trees—which are really just hypotheses about the ancestral

(*Continued*)

BOX 1.2 **INTEGRATIVE APPROACHES** *(continued)*

relationships among species—to examine the evolution of various behavioral and morphological traits. These traits will be "mapped" onto the tree, which means they will be recorded for each branch tip (species or other taxonomic unit, which in this case are X, Y, and Z). Using the comparative method, the relationships among different traits—such as the relationship between animal social and mating systems (see Chapter 12)—will be examined and traced back through the most recent common ancestors to determine how various traits are related to each other, as well as the sequence of events for how they might have coevolved. We will provide another detailed example of this comparative approach in Chapter 2 when we consider the evolutionary history of bird song.

Thinking Outside the Box

Which two species are the least closely related to each other? Redraw the tree using the two additional species below and then determine which species are now the least and most closely related. ■

Position	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Species Q	G	T	T	G	T	A	C	A	A	C	T	T	A	A	T
Species R	A	T	T	G	C	A	T	A	T	G	G	T	A	A	T

Examining the Adaptive Basis of Behavior

All three of these approaches—observational, experimental, and comparative—can provide information about one level of analysis or another. To see how these different approaches can be useful for studying the adaptive evolution of a particular behavior, let's examine the ultimate basis of one behavior: mobbing in gulls. Anyone who has ever stumbled upon a seabird colony during the nesting season knows to watch out! It would not be surprising to see an adult bird swoop about, yap loudly, dive at a person, and even attempt to bomb them with liquid excrement (**FIGURE 1.4**). It's not hard to see why birds become upset when a human, a potential predator, gets close to their nests—and their progeny. If the parents' assaults distract potential predators from their offspring, then mobbing birds may increase their own reproductive success, enabling them to pass on the hereditary basis for joining others in screaming at, defecating on, and even assaulting those who might eat their eggs or chicks. Yet, a single bird is unlikely to succeed in deterring a predator and so will often need the help of others. Thus, one's own reproductive success may require more than one's own solitary behavior. This possible explanation for such behavior led Hans Kruuk to investigate group mobbing in the black-headed gull (*Chroicocephalus ridibundus*), a colonial ground-nesting species that breeds across much of Europe and Asia (**FIGURE 1.5**) (Kruuk 1964). Because Kruuk was interested in studying the adaptive basis of mobbing, he did what behavioral biologists do to solve problems of this sort—he considered the costs and benefits of the behavior. His


Courtesy of John Alcock

FIGURE 1.4 Mobbing behavior of colonial, ground-nesting gulls. Silver gulls (*Chroicocephalus novaehollandiae*) reacting to a trespasser in their breeding colony in New Zealand.

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FIGURE 1.5 **Colonial-nesting black-headed gulls.** These birds build nests on the ground that are susceptible to predation.

working hypothesis was based on the notion that the costs to the mobbers (such as the time and energy expended by attacking potential predators, and the risk of getting injured or even killed) were outweighed by the fitness benefits to the birds from their social harassment of potential predators (such as increased offspring survival).

To examine the hypothesis that mobbing potential predators distracts them from depredating nests, Kruuk tested one of its central predictions, the idea that mobbing gulls should force distracted predators to expend more searching effort than they would otherwise. This prediction can be tested simply by watching gull–predator interactions using an observational approach (Kruuk 1964). Like most behavioral biologists studying animals in their natural habitat, Kruuk spent many hours watching the birds and observed that egg-hunting carrion crows (*Corvus corone*) must continually face gulls diving at them and so, while being mobbed, they cannot look around comfortably for their next meal (**FIGURE 1.6**). Because distracted crows are probably less likely to find their prey, Kruuk established that a probable benefit

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FIGURE 1.6 **Why do gulls mob predators?** Hans Kruuk proposed that the fitness costs to mobbers of harassing potential predators like this carrion crow were outweighed by the fitness benefits.

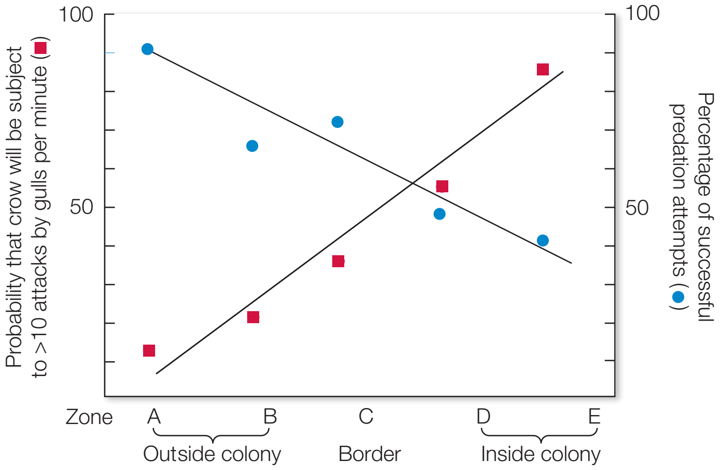


FIGURE 1.7 **Does mobbing protect eggs?** When chicken eggs were placed outside and inside a black-headed gull nesting colony, crows searching for the eggs within the colony were subject to more attacks by mobbing gulls (red squares), and as a result, they discovered fewer hen eggs (blue circles). (After H. Kruuk. 1964. *Behav Suppl* 11: 1–129.)

exists for mobbing. Moreover, the benefit of mobbing crows plausibly exceeds the costs, given that crows do not attack or injure adult gulls.

Although Kruuk's observations were consistent with the idea of predator distraction, the hypothesis yields much more demanding predictions that require an experimental approach. Because adaptations are better than the traits they replace, we can predict that the benefit experienced by mobbing gulls in protecting their eggs should be directly proportional to the extent that predators are actually mobbed. To test this prediction, Kruuk designed an experiment that involved placing 10 chicken eggs as stand-ins for gull eggs, one every 10 meters, along a line running from outside a black-headed gull nesting colony to inside it (Kruuk 1964). Eggs placed outside the colony, where mobbing pressure was low, were much more likely to be found and eaten by carrion crows and herring gulls (*Larus argentatus*) than were eggs placed inside the colony, where predators were communally harassed by the many parents whose offspring were threatened by the presence of a predator (**FIGURE 1.7**).

Kruuk assembled both observational and experimental evidence that was consistent with the hypothesis that mobbing is an adaptation that helps adult black-headed gulls protect their eggs and young. Field experiments, along with correlational and observational field data, are critical for deciphering the adaptive value of animal behaviors. However, we could also use the comparative approach to test Kruuk's explanation for mobbing by black-headed gulls by testing the following prediction: If mobbing by ground-nesting black-headed gulls is an evolved response to predation on gull eggs and chicks, then other gull species whose eggs and young are at low risk of predation should not exhibit mobbing behavior. The rationale behind this prediction is as follows: the various fitness costs of mobbing (such as the increased risk of being killed by a predator) will be outweighed only if sufficient fitness benefits are derived from distracting predators. If predators have not posed a problem, then the odds are that the costs of mobbing (such as the energy spent dive-bombing a non-predator) would be greater than the benefits, and we would not expect the behavior to have evolved in those species.

Inferring the Evolutionary History of Behavior

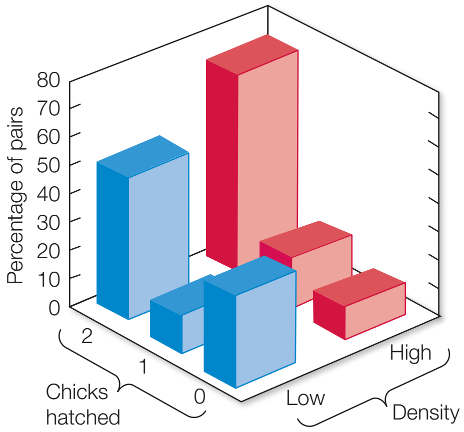
There is good reason to believe that the ancestral gull was a ground-nesting species with many nest-hunting predators against which the mobbing defense would have been effective (**BOX 1.3**). Of the 50 or so species of extant gulls, most nest on the ground and mob enemies that hunt for their eggs and chicks (Tinbergen 1959). These behavioral similarities among gulls, which also share many other features, are believed to exist in part because all gulls are the descendants of a relatively recent common ancestor, from which they all inherited the genetic material that predisposes many extant gull species to develop similar traits. Thus, all other things being equal, we expect most gulls to behave similarly.

Yet, some things are not equal, especially when it comes to gull reproductive behavior. For example, a few gull species nest on cliff ledges or on trees rather than on the ground. Perhaps these species are all the descendants of a more recent cliff-nesting gull species that evolved from a ground-nesting ancestor. The alternative hypothesis, that the original gull was a cliff nester, requires the cliff-nesting trait to have been lost and then regained, which produces an evolutionary scenario that

BOX 1.3 **EXPLORING BEHAVIOR BY INTERPRETING DATA**

The benefit of high nest density for the arctic skua

The arctic skua (*Stercorarius parasiticus*), a close relative of gulls, also nests on the ground and mobs colony intruders, including another relative, the great skua (*Stercorarius skua*), a larger predator that eats many arctic skua eggs and chicks. In one population, hatching success and postfledging survival were greater for arctic skuas that nested in dense colonies than for those in low-density groups (**FIGURE**); the number of near neighbors was, however, negatively correlated with the growth rate of their chicks (Phillips et al. 1998).



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Arctic skua

Arctic skuas nesting with many nearby neighbors were more likely to rear two chicks than were individuals nesting in areas with a lower density of breeding pairs. (After R. A. Phillips et al. 1998. *Biol Conserv* 86: 21–31.)

Thinking Outside the Box

Rephrase these findings in terms of the reproductive costs and benefits of communal nesting and mobbing by the arctic skua. If adaptation meant a perfect trait, would communal mobbing by arctic skuas be labeled an "adaptation"? ■

requires more changes than the competing one (**FIGURE 1.8**). Two changes, a loss and a reappearance, are simply less likely to happen than one change, an appearance that is maintained. Many evolutionary and behavioral biologists, although not all (Reeve and Sherman 2001), believe that simpler scenarios involving fewer transitions

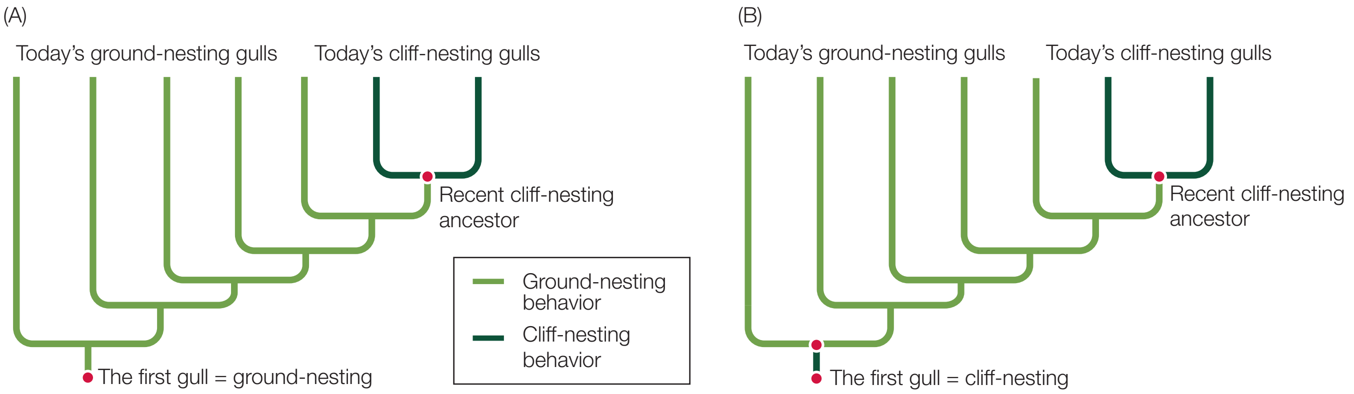
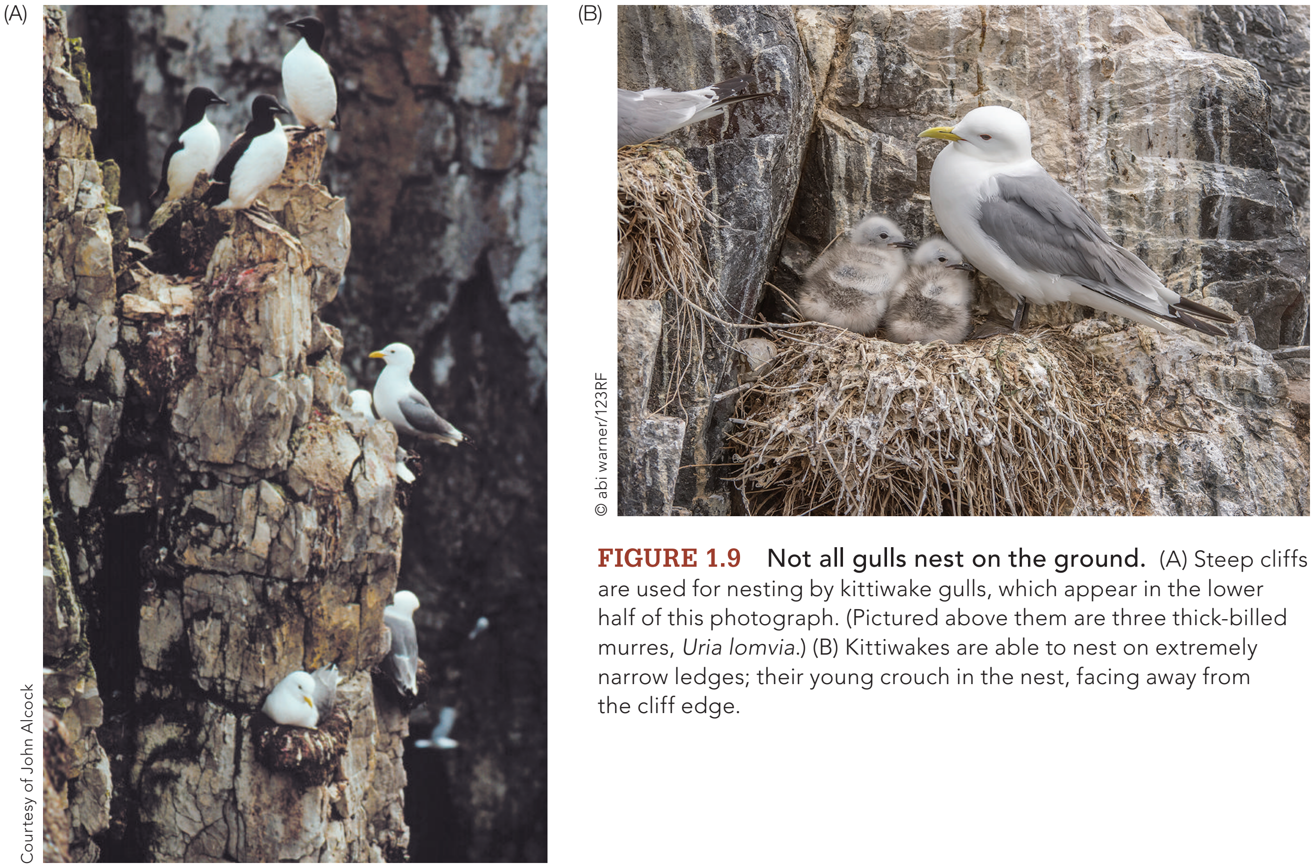


FIGURE 1.8 Gull phylogeny and two scenarios for the origin of cliff-nesting behavior. (A) Hypothesis A requires just one behavioral change, from ground nesting to cliff nesting. (B) Hypothesis B requires two behavioral changes, one from the ancestral cliff nester to ground nesting, and then another change back to cliff nesting.

are more likely than more complicated alternatives. This assumption is known as Occam's razor or the principle of **parsimony**, which holds that simpler explanations are more likely to be correct than complex ones—all other things being equal.

In any event, cliff-nesting gulls currently have relatively few nest predators because it is hard for small mammalian predators to scale cliffs in search of prey, and because predatory birds have a difficult time maneuvering near cliffs in turbulent coastal winds. Thus, a change in nesting environment surely led to a reduction in predation pressure, which should have altered the cost–benefit equation for mobbing by these gulls. If so, cliff-nesting gulls are predicted to have modified or lost the ancestral mobbing behavior pattern. For example, the black-legged kittiwake (*Rissa tridactyla*) nests on nearly vertical coastal cliffs, where its eggs are relatively safe from predators (**FIGURE 1.9**) (Massaro et al. 2001). The relatively small size of the kittiwakes may also make the adults themselves more vulnerable to attack by some nest predators, making the cost–benefit ratio for mobbing even less favorable. As predicted, groups of nesting adult kittiwakes do not mob their predators, despite sharing many other structural and behavioral features with black-headed gulls and other ground-nesting species. The kittiwake's distinctive behavior provides a case of **divergent evolution** and supports the hypothesis that mass mobbing by black-headed gulls evolved in response to predation pressure on the eggs and chicks of nesting adults (Cullen 1957). Take away the threat of predation, and over evolutionary time a gull will likely lose its mobbing behavior because it is no longer adaptive or useful to maintain.

Another use of the comparative approach for understanding the evolution of mobbing behavior is to test the idea that species from different evolutionary lineages that live in similar environments should experience similar selection pressures and thus can be predicted to evolve similar traits, resulting in **convergent evolution**. If this is true, these unrelated species will adopt the same adaptive solution to a



Courtesy of John Alcock

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FIGURE 1.9 **Not all gulls nest on the ground.** (A) Steep cliffs are used for nesting by kittiwake gulls, which appear in the lower half of this photograph. (Pictured above them are three thick-billed murres, *Uria lomvia*.) (B) Kittiwakes are able to nest on extremely narrow ledges; their young crouch in the nest, facing away from the cliff edge.

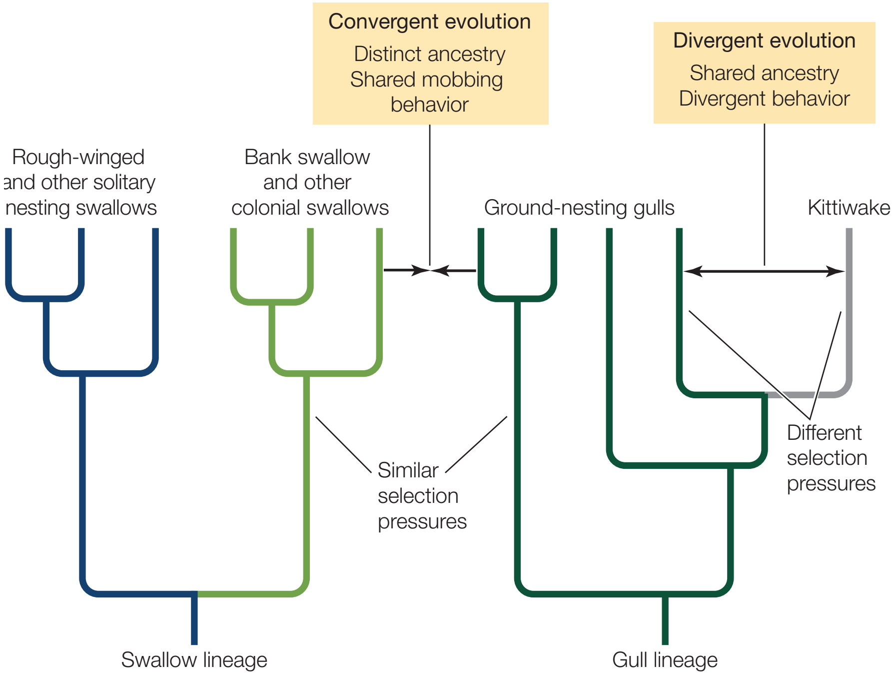

FIGURE 1.10 **The logic of the comparative method.** Since members of the same evolutionary lineage (such as gull species of the family Laridae) share a common ancestry and therefore share many of the same genes, they tend to have similar traits, such as mobbing behavior, which is widespread among ground-nesting gulls. But the effects of shared ancestry can be overridden by a novel selection pressure. A reduction in predation pressure has led to divergent evolution by the cliff-nesting kittiwake, which no longer mobs potential enemies. The other side of the coin is convergent evolution, which is illustrated by the mobbing behavior of some colonial swallows, even though gulls and swallows are not related, having come from different ancestors long ago. These colonial swallows and gulls have converged on a similar antipredator behavior in response to shared selection pressure from predators that have fairly easy access to their nesting colonies.

particular environmental obstacle to reproductive success (**FIGURE 1.10**). All other things being equal, unrelated species should behave differently, unless they have been subjected to the same **selection pressures**, or drivers of differential survival and reproduction.

As predicted, mobbing behavior has evolved convergently in many other birds only distantly related to gulls, particularly those that nest colonially (Sordahl 2004). Among these species is the bank swallow (*Riparia riparia*), which also nests in colonies where predatory snakes and jays come to eat swallow eggs and nestlings (Hoogland and Sherman 1976). The common ancestor of bank swallows and gulls occurred long, long ago, with the result that the lineages of the two groups have evolved separately for millions of years—a fact recognized by the taxonomic placement of gulls and swallows in two different families, Laridae and Hirundinidae. Yet, despite their evolutionary and genetic differences from gulls, bank swallows behave like gulls when they are nesting. As bank swallows swirl around and dive at their predators, they sometimes distract hunting jays or snakes that would otherwise kill their offspring.

Even some colonially nesting mammals have evolved mobbing behavior (Owings and Coss 1977). For example, adult California ground squirrels (*Otospermophilus beecheyi*), which live in groups and dig underground burrows, react to a hunting rattlesnake by gathering around it and shaking their infrared-emitting tails vigorously, a signal to the snake to encourage it to depart before the ground squirrels kick sand in its face (**FIGURE 1.11**) (Rundus et al. 2007). Rattlesnakes molested in this fashion cannot hunt leisurely for nest burrows to enter in search of vulnerable young

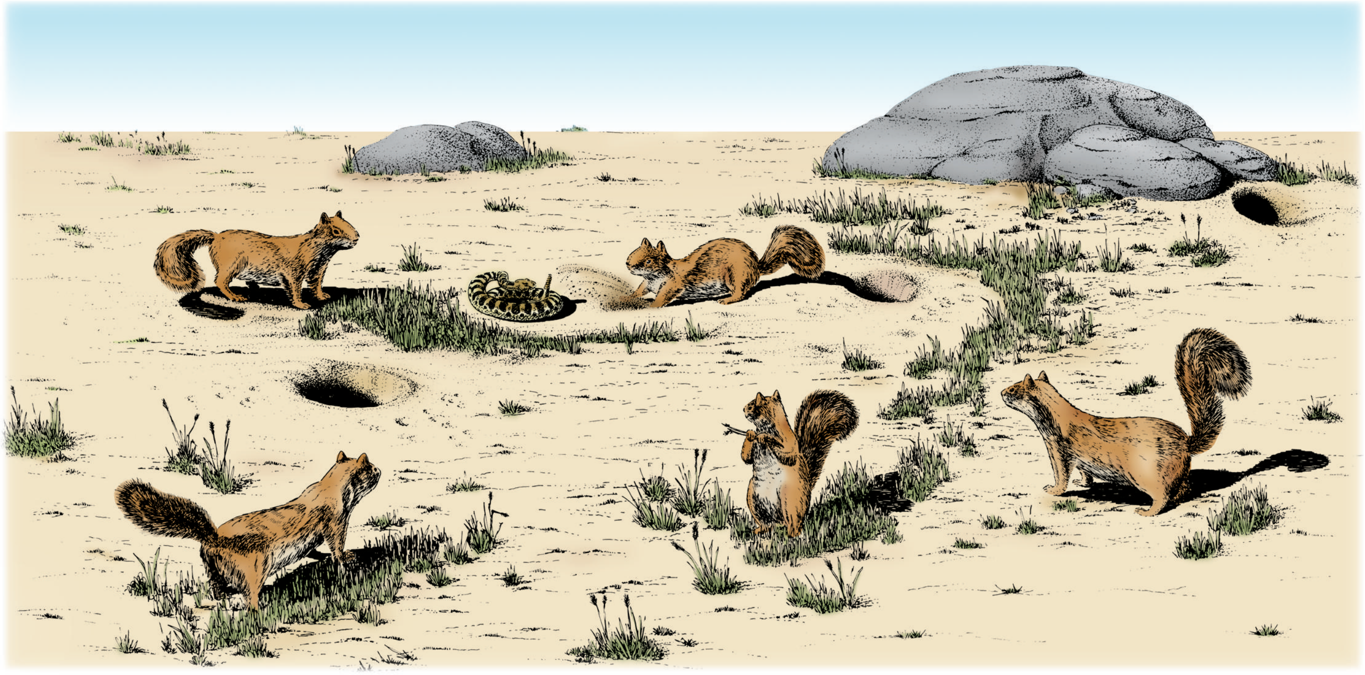

Illustration by R. G. Coss

FIGURE 1.11 **California ground squirrels signal to hunting rattlesnakes by shaking their tails.** The tail of this rodent emits infrared to signal to potential predators to leave.

ground squirrels. Thus, because mobbing behavior has evolved independently in several unrelated species whose adults can sometimes protect their vulnerable offspring by distracting predators, mobbing is almost certainly an antipredator adaptation. We will explore this and other antipredator behaviors further in Chapter 6.

Synthesis

Throughout the reading of this book, it is important to remember that behavioral biology is a scientific discipline. By this, we mean that researchers studying animal behavior use a particular kind of logic to evaluate potential explanations for puzzling phenomena. As we detailed previously, this logic is grounded in natural selection theory, and as we will see in subsequent chapters, this theory can be expanded to encompass a range of seemingly paradoxical behaviors, such as why males use and evolve elaborate traits that decrease their own survival, why individuals in some group-living animals forego their own reproduction to help raise others' offspring, and why females in some species have what look like penises but males of those species do not. We must also remember that animal behaviors are grounded in, and sometimes constrained by, both mechanism and evolutionary history. Therefore, integrative studies that cross levels of analysis can help explain how and why behaviors evolve. To ask questions at either level of analysis, behavioral biologists use the scientific method to develop hypotheses and then observationally, experimentally, or comparatively test predictions of those hypotheses using a variety of well-designed procedures. But at the heart of any good behavioral study remains the Darwinian logic to evaluate the puzzling phenomena in the world around us, the same logic that we used to determine why nesting black-headed gulls mob predators or how digger bees locate mates. Of course, caution must be used when interpreting why a particular behavior has evolved, as researchers often argue that natural selection has acted on a behavioral trait or that an animal actor has a purpose, yet animals do not know whether the choices they make are adaptive or not. Behavioral biologists sometimes use loose language to describe these issues, so we must be aware of what they really mean when they describe an adaptation or behavioral decision, remembering that the scientific method allows researchers to test and interpret alternative explanations about why animals have evolved to behave the way that they do. One of the book's primary goals is to encourage readers to realize how scientists evaluate hypotheses in ways that are generally considered fair and logical (at least by other scientists). Good science means that scientists approach a problem without preconceived answers. The scientific method allows researchers to distinguish among alternative explanations. The cases reviewed in the chapters

Synthesis (*continued*)

ahead have been selected with this goal in mind. After a discussion in Chapter 2 of how the integrative study of animal behavior can help us to better understand the evolution of song learning in birds, the book is organized to first present additional details about the proximate level of analysis, and then the ultimate level. Chapters 3, 4, and 5 emphasize the developmental, molecular, neural, physiological, and endocrine bases of behavior. From there, we begin to explore the adaptive behaviors that animals exhibit, with Chapter 6 emphasizing survival decisions (including how to avoid predators and find food) and Chapter 7 examining settlement and movement decisions (including territoriality, dispersal, and migration). In Chapter 8 we consider the evolution of communication and how individuals exchange information in ways that influence their reproduction and survival. From there, we move to a discussion of sexual behavior, examining reproductive behavior in Chapter 9 and mating systems in Chapter 10. Chapter 11 introduces the topic of parental care and transitions us into a discussion of social behavior. We use eusocial insects to introduce the principles of social evolution in Chapter 12, followed by a broader examination of social behavior and group living in vertebrates in Chapter 13. Finally, Chapter 14 offers examples of how both proximate and ultimate questions contribute to an understanding of our own behavior. Let's get started. ■

SUMMARY

1. Evolutionary theory provides the foundation for the study of animal behavior. Charles Darwin realized that evolutionary change would occur if "natural selection" took place. This process happens when individuals differ in their ability to reproduce successfully, as a result of their inherited attributes. If natural selection has shaped animal behavior, we expect that individuals will have evolved abilities that increase their chances of passing copies of their genes on to the next generation.

2. Most behavioral biologists now take a gene's eye view of evolution by natural selection. According to this view, adaptive evolution occurs through the differential survival of competing genes, which increases the frequency of those alleles whose phenotypic effects promote their own propagation.

3. Researchers interested in the adaptive value of behavioral traits use natural selection theory to develop particular hypotheses (tentative explanations) for how a specific behavior might enable individuals (not groups or species as a whole) to achieve higher reproductive success than individuals with alternative traits.

4. Behavioral traits have both ultimate (evolutionary) and proximate (immediate) causes that are complementary, not mutually exclusive. Questions about ultimate causes are those that focus on the possible adaptive value of a behavior as well as those that ask how an ancestral trait became modified over time, leading to a modern characteristic of interest. Questions about proximate causes can be categorized as those concerned with the genetic–developmental bases for behavior as well as those that deal with how physiological (neural and hormonal) systems provide the basis for behavior.

5. Adaptationist hypotheses can be tested in the standard manner of all scientific hypotheses by making predictions about what we must observe in nature in the outcome of an experiment or by comparatively exploring how traits evolved across a group of organisms over evolutionary time. Failure to verify these predictions constitutes grounds for rejecting the hypothesis; the discovery of evidence that supports the predictions means the hypothesis can be tentatively treated as true.

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2.1 The Development of Song Learning
Intraspecific Variation and Dialects
Social Experience and Song Development

2.2 Mechanisms of Song Learning
The Genetics of Song Learning
The Avian Song Control System

2.3 The Evolution of Song Learning
An Evolutionary History of Bird Song
Song Learning: A Comparative Approach

2.4 The Adaptive Value of Song Learning
Ecological and Social Correlates of Song Learning
Social Competition and Mate Choice

2

The Integrative Study of Behavior

- Recognize how questions and experiments conducted at multiple levels of analysis can generate a deeper understanding of how and why a behavior occurs.
- Synthesize proximate-level findings on the developmental and mechanistic processes underlying song learning in birds.
- Integrate knowledge of evolutionary history and adaptive benefits of bird song to consider the ultimate causes for the evolution of song learning and production.

As we learned in Chapter 1, animal behavior is a broad and varied discipline, and those who study it are becoming increasingly integrative in their approach. Although digger bees were used to illustrate how both proximate- and ultimate-level questions can be combined to create a richer understanding of bee behavior, this chapter takes the concept of integration a step further. The integrative study of animal behavior is most often described as simply using tools (including molecular, endocrine, or neural, but also statistical, computational, and phylogenetic) from other disciplines to enrich the study of behavior, particularly in the wild. For example, the application of tools to study hormones or DNA in blood samples or feces collected from free-living animals has changed the way behavioral biologists study almost every aspect of animal behavior. Moreover, evolutionary game theory (see Chapter 6), which comes directly from the field of economics, has enriched the way behavioral biologists think about topics as diverse as foraging behavior, social evolution, and sex allocation. Yet, since its inception, the field of animal behavior has always drawn links to other fields—ethology and psychology in the earliest days, then ecology and evolution, and increasingly molecular biology and neuroscience. True integration goes further than simply designing studies that cross levels of analysis or incorporating tools from other disciplines by enabling scientists to not only test long-standing hypotheses with new techniques, but also to generate novel hypotheses that would otherwise not have come to mind without new ways of thinking (MacDougall-Shackleton 2011, Hofmann et al. 2016). Although any number of behaviors could be used to illustrate this integrative approach to studying behavior, this chapter serves as a case study focused on song learning in birds.

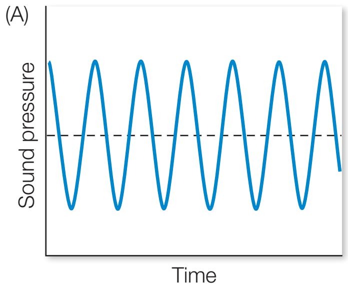
Bird song functions like many other animal sounds do, and it can be analyzed in much the same way (**BOX 2.1**). Here, however, we emphasize song learning—the ability to acquire vocalizations through imitation. This chapter focuses on both song

BOX 2.1 INTEGRATIVE APPROACHES

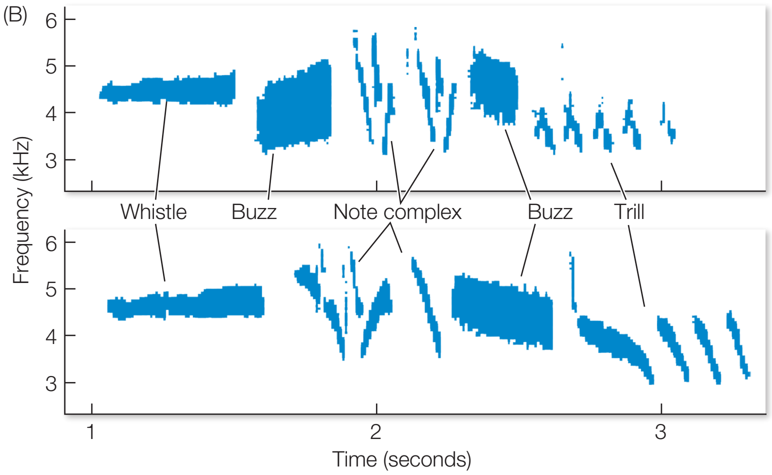
Characterizing sounds made by animals

Like all types of sounds, animal sounds are simply propagated disturbances in ambient pressure that travel in waves. Animal ears sense these changes in pressure and convert them to signals that are sent to the brain, much the way a microphone converts the same variations in pressure into electrical signals that are sent to a recording device. A **waveform** shows the changes in pressure over time that compose a sound. Imagine a waveform that looks like a repeating sine wave (**FIGURE A**). If the waveform changes in height (along the *y*-axis), we say that the **amplitude**—intensity—varies. If the waveform changes in width (along the *x*-axis), we say that the **frequency**—the rate at which amplitude increases and decreases—varies. Animals perceive changes in frequency as changes in pitch. The simplest way for behavioral biologists to analyze sounds is to use an **oscillogram**, a graph of amplitude as a function of time. However, since oscillograms do not reveal changes in frequency, researchers often use a **spectrogram** (sometimes referred to as a sonogram), a visual representation of sound frequencies over time. In a spectrogram, intensity is often shown using color or grayscale. Simply by looking at a spectrogram, we can learn something about whether an animal produces high- or low-frequency sounds, the intensity of those sounds, and how the different sounds are structured (say, into a song) over some period of time.

To illustrate how to interpret a spectrogram, let's examine the song of the white-crowned sparrow (*Zonotrichia leucophrys*), one of the most studied of all animal sounds. The male white-crowned sparrow song typically lasts 2 to 3 seconds and consists of several different elements, often referred to as **syllables**. Notice in the spectrogram that the shapes of these syllables differ greatly (**FIGURE B**) (Nelson et al. 2004). Now listen to some white-crowned sparrow songs. A typical song begins with a whistle, which sounds like one tone. The whistle is then followed by more



Sound waveform. The waveform of a pure sinusoidal tone at 1 kHz. (After J. W. Bradbury and S. K. Vehrencamp. 2011. *Principles of Animal Communication*, 2nd ed. Sunderland, MA: Oxford University Press/Sinauer.)



Two white-crowned sparrow songs from different dialect populations. The component parts of the song are labeled. (After D. A. Nelson et al. 2004. *Ethology* 110: 879–908.)

production and song perception, discussing not only how and why birds learn to sing, but also how the way in which birds learn and produce song influences its function, and vice versa. Although subsequent chapters in this book will also highlight some of the reasons that birds and other animals vocalize, as well as the developmental mechanisms that help them do so, this chapter briefly introduces these concepts in one place. It demonstrates how, by observing and recording singing birds in the field and lab, and by studying the brains, physiology, and genomes of birds during development and in adulthood, scientists can gain a richer and more integrative understanding of both the adaptive and mechanistic bases of song learning.

complex sounds consisting of frequency sweeps, buzzy vibrato elements, and trills (Chilton et al. 1995). There are also several other background noises in some of the recordings. From geese honking to cars driving to wind blowing, these sounds are not just distracting to us while listening, they can also influence how birds produce and hear song. As habitat is altered and humans encroach on more natural habitat, increasing anthropogenic noise may affect the way that many bird species produce and perceive song.

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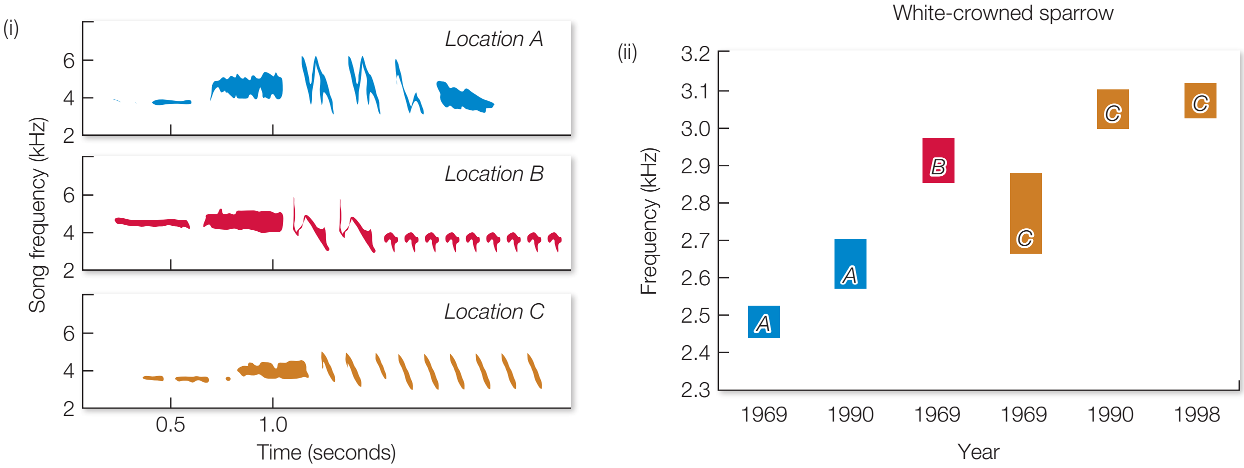
White-crowned sparrow

(C)



Dialects of white-crowned sparrows in three parts of San Francisco. (i) The three dialects, which were recorded over several decades at three locations that exhibited increasing urbanization at the three locations, each represented by a different color. (ii) The minimum frequency contained in the songs in the three locations (corresponding to those in panel i). The bars indicate SE of the birds captured at each location. (After D. Luther and L. Baptista. 2010. *Proc R Soc B* 277: 469–473.)

Thinking Outside the Box

In some cases, birds have adapted to environmental noise by altering the songs that they produce. Several researchers have wondered whether bird songs have changed in cities in response to traffic noise, which comprises primarily low-frequency sounds. In one study, the authors documented the minimum sound frequency employed in three dialects of white-crowned sparrow song recorded over a 30-year period in San Francisco (Luther and Baptista 2010). As we can see from the graph in **FIGURE C**, frequency increased over time. To help understand how behavioral biologists collected these data, reconstruct the science behind this research from the question that stimulated the study. Then, think about the conclusion the authors must have reached by determining why the minimum song frequency might have increased in urban birds over the course of three decades.

2.1 The Development of Song Learning

LEARNING OBJECTIVES

- Identify the contribution of genetic differences to song dialects across different geographic scales.
- Assess the role of early life social experiences and interactions on vocal development.
- Consider the interactive impact of genetics, acoustic stimuli, and social experience on song learning.

Our discussion begins with Peter Marler's classic work exploring why males in different populations of some bird species sing distinctive variants of their species' song, just as people in different parts of a country often speak different dialects. Marler became aware of bird dialects as a young scientist while traveling among British lakes conducting a study on lake ecology (Ball and Dooling 2017). As he listened to the local songs of chaffinches (*Fringilla coelebs*), he realized that each lake's population sang a slightly different version of this species' standard song, a rattling series of chips terminated by a descending flourish. It was these observations that changed Marler's scientific focus and set him along the path to studying bird song.

Intraspecific Variation and Dialects

When Marler moved to the University of California, Berkeley, in the 1960s, he and his students investigated the phenomenon of **song dialects** in the white-crowned sparrow, a common North American songbird. Many bird species exhibit dialects, but they are particularly conspicuous and delineated in white-crowned sparrows, which has made this species a model system for the study of bird song for more than 50 years since Marler's initial work (Toews 2017). Males of this species sing a complex vocalization, sounding like whistles, trills, and buzzes, during the breeding season. Marler and his colleagues found that sparrows living in Marin, north of San Francisco, sing a song type that is easily distinguished from that produced by birds living in Berkeley to the east, or in Sunset Beach to the south (**FIGURE 2.1**) (Marler and Tamura 1964). Although white-crowned sparrow dialects sometimes change gradually over time (Nelson et al. 2004), in at least some populations, local dialects tend to persist for decades with only modest changes (Harbison et al. 1999), showing that bird dialects can be relatively stable, just like those of humans.

What might cause birds to sing distinct dialects in different geographic areas, especially when the areas are relatively close to one another? There are several non-mutually exclusive hypotheses to explain how birds of the same species that live relatively close together can develop such different dialects (**HYPOTHESES 2.1**). A possible proximate explanation for the dialect differences was that Marin birds might differ genetically from those in Berkeley in ways that affected the construction of their neural development. One way to begin to test this **genetic differences hypothesis** is to test the prediction that groups of birds singing different dialects will be genetically distinct from one another. Although the tools to test this hypothesis did not exist when Marler began his work, researchers have subsequently found little genetic differentiation among six different dialect groups of white-crowned sparrows in the northern portions of their range (Soha et al. 2004, Poesel et al. 2017).

That is not to say, however, that there is no genetic differentiation among populations of white-crowned sparrows. The species occupies a wide geographic range, and in the western United States, some populations do not just sing unique songs, they are also morphologically distinct. Scientists have divided these groups into different subspecies: the Puget Sound subspecies (*Zonotrichia leucophrys pugetensis*) is migratory and breeds from northern California to southern British Columbia, whereas the Nuttall's subspecies (*Zonotrichia leucophrys nuttalli*) is a year-round resident that

HYPOTHESES 2.1

Non-mutually exclusive proximate hypotheses for the development of song and song dialects in birds

genetic differences hypothesis
Differences in song are the result of genetic differences.

acoustic stimulus hypothesis
Differences in song are the result of differences in a birds' acoustic environment.

social interaction hypothesis
Differences in song are the result of social interactions between a young bird and its tutor.

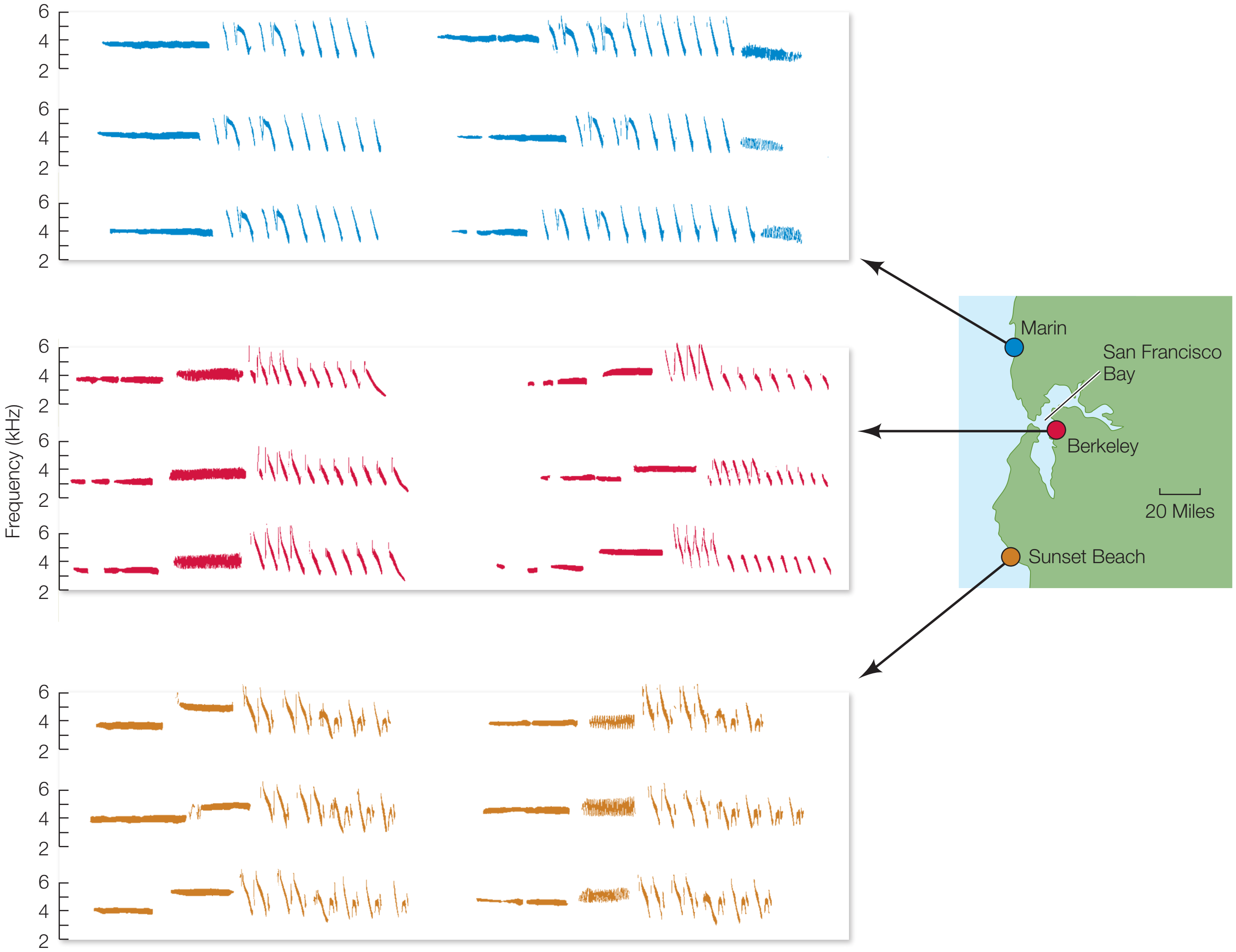


FIGURE 2.1 **Song dialects in white-crowned sparrows.** Males from Marin, Berkeley, and Sunset Beach, California, have their own distinctive song dialects, as revealed in these spectrograms of the songs of six birds from each location, provided by Peter Marler. Spectrograms shown in the same color are of songs with the same dialect. (From P. Marler and M. Tamura. 1964. *Science* 146: 1483–1486. Reprinted with permission from AAAS.)

breeds in coastal central and northern California. Although early studies found few genetic differences between these two subspecies (Weckstein and Zink 2001), subsequent work by Sara Lipshutz and colleagues using thousands of molecular markers scattered across the genome found that the regional subspecies do in fact separate into distinct genetic clusters (Lipshutz et al. 2017). These researchers also found that the two subspecies respond differently to each other's song, and that these different song preferences likely help limit gene flow between the subspecies. Thus, genetic differences exist at broad geographic scales (subspecies song differences), but not at the local scale that Marler used to first identify differences in song dialect. Although researchers have not yet examined the genes directly related to song learning in this species, there is no evidence that genetic differences give rise to distinct song dialects in nearby white-crowned sparrow populations.

If genetic differences are unlikely to explain the song differences among the local populations that Marler observed, then perhaps these differences might be caused by differences in the birds' social environments. According to the **acoustic stimulus hypothesis**, young males in Marin may *learn* to sing the dialect of that region by listening to what adult Marin males are singing, while farther south in Berkeley, young male white-crowned sparrows have different formative experiences as a result of hearing the local dialect. After all, a young person growing up in Mobile, Alabama, acquires a dialect different from someone in Bangor, Maine, simply because the Alabaman child hears a different brand of English than the youngster reared in Maine. Marler and his colleagues tested the hypothesis that differences in dialects may be the result of differences in the birds' social environments by taking eggs from white-crowned sparrow nests and hand-rearing them in the laboratory. Even when these young birds were kept isolated from the sounds made by singing birds and had no social guidance from adult sparrows, they still started singing when they were about 150 days old—but the best they could ever do was a twittering vocalization that never took on the rich character of the full song of a wild male white-crowned sparrow from Marin, Berkeley, or anywhere else (Marler 1970).

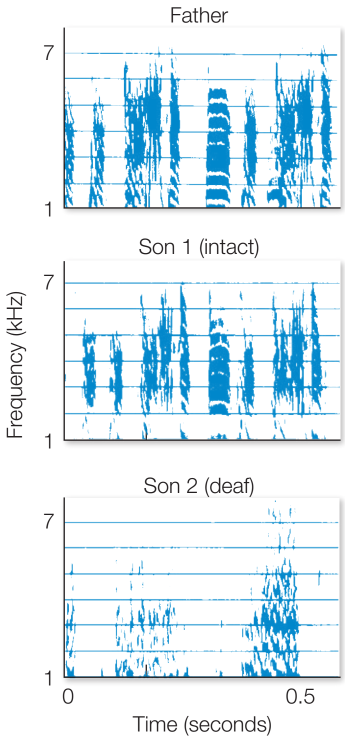
This result suggested that something critical was missing from the hand-reared birds' environment. If the opportunity to hear the songs of adult male white-crowned sparrows was the key factor that was missing, then a young male isolated in a soundproof chamber but exposed to recordings of white-crowned sparrow song should be able to learn to sing a complete white-crowned sparrow song. Indeed, that is exactly what happened when 10- to 50-day-old birds were allowed to listen to recordings of white-crowned sparrow song. As predicted by the acoustic stimulus hypothesis, these birds also started singing on schedule when they were about 150 days old. Although their songs were initially incomplete, by the age of 200 days, the isolated birds not only sang the species-typical form of their song, they closely mimicked the exact version that they had heard on recordings. Play a Berkeley song to an isolated young male white-crowned sparrow, and that male will come to sing the Berkeley dialect. Play a Marin song to another male, and he will eventually sing the Marin dialect. Thus, irrespective of where the bird was collected, it could readily be taught a new song.

These results offer strong support for the acoustic stimulus hypothesis and the idea that the experience of hearing neighboring male sparrows sing affects the development of white-crowned sparrow dialects in young males. Young male sparrows evidently store the acoustic information they acquire from their tutors and later match their own initially incomplete song versions against their memories of tutor song, gradually coming to duplicate a particular dialect. Along these lines, if a young hand-reared white-crowned sparrow is unable to hear itself sing (as a result of being deafened after hearing others sing but before beginning to vocalize itself), then it never produces a normal song, let alone a duplicate copy of the one it heard earlier in life (Konishi 1965). Indeed, the ability to hear oneself sing appears to be critical for the development of a complete song in a host of songbird species, including the commonly studied zebra finch (*Taeniopygia guttata*) (**FIGURE 2.2**).

Marler and others did many more experiments designed to determine how song development takes place in white-crowned sparrows. For example, they wondered whether young males were more easily influenced by the stimuli provided by singing adults of their own species than by those of other species. In fact, young, isolated, hand-reared birds that hear only songs of another species almost never come to sing that kind of song (although they may incorporate notes from the other species' song into their vocalizations). If 10- to 50-day-old birds listen only to recordings of song sparrows (*Melospiza melodia*) instead of white-crowned sparrows, they develop aberrant songs similar to the "songs" produced by males that never hear any bird song at all. But if an experimental bird has the chance to listen to recordings of the white-crowned sparrow along with songs of another sparrow species, then by 200 days of age it will sing the white-crowned sparrow dialect that it heard earlier (**FIGURE 2.3**) (Konishi 1985). The young bird's developmental

Courtesy of Atsuko Takahashi

Male zebra finch



From L. Wilbrecht et al. 2002. *J Neurosci* 22: 825–831

FIGURE 2.2 **Hearing and song learning.** In white-crowned sparrows and many other songbirds, young males have to hear themselves singing in order to produce an accurate copy of their species' song. A spectrogram of a male zebra finch's song is shown with those of two of his male offspring. The first son's hearing was intact, and he was able to copy his father's song. The second son was experimentally deafened early in life, and as a consequence, he never sang a typical zebra finch song, let alone one that resembled his father's song.

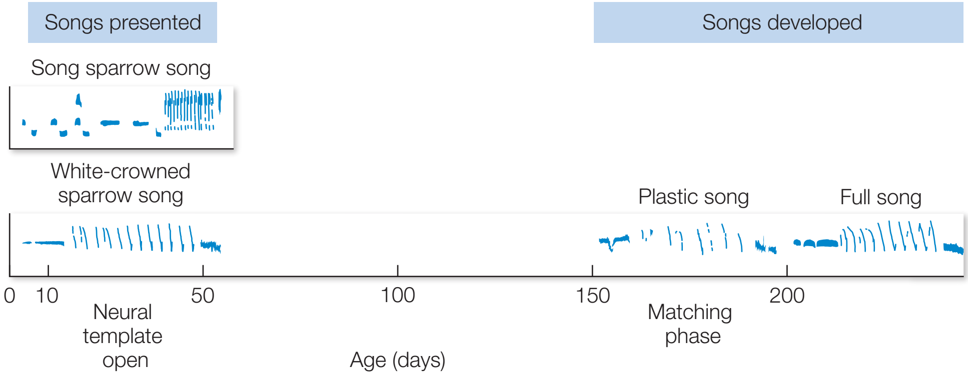


FIGURE 2.3 **Song-learning hypothesis based on laboratory experiments with white-crowned sparrows.** Young, male white-crowned sparrows have a special sensitive period 10 to 50 days after hatching, when their neural systems can acquire information from listening to their own species' song, but usually not to any other species' song. Later in life, the bird matches his own plastic song with his memory of the tutor's song and eventually imitates it perfectly—but does not sing elements of the song sparrow's song that he heard during his development. (After P. Marler. 1970. *J Compar Physiol Psychol* 71: 1–25. American Psychological Association.)

system is such that listening to the songs of other sparrow species has little effect on its later singing behavior, indicating that this is a genetically encoded perceptual predisposition. As we will see below, however, this type of filtering may not be the case for other bird species.

Although these studies demonstrate how dialects can be learned, they do not reveal how different dialects arise in the first place. Douglas Nelson proposed that white-crowned sparrow songs change gradually over time because of cultural evolution, whereby subtle, somewhat spontaneous changes to songs caused by imprecisions in imitative learning (analogous to mutations in DNA) are then learned by others and spread in the population (Nelson et al. 2004). Over time, the song a population sings will gradually change, resulting in a unique dialect. Nelson and colleagues demonstrated this process by examining white-crowned sparrow songs collected over a 30-year period, as did other researchers in a similar 31-year study of savannah sparrows (*Passerculus sandwichensis*) (Williams et al. 2013). In both studies, researchers traced the timing of specific changes to the song, observing when certain components were added or lost and new dialects produced or altered.

Although song dialects change gradually over time within populations, they generally tend to remain stable within geographic regions. Yet, this may not always be the case, as Ken Otter and colleagues showed in a study of male white-throated sparrows (*Zonotrichia albicolis*) (Otter et al. 2020). Prior to 1960, white-throated sparrow males across Canada sang a song that ended with a repeated triplet of notes, but sometime between 1960 and 2000, males west of the Rocky Mountains began ending their songs with a doublet-note, a dialect that had spread east of the Rocky Mountains by the 2000s. Indeed, by 2019, the doublet-ending song had spread to eastern Canada and completely replaced the triplet-ending song in every region in which it had been found. Within just two decades, the new dialect had spread more than 3000 miles across the continent. But the change is unlikely to stop there, as an even newer dialect with a modulated-doublet-ending song has emerged west of the Rocky Mountains and is rapidly spreading within the region, giving researchers the rare opportunity to track the spread of a new song dialect in real time.

Social Experience and Song Development

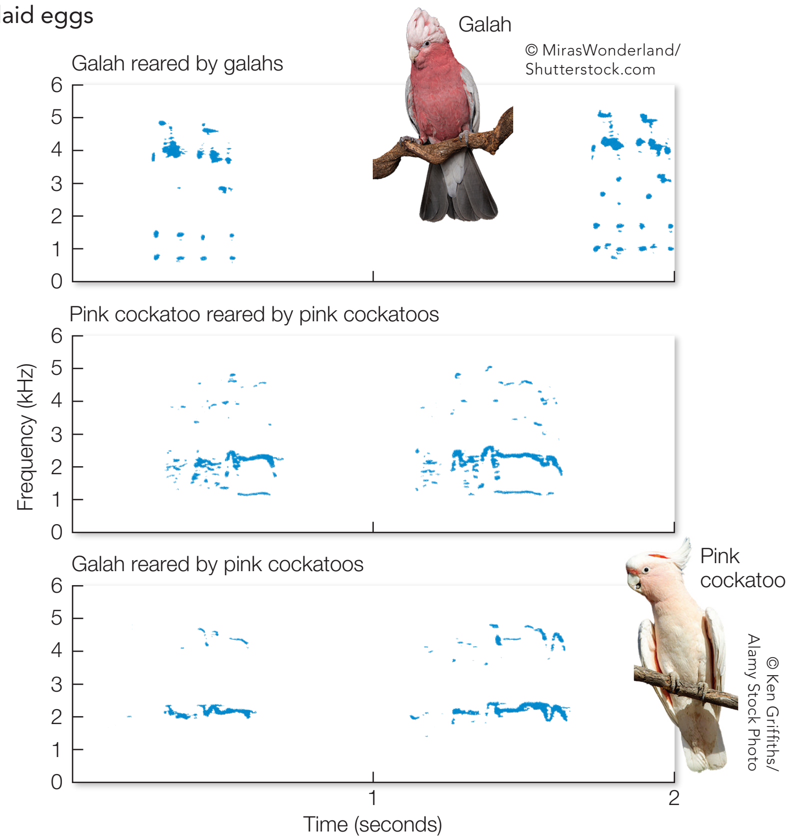
The experiments with isolated white-crowned sparrows exposed to recorded songs in laboratory cages led Marler to summarize the path of song development in this species (see Figure 2.3). At a very early age, the white-crowned sparrow's still immature brain is able to selectively store information about the sounds made by singing white-crowned sparrows while ignoring other species' songs. When the bird begins to sing months later, it accesses the memory that it stored earlier. By listening to its own rudimentary songs and comparing those sounds against its memories of the full song that it had heard, the maturing bird is able to slowly shape its own songs to match its memory. With repeated practice, the bird assembles and crystallizes a full song of its own, which it can then sing for the rest of its life.

The ability of male white-crowned sparrows to learn the songs of other males in their birthplace just by listening to them sing provides a plausible proximate explanation for how males come to sing a particular dialect of their species' full song. However, sometimes observers have heard wild white-crowned sparrows singing songs like those of other species. Such interspecific song learning also occurs occasionally in nature when one species tutors another (**BOX 2.2**). These rare exceptions

BOX 2.2 **EXPLORING BEHAVIOR BY INTERPRETING DATA**

Song learning in birds adopted by another species

A natural experiment occurred in Australian woodlands when galahs (*Eolophus roseicapilla*, a species of parrot) laid eggs in tree-hole nests that were stolen from them by pink cockatoos (another parrot species, *Lophochroa leadbeateri*), which then became unwitting foster parents for baby galahs. Listen to galahs and pink cockatoos calling. The young cockatoo-reared galahs produced begging and alarm calls that were identical to those produced by galahs cared for by their genetic parents. However, the adopted galahs eventually produced contact calls (used to promote flock cohesion) very much like those of their adoptive cockatoo parents, as seen from the spectrograms in the **FIGURE** (Rowley and Chapman 1986).



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Spectrograms of contact calls of two parrot species. The top panel shows the contact call of a galah reared by galahs; the middle panel shows the call of a pink cockatoo reared by cockatoos; the bottom panel shows the call of a galah reared by pink cockatoo foster parents. (After I. Rowley and G. Chapman. 1986. *Behaviour* 96: 1–16.)

Thinking Outside the Box

What can we make of these calls? If we were told that galah begging and alarm calls have a strong genetic basis, whereas contact calls are largely environmentally determined, what would we think? Why? But it does make sense to claim that the alarm calls of the adopted galahs and their cockatoo foster parents are different as a result of genetic differences between them. Why? What other behavioral differences are the result of differences between the social environment of the adopted galahs and that of certain other individuals? Are there other cases in nature where this type of interspecific vocal learning could occur?

led Luis Baptista to wonder whether some other factor, in addition to acoustic experience, might influence song development in white-crowned sparrows. One such factor might be social interactions, a variable excluded from Marler's famous experiments with isolated, hand-reared birds whose laboratory environments offered acoustic stimuli but not the opportunity to interact with living, breathing companions. To test whether social stimuli can influence song learning in white-crowned sparrows (**social interaction hypothesis**), Baptista and Lewis Petrinovich placed young hand-reared birds in cages where they could see and hear living adult white-crowned sparrows or strawberry finches (*Amandava amandava*) in various treatment combinations (Baptista and Petrinovich 1984). Under these circumstances, white-crowned sparrows learned heterospecific song from strawberry finches, even when they could hear, but not see, adult male white-crowned sparrows (**FIGURE 2.4**).

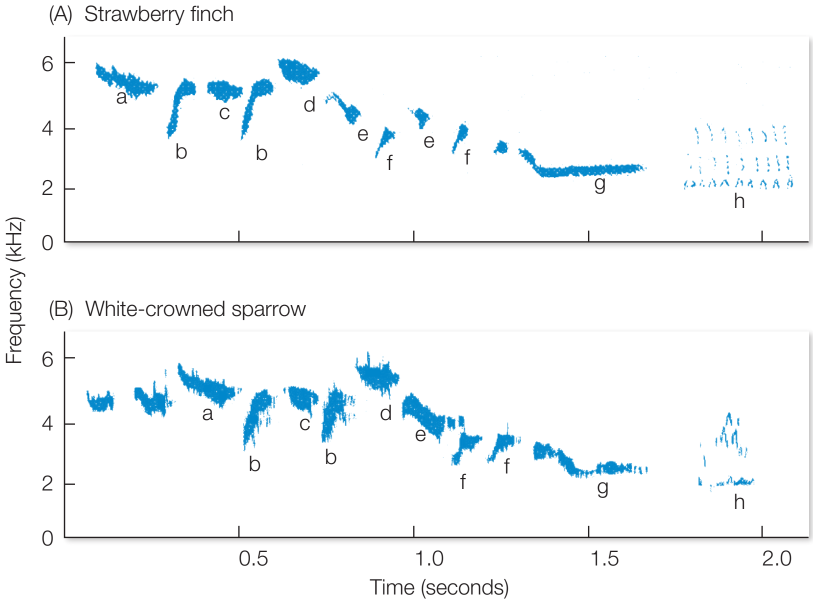


FIGURE 2.4 Social experience influences song development. A male white-crowned sparrow that has been caged next to a strawberry finch will learn the song of its social tutor but will not learn the song of a nearby, but unseen, white-crowned sparrow. (A) The song of a tutor strawberry finch. (B) The song of a white-crowned sparrow caged nearby. The letters beneath the spectrograms label the syllables of the finch song and their counterparts in the song learned by the sparrow. (From L. F. Baptista and L. Petrinovich. 1984. *Anim Behav* 32: 172–181.)

These results show how social acoustic experience can override purely acoustic stimulation during the development of white-crowned sparrow singing behavior, a finding that is not unique to this species. For example, researchers demonstrated in captive zebra finches that social interactions between young birds and their male tutors dramatically enhance vocal learning and neural development in the brain compared with simply hearing song alone without any physical contact (Chen et al. 2016). In a similar experiment in zebra finches using video playback for visual feedback rather than live birds, Samantha Carouso-Peck and Michael Goldstein demonstrated that, in addition to social feedback from male tutors, social feedback from females is also important (Carouso-Peck and Goldstein 2019). The researchers found that juvenile birds that received non-vocal female visual feedback when they sang immature songs learned significantly better and more accurate songs than did controls that received similar visual feedback that was dissociated from when they were singing. Thus, in white-crowned sparrows and other avian species, both social *and* acoustic cues influence song learning, highlighting how the acoustic stimulus and the social interaction hypotheses are not mutually exclusive.

social interaction hypothesis Differences in song are the result of social interactions between a young bird and its tutor.

2.2 Mechanisms of Song Learning

LEARNING OBJECTIVES

- Connect the underlying molecular mechanisms to the neurophysiological changes involved in the process of song learning.
- Describe the song control system and recognize the function of important brain regions such as the HVC in the learning experience.
- Compare the role of brain nuclei in song learning versus song production.

If we want to understand more about the ability of male white-crowned sparrows to learn a dialect of their species' song, we have to go beyond simply identifying those elements of the young bird's social acoustic environment that affect the development of its behavior at a later date. The process of development in a songbird results in the production of a fine-tuned brain, and understanding how a bird's brain works requires another level of analysis, a neurobiological one. For example, what drives a young male to attend to and memorize model songs? Where in a 1-month-old white-crowned sparrow's brain are memories stored of the songs it has listened to? What part of the brain controls the sounds that the bird will produce when it is 5 months old? And how does the young male come to match his song memories with his own initially simpler songs? These proximate questions require us to consider the internal devices that the young male possesses that are capable of using social and acoustic inputs to steer his singing behavior along a particular developmental pathway. And as we will see, considering how, for example, these mechanisms of song learning are shared in different bird species—and even lineages as diverse as birds and mammals—can shed light on why birds and other animals have evolved this ability.

The Genetics of Song Learning

When a young bird is bombarded with sounds produced by singing adults of its own species, these sounds must activate sensory signals that get relayed to particular parts of the brain. In response to these distinctive inputs, some cells in these locations must then alter their biochemistry and connectivity to change the bird's behavior. If we trace the biochemical changes taking place over time in the brain cells of a sparrow, we will eventually find that these are linked to changes in gene expression, where the information encoded in a gene is actually used to produce a gene product, such as a protein or an enzyme. So for example, when a young white-crowned sparrow hears its own species' song, certain patterns of sensory signals generated by acoustic receptors in the bird's ears are relayed to song control centers in the brain where learning occurs. These sensory inputs are believed to alter the activity of certain genes in the set of responding cells, leading to new patterns of protein production and follow-on changes in cell biochemistry that reshape those cells. Once the cells have been altered, the modified song control system can do things that it could not do before the bird was exposed to the song of other males of its species.

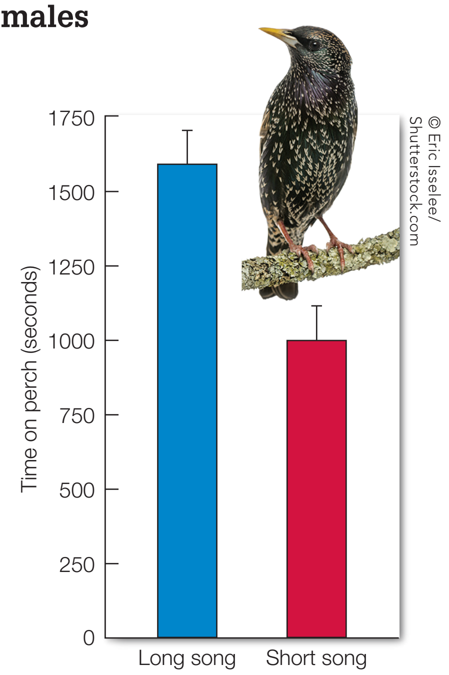
One of the genes that contributes to these changes is called *ZENK*, which codes for a protein called ZENK that is expressed in particular parts of the brain after a bird hears the songs of its own species (Mello and Ribeiro 1998). For birds that listen to these songs but do not sing in response, the protein can be detected only in certain brain structures associated with auditory processing. However, for birds that also respond vocally after hearing their species' song, the ZENK protein is similarly detected in the regions of the brain that control song production. The ZENK protein is a transcription factor (Moorman et al. 2011), meaning it is part of the regulatory apparatus that determines whether information in one or more genes is expressed and to what extent. In the case of bird song, these genes appear to affect which proteins are produced in the connections (synapses) between certain brain cells. Therefore, ZENK and the genes the protein regulates influence how one nerve cell communicates with another, and changes in these connections can alter a bird's behavior.

Studies of the relationship between genes and neural changes illustrate the intimate connection between the developmental and mechanistic levels of analysis of bird song. Changes in genetic activity in response to key environmental stimuli translate into changes in neurophysiological mechanisms that control the learning process, though how these mechanisms actually translate into memory remains an open question. Interestingly, these same mechanisms may be at play in female birds as well when it comes to learning song preferences (**BOX 2.3**). As we will see later in this chapter, an understanding of both developmental and neurophysiological systems is therefore necessary to give us a full account of the proximate causes of behavior.

BOX 2.3 **EXPLORING BEHAVIOR BY INTERPRETING DATA**

Proximate mechanisms underlying song preferences in females

Female European starlings possess the same *ZENK* gene that males do. In the female brain, the ventral caudomedial nidopallium, or NCMv, responds to signals sent to it from auditory neurons that fire when the bird is exposed to sounds, such as those made by singing male starlings. As we can see from the graph in the **FIGURE**, when captive female starlings are given a choice between perching next to a nest box where they can hear a long song versus perching next to another nest box where a shorter song is played, they spend more time at the long-song site.



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Song preferences of female European starlings. In this experiment, song preference was measured by the willingness of females to perch either near a nest box from which a long starling song (lasting about 50 seconds) was played or near one from which a shorter song (lasting about half as long) was played. Bars depict mean ± SE. (After T. Q. Gentner and S. Hulse. 2000. *Anim Behav* 59: 443–458.)

Thinking Outside the Box

What proximate hypothesis could account for the song preferences of female starlings? What prediction can be made about the activity of *ZENK* in the cells that make up the NCMv of female starlings exposed to long versus short songs? How might we test this prediction? What would be the scientific point of collecting the data necessary to evaluate this prediction? Finally, begin to think about *why* females might choose males that sing long songs. For an ultimate explanation for the female preference for long songs, see work by Farrell and colleagues (Farrell et al. 2012).

The Avian Song Control System

Having discussed just a few of the many factors involved in the operation of the avian song-learning mechanism, let's now consider the parts of the brain—the **song control system**—that are essential for learning a song dialect. The brains of white-crowned sparrows and other songbirds feature many anatomically distinct clusters of neurons, or **nuclei**, as well as neural connections that link one nucleus to another into a **neural circuit**. The various components of the brain are made up of cells (neurons) that communicate with one another via bioelectric messages (action potentials) that travel from one neuron to another (through synapses) via elongated extensions of the neurons (axons). Some components of the brain are deeply involved in the memory of songs, while others are necessary for the imitative production of memorized song patterns (Gobes and Bolhuis 2007).

Neurophysiologists have long focused on a region of the brain of white-crowned sparrows and other songbirds called the HVC, sometimes nicknamed the high vocal center. This dense collection of neurons connects to the robust nucleus of the arcopallium (mercifully shortened by anatomists to RA), which in turn is linked with the tracheosyringeal portion of the hypoglossal nucleus (whose less successful acronym is nXIIts). These connected brain elements send messages to the syrinx, the sound-producing structure of birds that is analogous to the larynx in humans. The

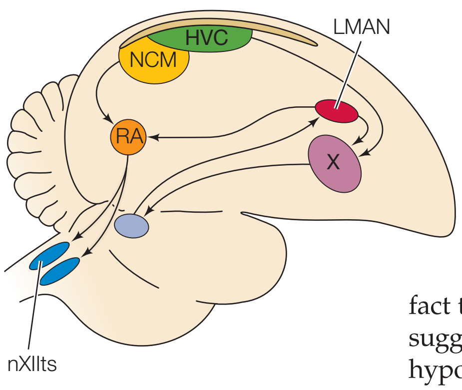
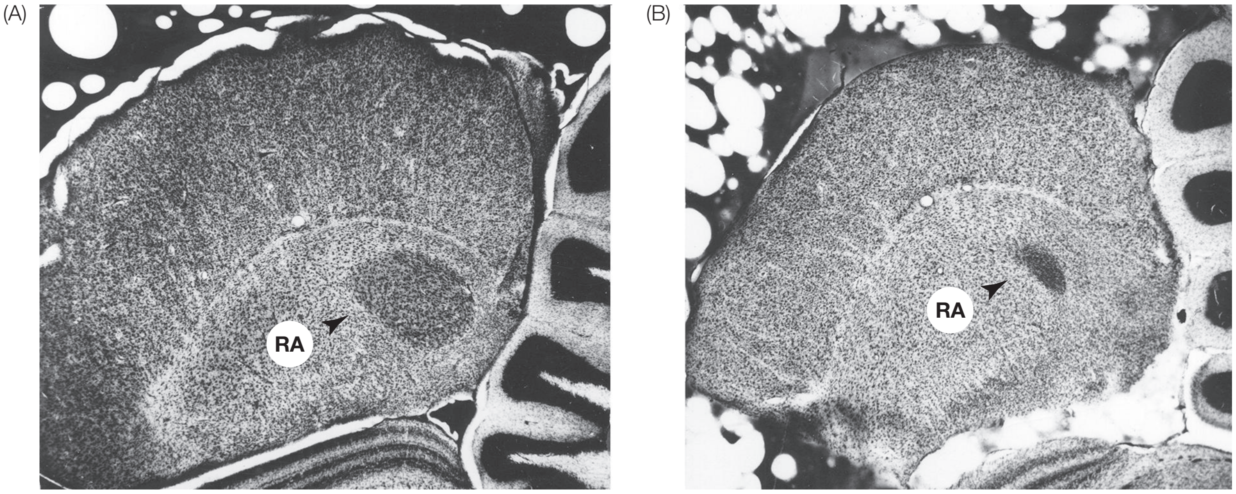


FIGURE 2.5 **Song control system of a typical songbird.** The major components, or nuclei, involved in song production include the robust nucleus of the arcopallium (RA), HVC, the lateral magnocellular nucleus of the anterior nidopallium (LMAN), the caudomedial nidopallium (NCM), and area X (X). Neural pathways carry signals from HVC to the tracheosyringeal portion of the hypoglossal nucleus (nXIIts) and then to the muscles of the song-producing syrinx. Other pathways connect the nuclei, such as LMAN and area X, that are involved in song learning rather than song production. (After E. A. Brenowitz et al. 1997. *J Neurobiol* 33: 495–500.)

fact that HVC and RA can communicate with nXIIts, which connects to the syrinx, suggests that these elements form a system that exerts control over singing behavior, a hypothesis about the neural control of bird song production that has been well tested (**FIGURE 2.5**). For example, if neural messages from RA cause songs to be produced, then the experimental destruction of this center, or surgical cuts through the neural pathway leading from RA to nXIIts, should have devastating effects on a bird's ability to sing, which they do (Catchpole and Slater 2008). If RA plays an important role in controlling bird song, then in species such as the white-crowned sparrow, in which males sing and females do not, RA should be larger in male brains than in female brains, and it is (**FIGURE 2.6**) (Nottebohm and Arnold 1976, Baker et al. 1984, Nealen and Perkel 2000). In addition, RA should also respond to the social environment of the bird. In European starlings (*Sturnus vulgaris*), for example, RA is the only song control nucleus that grows substantially in males that are exposed to high-quality (longer) songs of other males for a week (**FIGURE 2.7**) (Sockman et al. 2009). The suggestion here is that when some males are singing songs that are especially attractive to females, other eavesdropping males in the neighborhood benefit from expanding the motor pathway controlling their song production.

Other brain nuclei appear to be essential for song learning, rather than for song production. One such nucleus is the lateral magnocellular nucleus of the anterior nidopallium (LMAN), which projects to area X, another nucleus in the forebrain that is important for song learning. A team led by Arthur Arnold demonstrated that lesioning LMAN in juvenile male zebra finches disrupted song development, though only temporarily, as adults produced normal songs (Bottjer et al. 1984). Indeed, subsequent lesion studies in zebra finches demonstrated that LMAN plays a role in circuit plasticity necessary for song learning (Scharff and Nottebohm 1991, Braindard and Douple 2000), and chemical inactivation of LMAN in juvenile male zebra finches temporarily reduced song variability, a necessary ingredient for the reinforcement of song learning (Ölveczky et al. 2005).



Photographs courtesy of Fernando Nottebohm and Arthur Arnold

FIGURE 2.6 **Difference in the size of one nucleus of the song control system.** The robust nucleus of the arcopallium (RA) in (A) a male and (B) a female zebra finch.

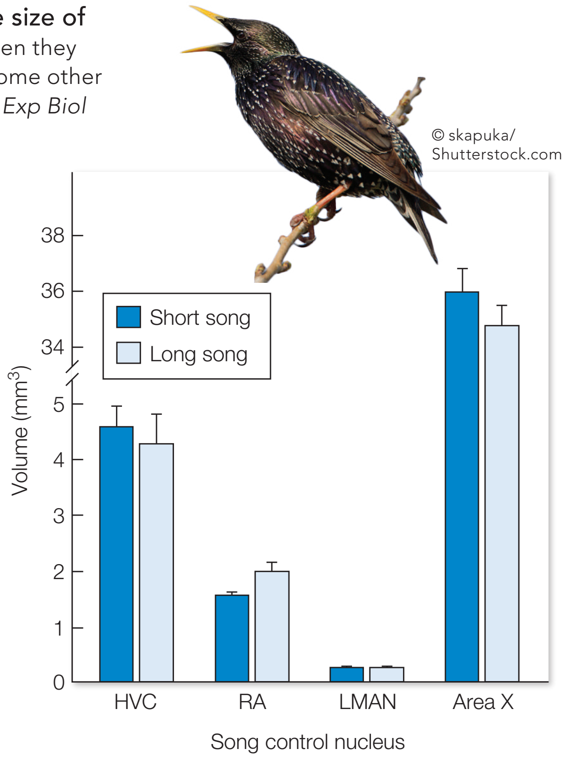


FIGURE 2.7 Song competition in the European starling changes the size of the brain. In males exposed to high-quality (long) songs of other starlings when they are adults, the robust nucleus of the arcopallium (RA) increases in size, unlike some other song control nuclei. Bars depict mean ± SE. (After K. W. Sockman et al. 2009. *J Exp Biol* 212: 2411–2418.)

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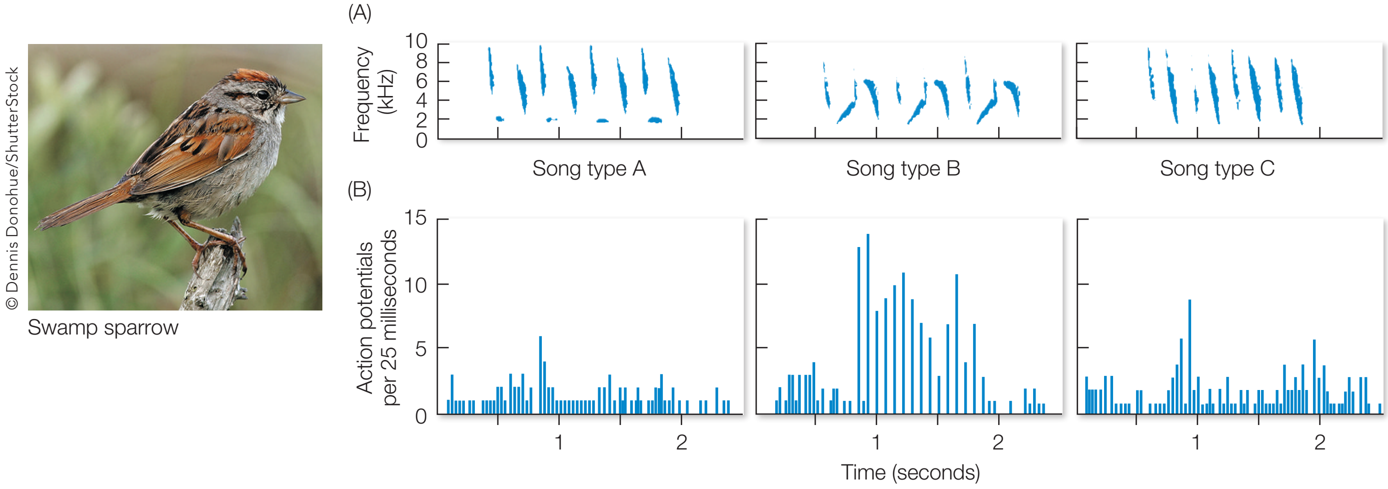
Relatedly, it has been proposed that large amounts of neural tissue are required for male songbirds to learn complex songs. Yet, one could argue instead that the experience of singing a complex song or acquiring a large repertoire causes HVC to expand in response to stimulation of this region of the brain. If this alternative explanation were true, then males reared in isolation should have smaller HVCs than males that learn songs. This experiment has been done with sedge warblers (*Acrocephalus schoenobaenus*), where isolated males had brains that were in no way different from those of males that had learned their songs by listening to the songs of other males (Leitner et al. 2002). Prior to this work, similar results came from a study in which some male marsh wrens (*Cistothorus palustris*) were given a chance to learn a mere handful of songs while another group listened to and learned up to 45 songs (Brenowitz et al. 1995). Thus, in both the warbler and the wren, the male brain develops largely independently of the learning experiences of its owner, suggesting that the production of a large HVC is required for learning, rather than the other way around.

Despite much work at the level of entire brain nuclei, some researchers have also examined how specific neurons within these nuclei contribute to communication between birds. For example, research by Richard Mooney and his coworkers has demonstrated that different song types are presumably stored as discrete memories in different parts of the brain, indicating a clear link between learning and perceptual distinctiveness (Mooney et al. 2001). Male swamp sparrows (*Melospiza Georgiana*) sing 2 to 5 song types, each type consisting of a "syllable" of sound that is repeated over and over in a trill that lasts for a few seconds. If a young male swamp sparrow is to learn a set of song types, he must be able to discriminate among the types being sung by males around him, and later, he must be able to tell the difference between his own song types as he listens to himself sing. One mechanism that could help a young male control his song type output would be a set of specialized neurons in the HVC that respond selectively to a specific song type. Activity in these cells could contribute to a bird's ability to monitor what he is singing so that he could adjust his repertoire in a strategic manner, say for a neighbor versus an intruder. By recording the responses of single cells in a swamp sparrow's HVC to playbacks of that bird's own songs, Mooney and his associates discovered several HVC relay neurons that generated intense volleys of action potentials when receiving neural signals from other cells upon exposure to one song type only (Mooney et al. 2001). Thus, one relay neuron, whose responses to three different song types are shown in **FIGURE 2.8**, produces large numbers of action potentials in a short period when the song stimulus is song type B. This same cell, however, is relatively unresponsive when the stimulus is song type A or C. Swamp sparrows therefore appear to exhibit a special kind of cell that could (in conjunction with many other neurons) help an individual identify which song type it is hearing, the better to select the appropriate response to that signal. Dana Moseley and colleagues further tested this hypothesis in swamp sparrows, showing that single cells in HVC carry information about both the bird's own song as well as the specific song tutor from which that song was learned (Moseley et al. 2017). Thus, specialized song learning depends on connectivity, selectivity, and biochemistry within specific brain regions like HVC.



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Swamp sparrow

FIGURE 2.8 **Single cells and song learning in the swamp sparrow.** (A) Spectrograms of three song types: A, B, and C. (B) When the three songs are presented to a male sparrow, one of his HVC relay neurons reacts substantially only to song type B. Other cells not shown here respond strongly only to song type A, while still others fire rapidly only when song type C is the stimulus. (After R. Mooney et al. 2001. *Proc Natl Acad Sci USA* 98: 12778–12783. © 2001 by the National Academy of Sciences, USA.)

2.3 The Evolution of Song Learning

LEARNING OBJECTIVES

- Link phylogenetic hypotheses and evolutionary history to subsequent conclusions about the evolution of song learning.
- Compare the arguments and evidence for the competing hypotheses of song learning evolution in birds.
- Use a comparative approach to consider the convergent evolution of vocalization in birds and humans.

Although a great deal has been learned about how the song control system of songbirds develops and operates, we still have much to discover about the underlying proximate mechanisms of singing behavior. But even if we had this information in hand, our understanding of singing by white-crowned sparrows would still be incomplete until we dealt with the ultimate causes of the behavior to determine why these mechanisms evolved. Since the complex and elaborate proximate mechanisms underlying bird song did not materialize out of thin air, we can take a comparative approach to ask questions such as, when in the distant past did an ancestral bird species start learning its species-specific song, thereby setting in motion the changes that led eventually to dialect-learning abilities in birds like the white-crowned sparrow?

An Evolutionary History of Bird Song

Interestingly, song learning occurs in members of just 3 of the 23 avian orders: the parrots, the hummingbirds, and the "songbirds," which belong to that portion of the Passeriformes—the oscines—that includes the sparrows, warblers, and more than 5000 other species (**FIGURE 2.9**) (Brenowitz 1991). The other group of Passeriformes is the suboscines, which comprise the non-learning singers. The suboscines and members of most of the remaining 20 orders of birds produce complex vocalizations, but they apparently do not have to learn how to do so, as shown in some cases by experiments in which young birds that were never permitted to hear a song tutor, or were deafened early in life prior to the onset of song practice, nevertheless came to sing normally (Kroodsma and Konishi 1991).

A central question about the historical sequence underlying the evolution of song learning is, did the song-learning ability exhibited by the three groups of birds evolve

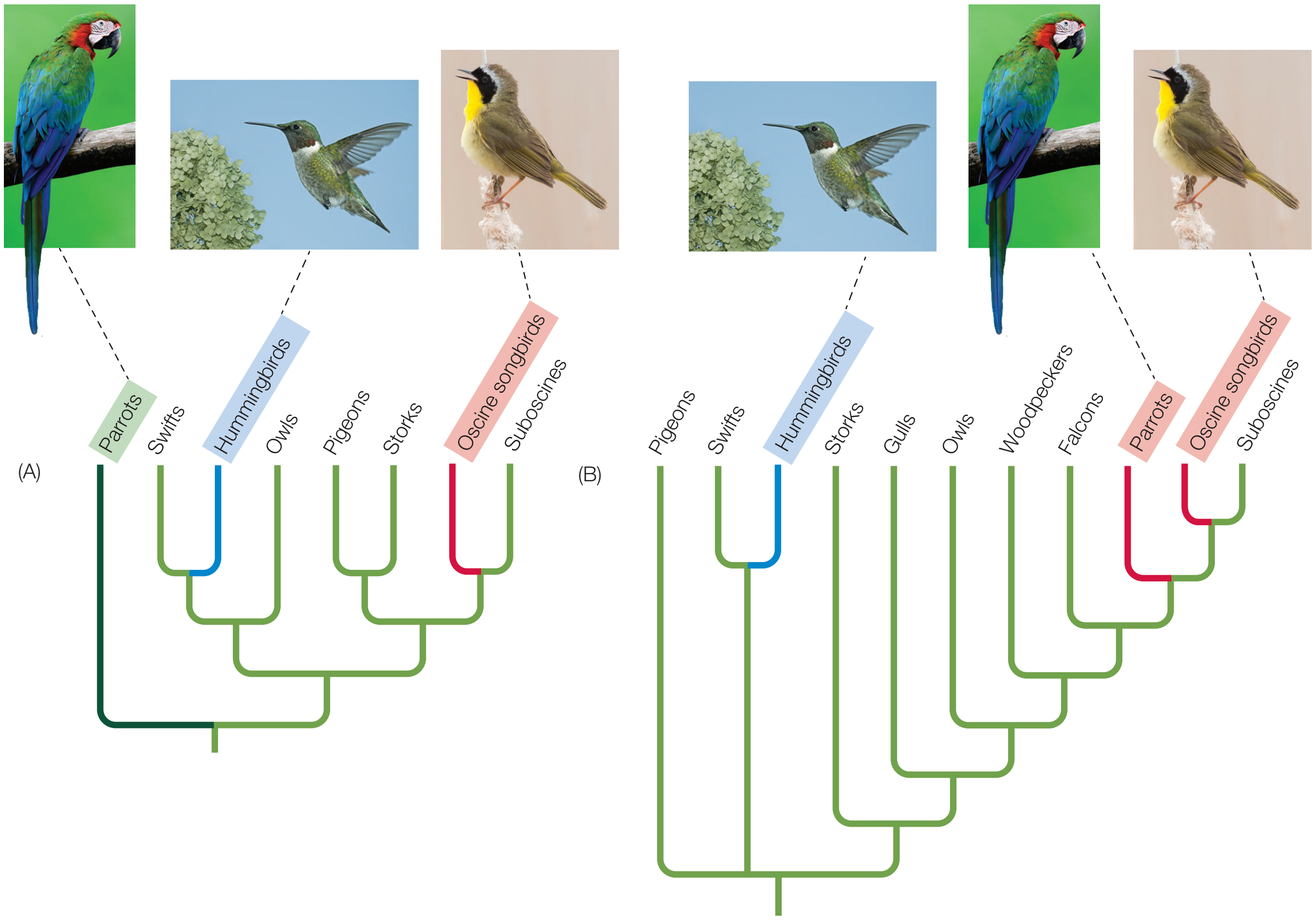

FIGURE 2.9 Two phylogenies of song learning in birds. (A) The bird phylogeny available in 1991 suggests that song learning evolved independently in three different lineages of modern birds: the oscine songbirds, the hummingbirds, and the parrots. (B) A newer phylogeny published in 2008 and confirmed in 2014 suggests that song learning may have evolved just twice, in the ancestor of the oscine songbirds and parrots, which are close relatives, and independently in the hummingbirds. Ancestral state reconstruction is only as good as the phylogeny being used. (A after C. G. Sibley et al. 1988. *Auk* 105: 409–423; B after S. J. Hackett et al. 2008. *Science* 320: 1763–1768.)

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independently or not? Answering this question requires extrapolation back in time from measured characters of extant species to their common ancestors, an approach called **ancestral state reconstruction**. Inferring the behavioral traits of extinct species is no easy task and requires several assumptions. Ancestral state reconstruction—as well as comparative analyses more generally—relies on two important factors: an accurate phylogeny, and reliable character or trait data. It is important to remember that, as we discussed in Chapter 1, phylogenies are simply hypotheses about the evolutionary relationships among species, and as more genetic data become available, the shape of the trees—and therefore the evolutionary hypothesis itself—can change. Birds are one such taxonomic group where the phylogeny has been a source of great debate, which in turn has led to considerable discussion about the phylogenetic relationships among the three orders of song learners.

To illustrate both the power and the challenge associated with ancestral state reconstruction, let's consider the evolutionary history of song learning in birds. If we were to accept a more traditional phylogenetic hypothesis (Figure 2.9A), we would conclude that the nearest living relatives of each of the three song-learning orders do not learn their songs. This conclusion suggests one of two scenarios: either song learning originated three different times in the approximately 65 million