

Lee Alan Dugatkin

third edition

PRINCIPLES OF
ANIMAL
BEHAVIOR





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PRINCIPLES OF ANIMAL BEHAVIOR

THIRD EDITION

Lee Alan Dugatkin

Principles of Animal Behavior

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Lee Alan Dugatkin

UNIVERSITY OF LOUISVILLE



W. W. NORTON & COMPANY | NEW YORK | LONDON

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Book Design: Leelo Märjamaa-Reintal / Rubina Yeh

Design Director: Rubina Yeh

Composition: TSI Graphics

Manufacturing: Courier Kendallville

The text of this book is composed in Fairfield LT with the display set in Meta Plus.

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Printed in the United States of America.

Library of Congress Cataloging-in-Publication Data

Dugatkin, Lee Alan, 1962-

Principles of animal behavior / Lee Alan Dugatkin. -- Third edition.

pages cm

Includes bibliographical references and index.

ISBN 978-0-393-92045-1 (pbk.)

1. Animal behavior. I. Title.

QL751.D748 2013

591.5--dc23

2013004071

W. W. Norton & Company, Inc., 500 Fifth Avenue, New York, NY 10110-0017

wwnorton.com

W. W. Norton & Company Ltd., Castle House, 75/76 Wells Street, London W1T 3QT

1 2 3 4 5 6 7 8 9 0

For Jerram L. Brown, my mentor and friend.



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Preface

Now is an exciting time to be participating in the field of animal behavior—whether as a researcher, an instructor, or a student. In particular, students taking courses in animal behavior today are getting their first glimpses of the field at a dynamic point in its history. The third edition of *Principles of Animal Behavior* aims to show why—by building on the work in the first two editions of this book and adding the latest, best, cutting-edge research being done in animal behavior. Much has happened in the field of animal behavior since the last edition of this book was published in 2009. Recent research findings have given me ample opportunity not only to update and expand on the studies presented in the book but also to reinforce the previous editions' focus on ultimate and proximate causation, as well as the book's unique emphasis on natural selection, learning, and cultural transmission. But there is more to this new edition of *Principles of Animal Behavior* than that.

The third edition greatly expands the discussion of proximate causation, so much so that I have added a new second “primer” chapter on this subject. Chapter 3 is now devoted to hormones, neurobiology, and behavior, while Chapter 4 focuses on molecular genetics, development, and behavior. This discussion of proximate causation introduces a line of inquiry that is sustained throughout the book, alongside ultimate causation. My goal is to weave together the most current knowledge on proximate and ultimate factors and present an integrated approach to animal behavior.

The process of natural selection produces the vast diversity of behavior we see within and across animal species. As such, I delve deeply into the adaptationist approach to animal behavior. In this edition of *Principles of Animal Behavior*, I have also added a great deal of new material on another way to study behavior in an evolutionary context—the phylogenetic approach to the study of behavior. Again, the aim is to produce an integrative overview of animal behavior: The tapestry of animal behavior is created from weaving all of its components into a beautiful whole.

A completely new feature in this edition is the Conservation Connection boxes in Chapters 2–17. Many students taking a course in animal behavior are interested in the course, in part, because they care about the natural world and the creatures that inhabit it. They want to make a difference, and some may even pursue careers in conservation biology. But most animal behavior textbooks barely touch on the subject of conservation biology, or they discuss it only in passing. The Conservation Connection boxes that run throughout the third edition of *Principles of Animal Behavior* give the topic of conservation and animal behavior the space it deserves. Each box focuses on a specific conservation issue related to the chapter topic—such as migration or foraging—and shows how ethology and conservation biology can inform each other in addressing that issue.

From the first edition of this book, my aim has been to explain underlying concepts in a way that is scientifically rigorous but, at the same time, accessible to students. Each chapter in the book provides a sound theoretical and conceptual basis upon which the empirical studies rest. The presentation of theory, sometimes in the form of mathematical models, is not meant to intimidate students but rather to illuminate the wonderful examples of animal behavior in that chapter. My goal has been to produce a book that students will actually enjoy and will recommend to their friends as a “keeper.” I also hope that instructors will find this book useful in their research programs, as well as in their courses.

MAJOR FEATURES

The book is written for both biology and psychology students. Its core strengths are:

- ▶ **A BALANCED TREATMENT OF PROXIMATE AND ULTIMATE FACTORS.** A comprehensive understanding of animal behavior requires a balanced and integrated approach to proximate and ultimate causation. Each of these perspectives informs the other, and both are necessary for an understanding of animal behavior. This book weaves together these two perspectives in ways that other books do not. In the third edition, coverage of proximate factors has been expanded from one chapter to two, allowing for greater depth of material in neurobiology, endocrinology, genetics, and development. Once these topics are thoroughly introduced, examples of proximate and ultimate factors are then integrated into every chapter that follows, reinforcing how modern ethologists study behavior.
- ▶ **LEARNING AND CULTURAL TRANSMISSION PRESENTED ALONGSIDE NATURAL SELECTION AND PHYLOGENY.** This book has always been distinctive in that it integrates learning, cultural transmission, natural selection, and phylogeny throughout the book, bringing together perspectives and research from various subdisciplines in biology, psychology, and anthropology. In recent years, these topics have only become more important to the study of animal behavior. The third edition’s coverage of them has been expanded to reflect this.

- ▶ **AN EXTENSIVE DISCUSSION OF PHYLOGENY.** Darwin spoke of two “great laws”: one centered on natural selection and the other on phylogeny. An emphasis on phylogeny has become more evident in animal behavior research in the last few years, so this edition delves more deeply into the role that phylogeny plays in understanding fundamental issues in animal behavior. Chapter 2 provides an overview of phylogenetic approaches to ethology, including a detailed description of how to build a phylogenetic tree, and later chapters include comprehensive discussions of the phylogeny of specific animal behaviors, including learning, parental care, cooperation, foraging, migratory behavior, and play.

- ▶ **A THOROUGHLY UPDATED ART PROGRAM.** The art program in this book has always included extensive data graphics, as well as photographs that convey the beauty of the natural world. But students often struggle to interpret the graphical representations of data that are so widely used for reporting results across the sciences. The third edition’s art program therefore has been updated to include a new element—extensive bubble captions that help students identify and interpret information conveyed in the figure.

- ▶ **NEW CONSERVATION CONNECTION BOXES.** Increasingly, conservation biologists and environmental scientists are using animal behavior research to maintain and improve ecosystems around the world. Chapters 2–17 in this book now each include a Conservation Connection box that describes both a current research inquiry and an application of that inquiry in nature.

- ▶ **EXTENSIVE VIDEO CLIPS OF ANIMAL BEHAVIOR.** To illustrate animal behavior in its entirety and to show students the behaviors about which they are learning, the text includes hundreds of beautiful photos and line drawings. But students in the twenty-first century have the opportunity to *see* animal behavior in action through video, as well as print. That is why, in addition to the photos and line art in the text, we provide a collection of over 200 wonderful videos—from the BBC, the Cornell Lab of Ornithology, and researchers cited in the book—that capture the beauty of studying animal behavior.

These clips are offered through two resources, the Norton Animal Behavior DVD, which includes descriptions of each clip and references to the book, and 60 new video clips, which are on the Web at wwnorton.com/college/biology/animalbehavior. Each of these clips is accompanied by assignable quizzes that test students’ grasp of core concepts, as well as their ability to analyze examples of animal behavior.

INSTRUCTOR RESOURCES

THE NORTON ANIMAL BEHAVIOR DVD



Available to instructors who adopt *Principles of Animal Behavior*, Third Edition. A resource of 200 video clips, accompanied by a booklet written by Jim Hare of the University of Manitoba, providing short descriptions of each clip. The footage is drawn from three sources:

1. **RESEARCHERS CITED IN THE TEXT.** Numerous adopters of the first and second editions of this book expressed a desire to show their students the studies described in the text. Many researchers generously provided their lab and field videos to make this desire a reality.
2. **BBC.** Most people who are familiar with the BBC's offerings rank their collection of animal behavior videos as among the best in the world. In reviewing the clips that are included on *The Norton Animal Behavior DVD*, I am inclined to agree. We are fortunate to be able to offer so many BBC video clips of animal behavior in this book.
3. **CORNELL LIBRARY OF ORNITHOLOGY.** The Cornell Library of Ornithology has an unparalleled collection of footage done by animal behavior researchers. The quality of both the production and the science in the CLO's collection is remarkable.

WEB-BASED VIDEO QUIZZES

Sixty new video clips, obtained from researchers around the world, serve as the basis to test students' ability to analyze examples of animal behavior and their mastery of core concepts. Students watch each clip and answer up to five questions on the specific behavior being illustrated or on the underlying theoretical concept being demonstrated. Quiz results report to an instructor grade book, making them easy to assign and grade.

All 60 clips and quiz questions have been converted to PowerPoint format for use in lecture as clicker questions.

INSTRUCTOR'S MANUAL

Ryan Earley of the University of Alabama has updated the *Instructor's Manual* to reflect changes in the third edition of the text. This resource includes in-depth answers to the end-of-chapter discussion questions in the text. It also includes a bank of multiple-choice questions, as well as review and challenge questions, from which instructors can draw when creating tests. The IM is available for download at wwnorton.com/books/Principles-of-Animal-Behavior.

NORTON MEDIA LIBRARY

Digital files of all drawn art and most photographs are available to adopters of the text at wwnorton.com/books/Principles-of-Animal-Behavior.

ACKNOWLEDGMENTS

I wish to thank my gifted editor, Betsy Twitchell, for shaping this third edition. Her editorial skills took the third edition to new heights. I would also like to thank Jack Repcheck, my editor on the first edition of this book, for all the time and effort that he invested in this project, and Michael Wright, who did a great job as editor for the second edition. Beth Ammerman's work as the developmental editor has been nothing short of fantastic. The same holds true for project editor Amy Weintraub's work. My thanks also go to Ryan Earley, who has been involved in all three editions of this book, producing a wonderful *Instructor's Manual* for each edition. I would also like to thank Jim Hare for his outstanding work on *The Norton Animal Behavior DVD* and the Web-based video quizzes. Jim not only selected every clip on the DVD but also wrote useful and succinct descriptions for each clip that will aid instructors in presenting the clips in their lectures. Jim's extensive field experience, and his deep understanding of the conceptual underpinnings of animal behavior, are evident in every description. I also extend my thanks to associate editor extraordinaire, Carson Russell, and production associate, Ashley Polikoff, for improving an already excellent DVD for this edition.

Each of the seventeen chapters in the book ends with an illuminating, in-depth interview with a leader in the field of animal behavior. I am deeply indebted to these seventeen brilliant (and busy) animal behaviorists who took time to allow me to interview them. So I extend a huge thank you on this front to E. O. Wilson, Alan Grafen, Geoffrey Hill, Gene Robinson, Sara Shettleworth, Cecilia Heyes, Anne Houde, Nick Davies, Francis Ratnieks, Kern Reeve, John Krebs, Anne Magurran, Rufus Johnstone, Judy Stamps, Karen Hollis, Marc Bekoff, and Sam Gosling.

The production of the text itself has benefited from the artistic skills of Dartmouth Publishing and the composition skills of TSI Graphics. The keen eyes of my photo editors, Stephanie Romeo and Julie Tesser, have taken the text and brought it to life through the beautiful new photos that they found. Production manager Eric Pier-Hocking and pinch-hitter Sean Mintus deserve thanks for managing the transformation of the manuscript files into a beautiful book and for coordinating the many aspects of the book's production. I am also grateful to Courtney Shaw for her assistance in helping us keep track of all the important details of the project. And all of this—the whole book—might have turned out differently had it not been for my remarkable agent, Susan Rabiner.

Literally dozens of my colleagues have read all or parts of *Principles of Animal Behavior*, and I extend my thanks to them all.

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The manuscript in each edition benefited from these reviewers' close reading and sound advice. Please credit these folks with all that is good about this book, and assign any problems you have to my hand.

Last, special thanks go to my wife Dana, who helped with almost every aspect of this project, and to my son Aaron for being such a special young man, and for keeping me smiling. Also thanks to 2R, who knows who he is.

L.A.D.
January 2013

Principles of Animal Behavior

THIRD EDITION

1



Types of Questions and Levels of Analysis

What Is Behavior?

Three Foundations

- ▶ Natural Selection
- ▶ Individual Learning
- ▶ Cultural Transmission

Conceptual, Theoretical, and Empirical Approaches

- ▶ Conceptual Approaches
- ▶ Theoretical Approaches
- ▶ Empirical Approaches

Interview with Dr. E. O. Wilson

An Overview of What Is to Follow

Principles of Animal Behavior



FIGURE 1.1. American cockroach. Almost everyone is familiar with the American cockroach, often a pest in households around the world. (Photo credit: Bates Littlehales/Animals Animals–Earth Scenes)

grew up in the heart of New York City. One animal that my family and I encountered on a fairly regular basis was the American cockroach (*Periplaneta americana*) (Figure 1.1). Much to my mother’s chagrin, we seemed locked in a never-ending battle with these creatures—a battle that we usually lost. And we probably lost because cockroaches have been subject to this sort of problem—other organisms trying to kill them—for tens of millions of years. As a result, they have evolved an exquisite set of antipredator behaviors, which have had the side effect of making them a thorn in the side of modern apartment dwellers.

As a very young boy, I had, of course, never heard of the **scientific method**—which, according to the Oxford English Dictionary, involves “scientific observation, measurement, and experiment, and the formulation, testing, and modification of hypotheses.” Nevertheless, I was able to draw some inferences and formulate some hypotheses about cockroach behavior by watching my mother put out the bug traps. First, it seemed to me that roaches liked to spend their time in dark places, and second, it appeared that most roaches agreed on what was a good place for roaches to be, as we kept putting the traps out in the same place. These two thoughts on cockroach behavior could easily be developed into the following hypotheses: (1) cockroaches will choose dark places over light places, and (2) roaches will return to the same places over and over, rather than moving randomly through their environment. Of course, as a child, I didn’t formally sit down and generate these hypotheses, and I surely didn’t run the controlled experiments that a scientist studying animal behavior would run to test these ideas, but I was nonetheless dabbling with scientific hypotheses about animal behavior—a field technically known as **ethology**.

Many people think like ethologists: from my mother, who understood roach behavior, to the farmer who has detailed knowledge about pigs, cows, chickens, and other domesticated farm animals. The girl who works to train her dog, and the outdoorsman who, on his camping vacation, searches for some animals and tries to avoid others also think like ethologists. Indeed, humans have always thought and acted like ethologists. If our hunter-gatherer ancestors had not thought like ethologists, and hadn’t, for example, understood the prey they were trying to catch, as well as the behavior of the predators that were trying to catch them, we humans wouldn’t be here today.

The study of animal behavior appears to have been so fundamental to human existence that the earliest cave paintings tended to depict animals. This choice of subject matter was certainly not inevitable—early cave drawings might have focused on any number of things, but apparently understanding something about the other life forms surrounding our ancestors was fundamental enough that they chose animals as the subjects for the earliest art. This focus on animals, and their behaviors, continued as humans began developing other types of art. For example, using artifacts from 4,000-year-old Minoan cultures, Marco Masseti argues that the Minoans had an advanced understanding of some aspects of animal behavior (Masetti, 2000). One fascinating example supporting this claim is a golden pendant from a Cretan cemetery that depicts two wasps transferring food to one another (Figure 1.2). Masseti hypothesizes that this kind of knowledge of insect food-sharing behavior could only have come from people who observed and studied the details of wasp life. A similar sort of argument is offered regarding a beautiful Minoan wall painting of “white antelopes.”



FIGURE 1.2. Art captures animal behavior. This pendant from the Chrysolakkos funeral complex in Crete suggests that some members of the ancient culture had a detailed knowledge of wasp behavior. (From Gianni Dagli Orti/*The Art Archive at Art Resource, NY*)

This painting probably depicts gazelles in the early stages of an aggressive interaction (Figure 1.3), and again it is the sort of art that is associated with an in-depth knowledge of the subject in question (Voultsiadou and Tatolas, 2005).

Spanning the millennia between ancient Cretan civilization and the present, literally thousands of amateur and professional naturalists have made some contribution to the study of animal behavior. These contributions have enabled ethologists to draw on a rich trove of information that has greatly expanded our understanding of animal behavior (Figure 1.4). Aristotle's work on animals, for example, though 2,500 years old, is a veritable treasure chest of ethological tidbits. Indeed, with Aristotle's books, *Physics* and *Natural History of Animals*, the field of natural history was born. In these and other works, Aristotle distinguished among 500 species of birds, mammals, and fish, and he wrote entire tracts on the behavior of animals.

In many ways, a course in animal behavior is where all the other biology and psychology classes that you have sat through up to this point in your academic career come together. Evolution, learning, genetics, molecular biology, development, neurobiology, and endocrinology congeal into one grand subject—animal behavior. The field of ethology is integrative in the true sense of the word, in that it combines the insights of biologists, psychologists, anthropologists, and even mathematicians and economists.

Types of Questions and Levels of Analysis

As you will learn in this book, ethologists have asked questions about almost every conceivable aspect of animal behavior—feeding, mating, fighting, and so on. At a broad level, however, ethologists pose four distinct *types of questions*,

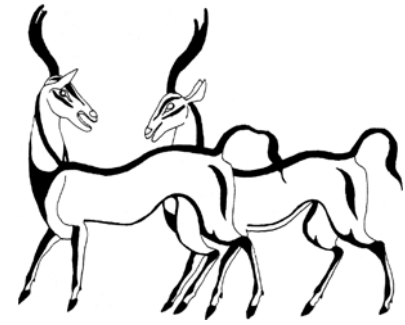


FIGURE 1.3. Minoan wall paintings of “white antelopes.” The drawing may depict a “lateral intimidation” during an aggressive encounter between the animals. (From Masseti. Courtesy Ministry of Culture, Hellenic Republic)



FIGURE 1.4. Fantastic images from a cave. A drawing of a herd of antelope found on the walls of a cave at Dunhuang, China. (Photo credit: Pierre Colombel/Corbis)

which Niko Tinbergen outlined in a classic paper entitled “On the Aims and Methods of Ethology” (N. Tinbergen, 1963). These questions center on:

- ▶ Mechanism—What stimuli elicit behavior? What sort of neurobiological and hormonal changes occur in response to, or in anticipation of, such stimuli?
- ▶ Development—How does behavior change as an animal matures? How does behavior change with the ontogeny, or development, of an organism? How does developmental variation affect behavior later in life?
- ▶ Survival value—How does behavior affect survival and reproduction?
- ▶ Evolutionary history—How does behavior vary as a function of the evolutionary history, or **phylogeny**, of the animal being studied? When did a behavior first appear in the evolutionary history of the species under study?

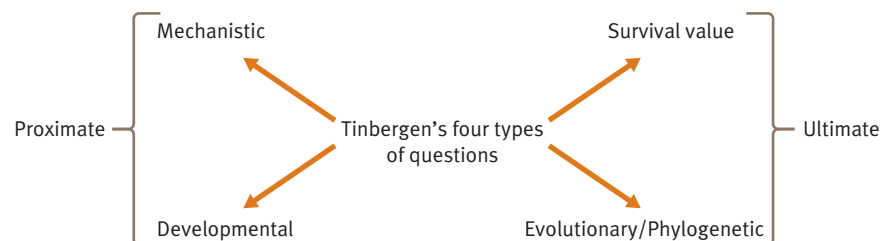
Thousands of studies have been undertaken on each of these four types of questions. Tinbergen’s four questions can be captured in two different kinds of analyses—proximate analysis and ultimate analysis (Alcock and Sherman, 1994; Dewsbury, 1992, 1994; Hailman, 1982; Hogan, 1994; J. Huxley, 1942; Mayr, 1961; Orians, 1962; Reeve and Sherman, 1993). **Proximate analysis** focuses on *immediate causes*, whereas **ultimate analysis** is defined in terms of the *evolutionary forces* that have shaped a trait over time. As such, proximate analysis incorporates Tinbergen’s first two types of questions, whereas ultimate analysis covers the latter two types (Figure 1.5). We could ask, for example, the following questions: Why do some bird chicks peck at red stimuli but not stimuli of other colors? Does red trigger a set of neuronal responses that are not triggered otherwise? If so, exactly which neurons and when? An analysis at the ultimate level, on the other hand, would ask: What selective forces in the birds’ evolutionary past would have favored individuals that had responses to red stimuli? Was the color red associated with a particular food source? Do other closely related bird species show similar responses to red stimuli?

Every chapter of this book examines animal behavior from both proximate and ultimate perspectives.

What Is Behavior?

What do ethologists mean by the word *behavior*? It turns out that this is not a trivial question, and it is one that ethologists have grappled with for some time. Early on, ethologists such as Niko Tinbergen defined behavior as “the total movements made by the intact animal,” but that definition seems far too general, incorporating almost everything an animal does. But if a definition proposed by Tinbergen—who shared a Nobel Prize as a founder of the study of animal behavior—doesn’t work, how can a satisfactory definition be achieved?

FIGURE 1.5. Tinbergen’s four types of questions. A diagrammatic representation of the four different types of questions asked by ethologists. Two of these types of questions are proximate and two are ultimate.



One solution is to survey ethologists to get a discipline-wide view of the way the term *behavior* is employed. In a review paper on definitions of behavior, Daniel Levitis and his colleagues surveyed 174 members of three professional societies that focus on behavior to try and determine what researchers meant when they used the term (Levitis et al., 2009). What they found was a great deal of variation among ethologists on how behavior was defined. Based on their survey results, Levitis and his colleagues argued that many of the definitions that ethologists use can be captured by a few published, but quite dated, definitions already in the literature. These include Tinbergen's 1952 definition of behavior, as well as the following:

- ▶ “Externally visible activity of an animal, in which a coordinated pattern of sensory, motor and associated neural activity responds to changing external or internal conditions” (Beck et al., 1981).
- ▶ “A response to external and internal stimuli, following integration of sensory, neural, endocrine, and effector components. Behavior has a genetic basis, hence is subject to natural selection, and it commonly can be modified through experience” (Starr and Taggart, 1992).
- ▶ “Observable activity of an organism; anything an organism does that involves action and/or response to stimulation” (R. Wallace et al., 1991).
- ▶ “Behavior can be defined as the way an organism responds to stimulation” (D. Davis, 1966).
- ▶ “What an animal does” (Raven and Johnson, 1989).
- ▶ “All observable or otherwise measurable muscular and secretory responses (or lack thereof in some cases) and related phenomena such as changes in blood flow and surface pigments in response to changes in an animal's internal and external environment” (Grier and Burk, 1992).

As with all definitions, each of these has its pluses and minuses. If “behavior has a genetic basis,” as it certainly does in many instances, does that mean that we should exclude all actions that have not been studied from a genetic perspective when we speak of behavior? Surely not. For any of the definitions above we could pose equally strong challenges. That said, I needed to adopt a consistent definition of behavior in this book. I chose one that is a slight modification of a suggestion by Levitis and his colleagues—namely, that behavior is the coordinated responses of whole living organisms to internal and/or external stimuli. This definition is appropriate for a number of reasons (all of which are somewhat subjective): (1) it seems to capture what most modern ethologists and behavioral ecologists mean when they use the term behavior, (2) it works fairly well for the behaviors covered in detail in Chapters 6–17 of this book, and (3) it makes an important distinction between organism and organ. What this third point means is that, as Levitis and his colleagues note, sweating in response to increasing body temperature is not generally thought of as a behavior per se. But when an animal moves to the shade in response to heat and its own sweating, most ethologists would agree that this is a behavioral response.

Three Foundations

Incredible tales and fascinating natural history make a textbook on animal behavior different from a textbook on organic chemistry or molecular genetics. What links animal behavior to all scientific endeavors, however, is a structured system for developing and testing hypotheses and a bedrock set of foundations on

which such hypotheses can be built. Throughout this book, the force of natural selection, the ability of animals to learn, and the power of transmitting learned information to others (cultural transmission) will serve as the foundations upon which we build our approach to ethology.

In his classic book, *On the Origin of Species*—a text widely regarded as the most important biology book ever written—Charles Darwin laid out general arguments for how evolutionary change has shaped the diversity of life and how the primary engine of that change is a process that he dubbed **natural selection** (Darwin, 1859). In a nutshell, Darwin argued that any trait that provided an animal with some sort of reproductive advantage over others in its population would be favored by natural selection. Natural selection is, then, the process whereby traits that confer the highest relative reproductive success on their bearers and that are heritable—that is, can be passed down across generations—increase in frequency over generations.

Whereas natural selection changes the frequency of different behaviors over the course of many generations, **individual learning** can alter the frequency of behaviors displayed within the lifetime of an organism. Animals learn about everything from food and shelter to predators and familial relationships. If we study how learning affects behavior *within the lifetime* of an organism, we are studying learning from a proximate perspective. If we study how natural selection affects the *ability* of animals to learn, we are approaching learning from an ultimate perspective. Later in this chapter, an example is used from a study on learning and foraging (feeding) behavior in grasshoppers. When we ask what sort of cues grasshoppers use to learn where to forage, we are addressing learning from a proximate perspective. When we examine how a grasshopper's learning about food sources affects its reproductive success, we are studying learning from an ultimate perspective. Both approaches can shed light on animal behavior, and this book employs both of these complementary approaches to learning throughout.

Cultural transmission also affects the type of behavior animals exhibit and the frequency with which behaviors occur. While definitions vary across disciplines, this book uses the term *cultural transmission* to refer to situations in which animals learn something by copying the behavior of others, through what is typically referred to as **social learning**. Cultural transmission can allow newly acquired traits to spread through populations at a very quick rate, as well as permit the rapid transmission of information across generations. As with individual learning, natural selection can also act on animals' ability to transmit, acquire, and act on culturally transmitted information.

NATURAL SELECTION

Darwin recognized that his theory of natural selection applied to behavioral traits as well as morphological, anatomical, and developmental traits. Indeed, morphological traits are often the physical underpinning for the production of behavior, so morphology and behavior are linked at many levels. More detail about this linkage is provided below and throughout the book, but for the moment, the key point is that Darwin's ideas on evolution, natural selection, and behavior were revolutionary, and ethology today would look very different were it not for the ideas that Darwin set forth in *On the Origin of Species*. A fascinating example involving mating and parasites in Hawaiian crickets illustrates how natural selection operates on animal behavior in the wild.

In the evening on the Hawaiian Islands, male crickets sing to attract their mates. This “singing” results when the male cricket rapidly moves the smooth scraper on the front of one wing against the serrated file on the other wing. Females cue in on male songs, and they typically will not mate with males that do not produce songs. But as with many behavioral traits associated with attracting mates, male singing is not cost free. Just as females are attracted to male song, so are potentially very dangerous parasites (Zuk and Kolluru, 1998).

Marlene Zuk and her colleagues have been studying this trade-off in male song production—between attracting females and attracting parasites—in the field cricket *Teleogryllus oceanicus* (Zuk et al., 2006). These crickets are parasitized by the fly *Ormia ochracea*, a species that is attracted to the singing male *T. oceanicus*. If a fly finds a singing cricket, it lays its eggs on the cricket, and then the fly larvae burrow their way into the cricket and grow. When the flies emerge from the larvae, they kill the cricket.

Parasitic flies are found on three of the Hawaiian Islands—Oahu, Hawaii, and Kauai—that are also home to *T. oceanicus*. The flies are most prevalent on the island of Kauai, where 30 percent of the crickets are parasitized. Zuk and her team have been studying the relationship between crickets and parasitic flies since 1991, and over time, they noted what appeared to be a significant decline in the cricket population on Kauai. Over the years, they heard fewer and fewer singing males on this island, and they assumed that the parasitic fly was slowly causing the extinction of *T. oceanicus* on Kauai. Indeed, in 2003 they heard only a single male singing. Nonetheless, when they got down on their hands and knees and searched for crickets, Zuk and her team found *T. oceanicus* in abundance. How can we explain these seemingly contradictory findings?

What Zuk and her team found was that most of the males on Kauai had modified wings that were not capable of producing song (Figure 1.6). The file section of the wings of these Kauai males (called “flatwing males”) was significantly reduced compared to that of normal males, and its position on

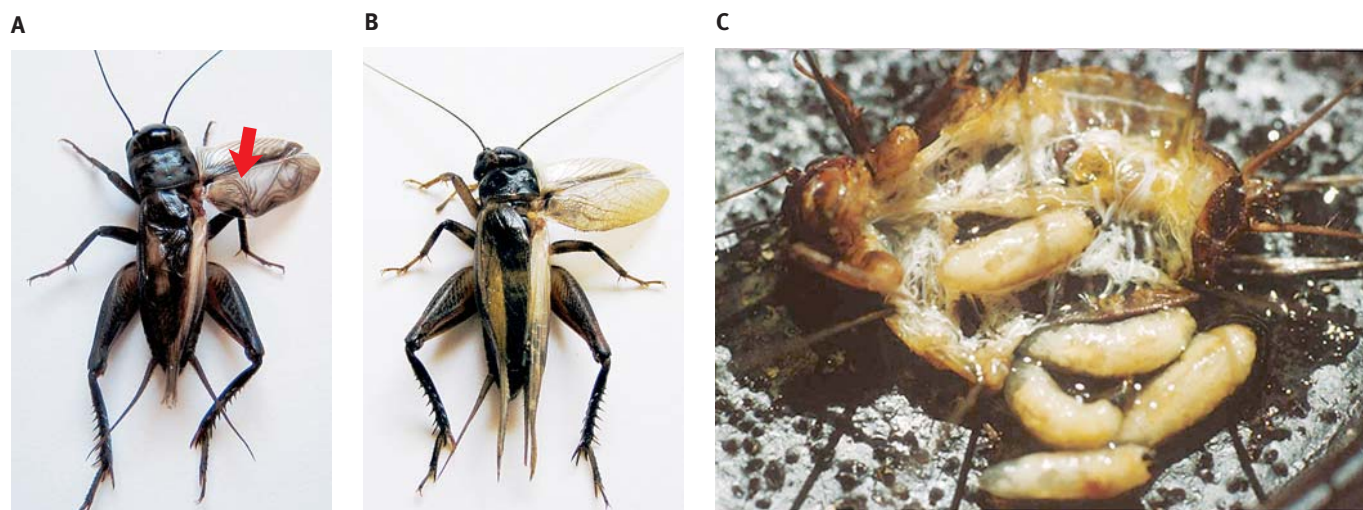


FIGURE 1.6. Natural selection in crickets. Marlene Zuk and her colleagues have been studying the field cricket *Teleogryllus oceanicus*. Pictured here are (A) a field cricket with normal wings (the arrow points to the file on its outstretched wing); (B) a field cricket with flat wings, in which the file section on the outstretched wing has evolved to a much smaller size and is visible only under a high-powered microscope; and (C) fly larvae in a parasitized cricket. (Photo credits: Robin Tinghitella)