8TH EDITION

HOW HUMANS EVOLVED

Robert Boyd   Joan B. Silk

EIGHTH EDITION

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Arizona State University

W. W. NORTON & COMPANY
NEW YORK • LONDON

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Composition: Brad Walrod/Kenoza Type, Inc.
Illustrations: Imagineering Art
Manufacturing: Transcontinental

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Library of Congress Cataloging-in-Publication Data

Names: Boyd, Robert (Professor of cultural evolution), author. | Silk, Joan B., author.
Title: How humans evolved / Robert Boyd and Joan B. Silk, Arizona State University.
Description: Eighth edition. | New York : W. W. Norton & Company, [2018] | Includes bibliographical references and index.
Identifiers: LCCN 2017021652 | **ISBN 9780393603453 (pbk.)**
Subjects: LCSH: Human evolution.
Classification: LCC GN281 .B66 2018 | DDC 599.93/8—dc23 LC record available at https://lccn.loc.gov/2017021652

W. W. Norton & Company, Inc., 500 Fifth Avenue, New York, NY 10110
wwnorton.com
W. W. Norton & Company Ltd., 15 Carlisle Street, London W1D 3BS

1 2 3 4 5 6 7 8 9 0

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Part Three: The History of the Human Lineage

PREFACE

How Humans Evolved focuses on the processes that have shaped human evolution. This approach reflects our training and research interests. As anthropologists, we are interested in the evolutionary history of our own species, *Homo sapiens*, and the diversity of contemporary human societies. As evolutionary biologists, we study how evolution works to shape the natural world. In this book, we integrate these two perspectives. We use current theoretical and empirical work in evolutionary theory, population genetics, and behavioral ecology to interpret human evolutionary history. We describe the changes that have occurred as the human lineage has evolved, and we consider why these changes may have happened. By focusing on the processes that generate change, create adaptations, and shape bodies and behavior, we try to give life to the creatures that left the bones and made the artifacts that paleontologists and archaeologists painstakingly excavate. We also pay serious attention to the role of evolution in shaping contemporary human behavior. There is considerable controversy over evolutionary approaches to human behavior within the social sciences, but we think it is essential to confront these issues clearly and openly. Positive responses to the first seven editions of *How Humans Evolved* tell us that many of our colleagues endorse this approach.

One of the problems in writing a textbook about human evolution is that there is considerable debate on many topics. Evolutionary biologists disagree about how new species are formed and how they should be classified; primatologists argue about whether large primate brains are adaptations to social or ecological challenges and whether reciprocity plays an important role in primate societies; paleontologists disagree about the taxonomic relationships among early hominin species and the emergence of modern humans; and people who study modern humans disagree about the meaning and significance of race, the role of culture in shaping human behavior and psychology, the adaptive significance of many aspects of modern human behavior, and several other things. Sometimes multiple interpretations of the same data can be defended; in other cases, the facts seem contradictory. Textbook writers can confront this kind of uncertainty in two ways. They can weigh the evidence, present the ideas that best fit the available evidence, and ignore the alternatives. Or they can present opposing ideas, evaluate the logic underlying each idea, and explain how existing data support each of the positions. We chose the second alternative, at the risk of complicating the text and frustrating readers looking for simple answers. We made this choice because we believe that this approach is essential for understanding how science works. Students need to see how theories are developed, how data are accumulated, and how theory and data interact to shape our ideas about how the world works. We hope that students remember this long after they have forgotten many of the facts that they will learn in this book.

We wrote this book with undergraduates in mind and have designed several features to help students use the book effectively. We have retained the "key idea" statements (now printed in blue-green type), and we recommend that students use these key ideas to keep track of important concepts and facts and to structure their review of the material. Important terms that may be unfamiliar are set in boldface type when they first appear. Readers can find definitions for these terms in the Glossary. Discussion questions appear at the end of each chapter. These questions are meant to help students synthesize material presented in the text. Some of the questions are designed to help students review factual material, but most are intended to help students think about the processes or theoretical principles they have learned. Some questions are open-ended and meant to encourage students to apply their own values and judgment to the material presented in the text. Students tell us that they find these questions useful as they attempt to master the material and prepare for exams. The list of references for further reading at the end of each chapter provides a starting point for students who want to delve more deeply into the material covered in that chapter.

The book is richly illustrated with photographs, diagrams, figures, and graphs. These illustrations provide visual information to complement the text. For some subjects, a picture is clearly worth a thousand words—no amount of description can enable students to conjure up an image of an aye-aye or appreciate how much more similar the australopith pelvis is to the modern human pelvis than to the chimpanzee pelvis. The diagrams of evolutionary processes that appear in Part One are designed to help students visualize how natural selection works. The figures depicting the hominin fossils are drawn to scale, so each is presented in the same orientation and to the same scale. This should help students compare one hominin specimen with another. We have often been advised that you cannot put graphs in an undergraduate textbook, but we think that the graphs help students understand the evidence more fully. For us, it is easier to remember data that are portrayed graphically than to recall verbal descriptions of results.

New in the Eighth Edition

The study of human evolution is a dynamic field. No sooner do we complete one edition of this book than researchers make new discoveries that fundamentally change our view of human evolution. New developments in human evolutionary studies require regular updates of the textbook. Although we have made several changes throughout the book to reflect new findings, clarify concepts, and improve the flow of the text, readers familiar with prior editions will find the most substantive changes in Part Three, "The History of the Human Lineage."

In Part Three, we reorganized the treatment of early *Homo*, the development of stone tools, and the evolution of the distinctive human life history. Although the earliest stone tools now date to 3.3 million years ago (Ma), such tools don't become common in the archaeological record until about 2 Ma. These findings, combined with new analyses of brain size in early *Homo* species, suggest that flaked stone tools became a crucial part of human adaptation with the advent of early *Homo*, which also coincided with the evolution of larger brains and a slower life history. As usual, new fossil and archaeological finds have been incorporated into Part Three. For example, Chapter 10 discusses the tools found at Lomekwi and Chapter 11 includes a description of the morphology of *Homo naledi*. Chapter 13 has been extensively revised to reflect new insights from analyses of genetic data. We now have complete genomes for several late Pleistocene modern human fossils dating from 35 thousand years ago (ka) to 45 ka. In addition, we have complete sequences for a large, worldwide sample of living people, and these data provide rich information about the expansion of modern humans across the globe and about their interactions with Neanderthals and Denisovans. It now seems that modern humans interbred with these earlier hominins for thousands of years. New archaeological evidence suggests that the spread of modern humans across Eurasia may have occurred in several waves, perhaps beginning as early as 120 ka.

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Prepared by Ashley Hurst, University of Texas—San Antonio.

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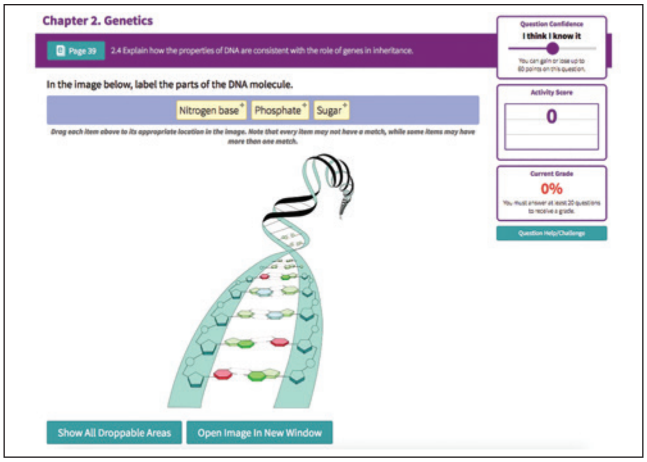

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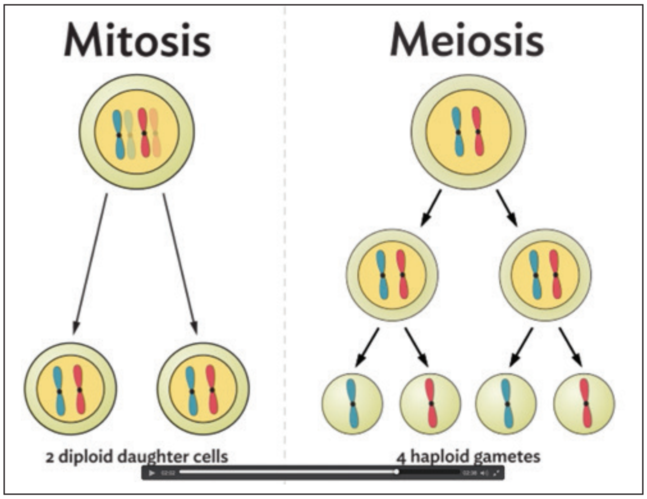

Physical Anthropology Animations and Videos

Animations of key concepts from the text, as well as curated real-world videos, are available to instructors and students in several ways, including via the coursepack, in the Interactive Instructor's Guide, and at **digital.wwnorton.com/howhumans8**. These features are brief, easy to use, and great for explaining and helping students better visualize and understand concepts, either in class or as a self-study tool.

Coursepacks

Prepared by Tracy Betsinger, State University of New York at Oneonta.

Available at no cost to professors and students, Norton Coursepacks for online or hybrid courses are available in a variety of formats, including Blackboard, WebCT, Moodle, Canvas, and D2L. With just a simple download from the Norton instructor website, instructors can bring high-quality Norton digital media into a new or existing online course (no extra student passwords required). Content includes the full suite of animations and streaming videos that accompanies the text, available here to integrate into your lectures or for students to view outside of class. Engaging visual questions are specially designed for the distance or blended learning environment. Norton test banks and chapter quizzes are also all available for your use, and vocabulary flash cards are included for student self-study. Additionally, if InQuizitive will be in use, contact your local Norton representative to learn about our easy integration options for a single-sign-on and gradebook-reporting experience with your Norton Coursepack. All visual materials in Norton Coursepacks are ADA compliant.

PowerPoint Package

Prepared by Melissa Torpey, University of North Carolina—Wilmington.

The PowerPoint slides for this edition retain their richly illustrated format and extensive lecture notes. Designed to cover the core material in a highly visual way by using photography and art from the text, these PowerPoint slides bring the concepts in each chapter to life with additional photography and design. These slides also include a lecture script in the notes field. Download these resources from wwnorton.com/instructors or from the Interactive Instructor's Guide.

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To help you improve your class, JPEGs of all the art and photographs are available for download from the Norton instructor website.

Instructor's Manual

Prepared by Susan Kirkpatrick Smith, Kennesaw State University.

The Instructor's Manual provides an overview of each chapter's key concepts with additional explanation for topics that students may find more challenging as well as answers to the end-of-chapter Study Questions found in the text. The Instructor's Manual is available for download at the Norton instructor website.

Test Bank

Prepared by Greg Laden, Century College.

The Test Bank offers teachers approximately 60 multiple-choice and essay questions (organized by difficulty level and topic) for each chapter. Every question is keyed according to Bloom's knowledge types and the corresponding learning objective from the textbook. The Test Bank is available in downloadable formats in the Exam View Assessment Suite, as a PDF, and in formats compatible with MS Word and other word processors.

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Acknowledgments

Over the last 25 years, many of our colleagues have provided new information, helpful comments, and critical perspectives that have enriched this book. We are grateful for all those who have responded to our requests for photographs, clarifications, references, and opinions. For the Eighth Edition, we are grateful to our ASU colleagues, particularly William Kimbel, Kaye Reed, and Gary Schwartz, for their generous help with revisions of Part Three. We also thank Melissa Wilson Sayers and Luca Pagani for their assistance with material in Chapter 13. For the Seventh Edition we thank Curtis Marean for reviewing Chapter 13 and Kim Hill for reading Chapter 16. For the Sixth Edition, we thank Christopher Kirk for reviewing Chapter 5, Leanne Nash for reviewing Chapters 4 and 8, Roberto Delgano for reviewing Chapters 6 and 7, and Carol Ward and Jeremy DeSilva for help with Chapter 9. For the Fourth Edition, Laura MacLatchy provided help with the Miocene apes in Chapter 10, Dan Fessler and David Schmitt gave us access to material for Chapter 16, and Kermyt Anderson dug up original data for figures in Chapter 17. Steven Reznik reviewed our discussion of the rapid evolution of placentas in the minnows he studies and kindly provided an image. Leslie Aiello helped with our discussion of hominin developmental rates. For help with the Third Edition, we thank Carola Borries, Colin Chapman, Richard Klein, Cheryl Knott, Sally McBrearty, Ryne Palombit, Steve Pinker, Karin Stronswold, and Bernard Wood. For help with the Second Edition, we also thank Tom Plummer, Daniel Povinelli, Beverly Strassman, and Patricia Wright. We remain grateful for the help we received for the First Edition from Leslie Aiello, Monique Borgerhoff Mulder, Scott Carroll, Dorothy Cheney, Glenn Conroy, Martin Daly, Robin Dunbar, Lynn Fairbanks, Sandy Harcourt, Kristin Hawkes, Richard Klein, Phyllis Lee, Nancy Levine, Jeff Long, Joseph Manson, Henry McHenry, John Mitani, Jocelyn Peccei, Susan Perry, Steve Pinker, Tom Plummer, Tab Rasmussen, Mark Ridley, Alan Rogers, Robert Seyfarth, Frank Sulloway, Don Symons, Alan Walker, Tim White, and Margo Wilson.

Several people have provided reviews of all or parts of the text and accompanying resource suite. We thank the following: Stephanie Anestis, Thad Bartlett, AnnMarie Beasley, Rene Bobe, Barry Bogin, Doug Broadfield, Bryce Carlson, Joyce Chan, Margaret Clarke, Steve Corbett, Julie Cormack, Douglas Crews, Roberto Delgado, Arthur Durband, Charles Edwards, Donald Gaff, Renee Garcia, Susan Gibson, Peter Gray, Mark Griffin, Corinna Guenther, Sharon Gursky, Kim Hill, Kevin Hunt, Andrew Irvine, Trine Johansen, Andrea Jones, Barbara King, Richard Klein, Sam Kobari, Jeremy Koster, Kristin Krueger, Darrell La Lone, Clark Larsen, Lynette Leidy, Joseph Lorenz, Laura MacLatchy, Lara McCormick, Elizabeth Miller, Shannon Mills, John Mitani, Gilliane Monnier, Peer Moore-Jansen, M. J. Mosher, Martin Muller, Marilyn Norconk, Ann Palkovich, Amanda Wolcott Paskey, James Paterson, Michael Pietrusewsky, Mindy Pitre, Barbara Quimby, Corey Ragsdale, Kristin Rauch, Ulrich Reichard, Laurie Reitsema, Michael Robertson, Stacey Rucas, Michael Schillaci, Eric Schnicter, Liza Shapiro, Beth Shook, Eric Smith, K. Elizabeth Soluri, Craig Stanford, Horst Steklis, Joan Stevenson, Mark Stoneking, Rebecca Storey, Rebecca Stumpf, Roger Sullivan, Yanina Valdos, Timothy Weaver, Elizabeth Weiss, Jill Wenrick, Patricia Wright, and Alexandra Zachwieja. Although we are certain that we have not satisfied all those who read and commented on parts of the book over the years, we have found all the comments helpful as we revised the text.

Richard Klein provided us with many exceptional drawings of fossils that appear in Part Three—an act of generosity that we continue to appreciate. We also give special thanks to Neville Agnew and the Getty Conservation Institute for granting us permission to use images of the Laetoli conservation project for the cover of the Second Edition.

We also acknowledge the thousands of students and dozens of teaching assistants at ASU and UCLA who have used various versions of this material over the years. Student evaluations of the original lecture notes, the first draft of the text, and the first seven editions were helpful as we revised and rewrote various parts of the book. The teaching assistants helped us identify many parts of the text that needed to be clarified, corrected, or reconsidered.

We thank all the people at Norton who helped us produce this book, particularly our current editor, Jake Schindel, and his predecessors, Leo Wiegman, Pete Lesser, Aaron Javsicas, and Eric Svendsen. We are also grateful to the assistant editor, Rachel Goodman, and project editor, Carla Talmadge. We also thank all the other people who saw the book through the production and marketing process, including Sarah Rose Aquilina, Tacy Quinn, Donna Ranieri, Benjamin Reynolds, Bethany Salminen, Megan Schindel, Lissi Sigillo, Katie Sweeney, and Ted Szczepanski.

PROLOGUE

WHY STUDY HUMAN EVOLUTION?

Origin of man now proved—Metaphysics must flourish—He who understand baboon would do more toward metaphysics than Locke.

—Charles Darwin,* M Notebook*, August 1838

In 1838, Charles Darwin discovered the principle of evolution by natural selection and revolutionized our understanding of the living world. Darwin was 28 years old, and it was just two years since he had returned from a five-year voyage around the world as a naturalist on the HMS *Beagle* (**Figure P.1**). Darwin's observations and experiences during the journey had convinced him that biological species change through time and that new species arise by the transformation of existing ones, and he was avidly searching for an explanation of how these processes worked.

In late September of the same year, Darwin read Thomas Malthus's *Essay on the Principle of Population*, in which Malthus (**Figure P.2**) argued that human populations invariably grow until they are limited by starvation, poverty, and disease. Darwin realized that Malthus's logic also applied to the natural world, and this intuition inspired the conception of his theory of evolution by natural selection. In the intervening century and a half, Darwin's theory has been augmented by discoveries in genetics and amplified by studies of the evolution of many types of organisms. It is now the foundation of our understanding of life on Earth.

This book is about human evolution, and we will spend a lot of time explaining how natural selection and other evolutionary processes have shaped the human species. Before we begin, it is important to consider why you should care about this topic. Many of you will be working through this book as a requirement for an undergraduate class in biological anthropology and will read the book in order to earn a good grade. As instructors of a class like this ourselves, we approve of this motive. However, there is a much better reason to care about the processes that have shaped human evolution: Understanding how humans evolved is the key to understanding why people look and behave the way they do.

The profound implications of evolution for our understanding of humankind were apparent to Darwin from the beginning. We know this today because he kept notebooks in which he recorded his private thoughts about various topics. The quotation that begins this prologue is from the *M Notebook*, begun in July 1838, in which Darwin jotted down his ideas about humans, psychology, and the philosophy of science. In the nineteenth century, metaphysics involved the study of the human mind. Thus Darwin was saying that because he believed humans evolved from a creature something like a baboon, it followed that an understanding of the mind of a baboon would contribute more to an understanding of the human mind than would all the works of the great English philosopher John Locke.

Darwin's reasoning was simple. Every species on this planet has arisen through the same evolutionary processes. These processes determine why organisms are the way they are by shaping their morphology, physiology, and behavior. The traits that characterize the human species are the result of the same evolutionary processes that created all other species. If we understand these processes and the conditions under which the human species evolved, then we will have the basis for a scientific understanding of human nature. Trying to comprehend the human mind without an understanding of human evolution is, as Darwin wrote in another notebook that October, "like puzzling at astronomy without mechanics." By this, Darwin meant that his theory of evolution could play the same role in biology and psychology that Isaac Newton's laws of motion had played in astronomy. For thousands of years, stargazers, priests, philosophers, and mathematicians had struggled to understand the motions of the planets without success. Then, in the late 1600s, Newton discovered the laws of mechanics and showed how all the intricacies in the dance of the planets could be explained by the action of a few simple processes (**Figure P.3**).

In the same way, understanding the processes of evolution enables us to account for the stunning sophistication of organic design and the diversity of life and to understand why people are the way they are. As a consequence, understanding how natural selection and other evolutionary processes shaped the human species is relevant to all the academic disciplines that are concerned with human beings. This vast intellectual domain includes medicine, psychology, the social sciences, and even the humanities. Beyond academia, understanding our own evolutionary history can help us answer many questions that confront us in everyday life. Some of these questions are relatively trivial: Why do we sweat when hot or nervous? Why do we crave salt, sugar, and fat, even though large amounts of these substances cause disease (**Figure P.4**)? Why are we better marathon runners than mountain climbers? Other questions are more profound: Why do only women nurse their babies? Why do we grow old and eventually die? Why do people around the world look so different? As you will see, evolutionary theory provides answers or insights about all these questions. Aging, which eventually leads to death, is an evolved characteristic of humans and most other creatures. Understanding how natural selection shapes the life histories of organisms tells us why we are mortal, why our life span is about 70 years, and why other species live shorter lives. In an age of horrific ethnic conflicts and growing respect for multicultural diversity, we are constantly reminded of the variation within the human species. Evolutionary analyses tell us that genetic differences between human groups are relatively minor and that our notions of race and ethnicity are culturally constructed categories, not biological realities.

FIGURE P.1

When this portrait of Charles Darwin was painted, he was about 30 years old. He had just returned from his voyage on the HMS *Beagle* and was still busy organizing his notes, drawings, and vast collections of plants and animals.

FIGURE P.2

Thomas Malthus was the author of *An Essay on the Principle of Population*, a book Charles Darwin read in 1838 that profoundly influenced the development of his theory of evolution by natural selection.

FIGURE P.3

Sir Isaac Newton discovered the laws of celestial mechanics, a body of theory that resolved age-old mysteries about the movements of the planets.

FIGURE P.4

A strong appetite for sugar, fat, and salt may have been adaptive for our ancestors, who had little access to these foods. We have inherited these appetites and now have easy access to sugar, fat, and salt. As a consequence, many of us suffer from obesity, high blood pressure, diabetes, and heart disease.

All these questions deal with the evolution of the human body. However, understanding evolution is also an important part of our understanding of human behavior and the human mind. The claim that understanding evolution will help us understand contemporary human behavior is much more controversial than the claim that it will help us understand how human bodies work. But it should not be. The human brain is an evolved organ of great complexity, just like the endocrine system, the nervous system, and all the other components of the human body that regulate our behavior. Understanding evolution helps us understand our mind and behavior because evolutionary processes forged the brain that controls human behavior, just as they forged the brain of the chimpanzee and the salamander.

One of the great debates in Western thought centers on the essence of human nature. One view is that people are basically honest, generous, and cooperative creatures who are corrupted by an immoral economic and social order. The opposing view is that we are fundamentally amoral, egocentric beings whose antisocial impulses are held in check by social pressures. This question turns up everywhere. Some people believe that children are little barbarians who are civilized only through sustained parental effort; others think that children are gentle beings who are socialized into competitiveness and violence by exposure to negative influences such as toy guns and violent TV programs (**Figure P.5**). The same dichotomy underpins much political and economic thought. Economists believe that people are rational and selfish, but other social scientists, particularly anthropologists and sociologists, question and sometimes reject this assumption. We can raise an endless list of interesting questions about human nature: Does the fact that, in most societies, women rear children and men make war mean that men and women differ in their innate predispositions? Why do men typically find younger women attractive? Why do some people neglect and abuse their children, whereas others adopt and lovingly raise children who are not their own?

FIGURE P.5

One of the great debates in Western thought focuses on the essential elements of human nature. Are people basically moral beings corrupted by society or fundamentally amoral creatures socialized by cultural conventions, social strictures, and religious beliefs?

Understanding human evolution does not reveal the answers to all these questions or even provide a complete answer to any one of them. As we will see, however, it can provide useful insights about all of them. An evolutionary approach does not imply that behavior is genetically determined or that learning and culture are unimportant. In fact, we will argue that learning and culture play crucial roles in human behavior. Behavioral differences among peoples living in different times and places result mainly from flexible adjustments to different social and environmental conditions. Understanding evolution is useful precisely because it helps us understand why humans respond in different ways to different conditions.

Overview of the Book

Humans are the product of organic evolution. By this we mean that there is an unbroken chain of descent that connects every living human being to a bipedal, apelike creature that walked through the tall grasses of the African savanna 3 million years ago (Ma); to a monkeylike animal that clambered through the canopy of great tropical forests covering much of the world 35 Ma; and, finally, to a small, egg-laying, insect-eating mammal that scurried about at night during the age of the dinosaurs 100 Ma. To understand what we are now, you have to understand how this transformation took place. We tell this story in four parts.

Part One: How Evolution Works

More than a century of hard work has given us a good understanding of how evolution works. The transformation of apes into humans involved the assembly of many new, complex adaptations. For example, for early humans to walk upright on two legs, there had to be coordinated changes in many parts of their bodies, including their feet, legs, pelvis, backbone, and inner ear. Understanding how natural selection gives rise to such complex structures and why the genetic system plays a crucial role in this process is essential for understanding how new species arise. Understanding these processes also allows us to reconstruct the history of life from the characteristics of contemporary organisms.

FIGURE P.6

We will draw on information about the behavior of living primates, such as this chimpanzee, to understand how behavior is molded by evolutionary processes, to interpret the hominin fossil record, and to draw insights about the behavior of contemporary humans.

Part Two: Primate Ecology and Behavior

In the second part of the book, we consider how evolution has shaped the behavior of nonhuman primates—an exercise that helps us understand human evolution in two ways. First, humans are members of the primate order: We are more similar to other primates, particularly the great apes, than we are to wolves, raccoons, or other mammals. Studying how primate morphology and behavior are affected by ecological conditions helps us determine what our ancestors might have been like and how they may have been transformed by natural selection. Second, we study primates because they are an extremely diverse order and are particularly variable in their social behavior. Some are solitary, others live in pair-bonded groups, and some live in large groups that contain many adult females and males. Data derived from studies of these species help us understand how social behavior is molded by natural selection. We can then use these insights to interpret the hominin fossil record and the behavior of contemporary people (**Figure P.6**).

Part Three: The History of the Human Lineage

General theoretical principles are not enough to understand the history of any lineage, including our own. The transformation of a shrewlike creature into the human species involved many small steps, and each step was affected by specific environmental and biological circumstances. To understand human evolution, we have to reconstruct the actual history of the human lineage and the environmental context in which these events occurred. Much of this history is chronicled in the fossil record. These bits of mineralized bone, painstakingly collected and reassembled by paleontologists, document the sequence of organisms that links early mammals to modern humans. Complementary work by geologists, biologists, and archaeologists allows us to reconstruct the environments in which the human lineage evolved (**Figure P.7**).

FIGURE P.7

Fossils painstakingly excavated from many sites in Africa, Europe, and Asia provide us with a record of our history as a species. Two million years ago in Africa, there were several apelike species that walked bipedally but still had ape-size brains and apelike developmental patterns. These are the fossilized remains of *Homo habilis*, a species that some think is ancestral to modern humans.

Part Four: Evolution and Modern Humans

Finally, we turn our attention to modern humans and ask why we are the way we are. Why is the human species so variable? How do we acquire our behavior? How has evolution shaped human psychology and behavior? How do we choose our mates? Why do people commit infanticide? Why have humans succeeded in inhabiting every corner of Earth when other species have more limited ranges? We will explain how an understanding of evolutionary theory and a knowledge of human evolutionary history provide a basis for addressing such questions.

The history of the human lineage is a great story, but it is not a simple one. The relevant knowledge is drawn from many disciplines in the natural sciences, such as physics, chemistry, biology, and geology, and from the social sciences, mainly anthropology, psychology, and economics. Learning this material is an ambitious task, but it offers a very satisfying reward. The better you understand the processes that have shaped human evolution and the historical events that took place in the human lineage, the better you will understand how we came to be and why we are the way we are.

1

PART ONE

HOW EVOLUTION WORKS

1

ADAPTATION BY NATURAL SELECTION

CHAPTER OBJECTIVES

By the end of this chapter you should be able to

A. Describe why our modern understanding of the diversity of life is based on the ideas of Charles Darwin.

B. Explain how competition, variation, and heritability lead to evolution by natural selection.

C. Explain why natural selection sometimes causes species to become better adapted to their environments.

D. Explain why natural selection can produce change or cause species to remain the same over time.

E. Describe how natural selection can produce very complex adaptations such as the human eye.

F. Assess why natural selection usually works at the level of the individual, not at the level of the group or species.

Explaining Adaptation before Darwin

Animals and plants are adapted to their conditions in subtle and marvelous ways. Even the casual observer can see that organisms are well suited to their circumstances. For example, fish are clearly designed for life underwater, and certain flowers are designed to be pollinated by particular species of insects. More careful study reveals that organisms are more than just suited to their environments: They are complex machines, made up of many exquisitely constructed components, or **adaptations**, that interact to help the organism survive and reproduce.

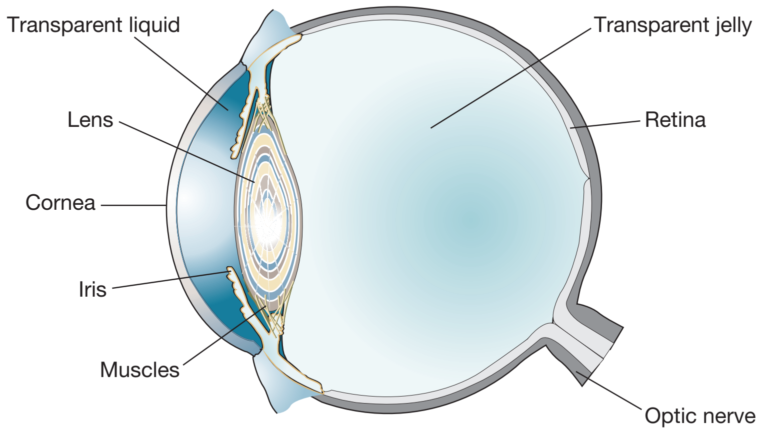


FIGURE 1.1

A cross section of the human eye.

The human eye provides a good example of an adaptation. Eyes are amazingly useful: They allow us to move confidently through the environment, to locate critical resources such as food and mates, and to avoid dangers such as predators and cliffs. Eyes are extremely complex structures made up of many interdependent parts (**Figure 1.1**). Light enters the eye through a transparent opening, then passes through a diaphragm called the iris, which regulates the amount of light entering the eye and allows the eye to function in a wide range of lighting conditions. The light then passes through a lens that projects a focused image on the retina on the back surface of the eye. Several kinds of light-sensitive cells then convert the image into nerve impulses that encode information about spatial patterns of color and intensity. These cells are more sensitive to light than the best photographic film. The detailed construction of each of these parts of the eye makes sense in terms of the eye's function: seeing. If we probed into any of these parts, we would see that they, too, are made of complicated, interacting components whose structure is understandable in terms of their function.

Differences between human eyes and the eyes of other animals make sense in terms of the types of problems each creature faces. Consider, for example, the eyes of fish and humans (**Figure 1.2**). The lens in the eyes of humans and other terrestrial mammals is much like a camera lens; it is shaped like a squashed football and has the same index of refraction (a measure of light-bending capacity) throughout. In contrast, the lens in fish eyes is a sphere located at the center of the curvature of the retina, and the index of refraction of the lens increases smoothly from the surface of the lens to the center. It turns out that this kind of lens, called a spherical gradient lens, provides a sharp image over a full 180° visual field, a very short focal length, and high light-gathering power—all desirable properties. Terrestrial creatures like us cannot use this design because light is bent when it passes from the air through the cornea (the transparent cover of the pupil), and this fact constrains the design of the remaining lens elements. In contrast, light is not bent when it passes from water through the cornea of aquatic animals, and the design of their eyes takes advantage of this fact.

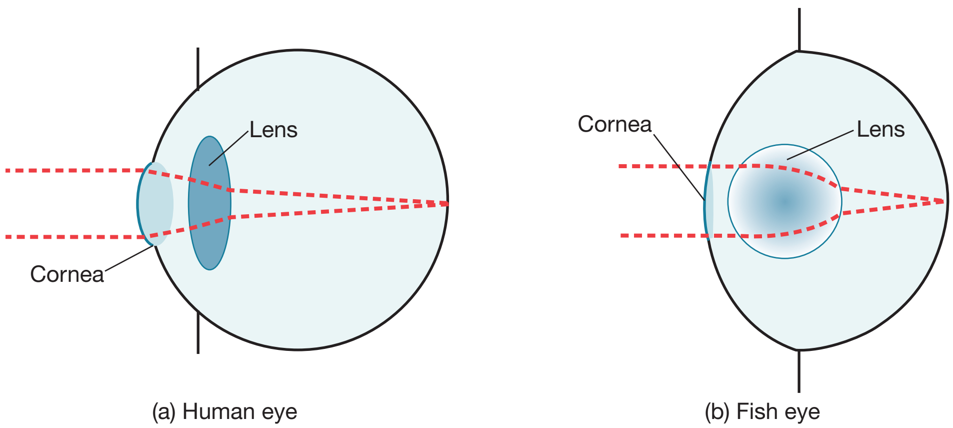


FIGURE 1.2

(a) Like those of other terrestrial mammals, human eyes have more than one light-bending element. A ray of light entering the eye (*dashed lines*) is bent first as it moves from the air to the cornea and then again as it enters and leaves the lens. (b) In contrast, fish eyes have a single lens that bends the light throughout its volume. As a result, fish eyes have a short focal length and high light-gathering power.

Before Darwin there was no scientific explanation for the fact that organisms are well adapted to their circumstances.

As many nineteenth-century thinkers were keenly aware, complex adaptations such as the eye demand a different kind of explanation from other natural objects. This is not simply because adaptations are complex, since many other complicated objects exist in nature. Adaptations require a special kind of explanation because they are complex in a particular, highly improbable way. For example, the Grand Canyon, with its maze of delicate towers intricately painted in shades of pink and gold, is byzantine in its complexity (**Figure 1.3**). Given a different geological history, however, the Grand Canyon might be quite different—different towers in different hues—yet we would still recognize it as a canyon. The particular arrangement of painted towers of the Grand Canyon is improbable, but the existence of a spectacular canyon with a complex array of colorful cliffs in the dry sandstone country of the American Southwest is not unexpected at all; and in fact, wind and water produced many such canyons in this region. In contrast, any substantial changes in the structure of the eye would prevent the eye from functioning, and then we would no longer recognize it as an eye. If the cornea were opaque or the lens on the wrong side of the retina, then the eye would not transmit visual images to the brain. It is highly improbable that natural processes would randomly bring together bits of matter having the detailed structure of the eye because only an infinitesimal fraction of all arrangements of matter would be recognizable as a functioning eye.

FIGURE 1.3

Although an impressive geological feature, the Grand Canyon is much less remarkable in its complexity than the eye.

In Darwin's day, most people were not troubled by this problem because they believed that adaptations were the result of divine creation. In fact, the theologian William Paley used a discussion of the human eye to argue for the existence of God in his book *Natural Theology,* published in 1802. Paley argued that the eye is clearly *designed* for seeing, and where there is design in the natural world, there certainly must be a heavenly designer.

Although most scientists of the day were satisfied with this reasoning, a few, including Charles Darwin, sought other explanations.

Darwin's Theory of Adaptation

Charles Darwin was expected to become a doctor or clergyman, but instead he revolutionized science.

Charles Darwin was born into a well-to-do, intellectual, and politically liberal family in England. Like many prosperous men of his time, Darwin's father wanted his son to become a doctor. But after failing at the prestigious medical school at the University of Edinburgh, Charles went on to Cambridge University, resigned to becoming a country parson. He was, for the most part, an undistinguished student—much more interested in tramping through the fields around Cambridge in search of beetles than in studying Greek and mathematics. After graduation, one of Darwin's botany professors, John Stevens Henslow, provided him with a chance to pursue his passion for natural history as a naturalist on the HMS *Beagle*.

The *Beagle* was a Royal Navy vessel whose charter was to spend two to three years mapping the coast of South America and then to return to London, perhaps by circling the globe (**Figure 1.4**). Darwin's father forbade him to go, preferring that Charles get serious about his career in the church, but Darwin's uncle (and future father-in-law) Josiah Wedgwood II intervened. The voyage was the turning point in Darwin's life. His work during the voyage established his reputation as a skilled naturalist. His observations of living and fossil animals ultimately convinced him that plants and animals sometimes change slowly through time and that such evolutionary change is the key to understanding how new species come into existence. This view was rejected by most scientists of the time and was considered heretical by the general public.

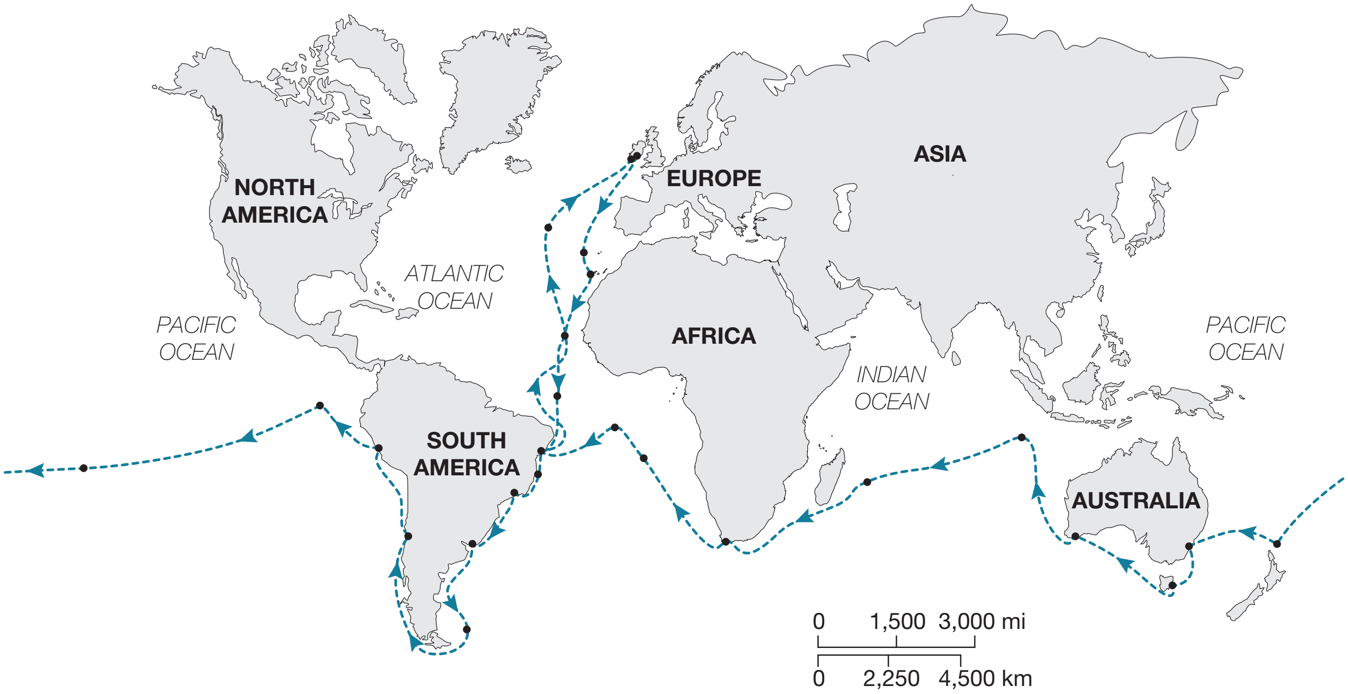


FIGURE 1.4

Darwin circumnavigated the globe during his five-year voyage on the HMS *Beagle*.

Darwin's Postulates

Darwin's theory of adaptation follows from three postulates: (1) the struggle for existence, (2) the variation in fitness, and (3) the inheritance of variation.

In 1838, shortly after the *Beagle* returned to London, Darwin formulated a simple mechanistic explanation for *how* species change through time. His theory follows from three postulates:

1. The ability of a population to expand is infinite, but the ability of any environment to support populations is always finite.
2. Organisms within populations vary, and this variation affects the ability of individuals to survive and reproduce.
3. This variation is transmitted from parents to offspring.

Darwin's first postulate means that populations grow until they are checked by the dwindling supply of resources in the environment. Darwin referred to the resulting competition for resources as "the struggle for existence." For example, animals require food to grow and reproduce. When food is plentiful, animal populations grow until their numbers exceed the local food supply. Because resources are always finite, it follows that not all individuals in a population will be able to survive and reproduce. According to the second postulate, some individuals will possess traits that enable them to survive and reproduce more successfully (producing more offspring) than others in the same environment. The third postulate holds that if the advantageous traits are inherited by offspring, then these traits will become more common in succeeding generations. Thus traits that confer advantages in survival and reproduction are retained in the population, and traits that are disadvantageous disappear. When Darwin coined the term **natural selection** for this process, he was making a deliberate analogy to the artificial selection practiced by animal and plant breeders of his day. A much more apt term would be "evolution by variation and selective retention."

(a)

(b)

FIGURE 1.5

(a) The islands of the Galápagos, which are located off the coast of Ecuador, house a variety of unique species of plants and animals. (b) Cactus finches from Charles Darwin's *The Zoology of the Voyage of H.M.S. Beagle* (1840).

An Example of Adaptation by Natural Selection

Contemporary observations of Darwin's finches provide a particularly good example of how natural selection produces adaptations.

In his autobiography, first published in 1887, Darwin claimed that the curious pattern of adaptations he observed among the several species of finches that live on the Galápagos Islands off the coast of Ecuador—now referred to as "Darwin's finches"—was crucial in the development of his ideas about evolution (**Figure 1.5**). Some evidence suggests that Darwin was actually confused about the Galápagos finches during his visit, and they played little role in his discovery of natural selection. Nonetheless, Darwin's finches hold a special place in the minds of most biologists.

Peter and Rosemary Grant, biologists at Princeton University, conducted a landmark study of the ecology and evolution of one particular species of Darwin's finches on one of the Galápagos Islands. The study is remarkable because the Grants were able to directly document how Darwin's three postulates led to evolutionary change. The island, Daphne Major, is home to the medium ground finch (*Geospiza fortis*), a small bird that subsists mainly by eating seeds (**Figure 1.6**). The Grants and their colleagues caught, measured, weighed, and banded nearly every finch on the island each year of their study—some 1,500 birds in all. They also kept track of critical features of the birds' environment, such as the distribution of seeds of various sizes, and they observed the birds' behavior.

A few years into the Grants' study, a severe drought struck Daphne Major (**Figure 1.7**). During the drought, plants produced far fewer seeds, and the finches soon depleted the stock of small, soft, easily processed seeds, leaving only large, hard seeds that were difficult to process (**Figure 1.8**). The bands on the birds' legs enabled the Grants to track the fate of individual birds during the drought, and the regular measurements that they had made of the birds allowed them to compare the traits of birds that survived the drought with the traits of those that perished. The Grants also kept detailed records of the environmental conditions, which allowed them to determine how the drought affected the birds' habitat. It was this vast body of data that enabled the Grants to document the action of natural selection among the finches of Daphne Major.

FIGURE 1.6

The medium ground finch, *Geospiza fortis,* uses its beak to crack open seeds.

(a)

(b)

FIGURE 1.7

Daphne Major (a) after a year of good rains, and (b) after a year of very little rain.

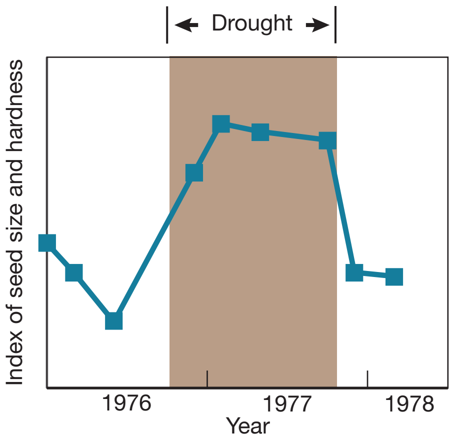
The Grants' data show how the processes identified in Darwin's postulates lead to adaptation.

The events on Daphne Major embodied all three of Darwin's postulates. First, the supply of food on the island was not sufficient to feed the entire population, and many finches did not survive the drought. From the beginning of the drought in 1976 until the rains came nearly two years later, the population of medium ground finches on Daphne Major declined from 1,200 birds to only 180.

Second, beak depth (the top-to-bottom dimension of the beak) varied among the birds on the island, and this variation affected the birds' survival. Before the drought began, the Grants and their colleagues had observed that birds with deeper beaks were able to process large, hard seeds more easily than birds with shallower beaks. Deep-beaked birds usually concentrated on large seeds, whereas shallow-beaked birds normally focused their efforts on small seeds. The open bars in the histogram in **Figure 1.9a** show what the distribution of beak sizes in the population was like before the drought. The height of each open bar represents the number of birds with beaks in a given range of depths—for example, 8.8 to 9.0 mm, or 9.0 to 9.2 mm. During the drought, the relative abundance of small seeds decreased, forcing shallow-beaked birds to shift to larger and harder seeds. Shallow-beaked birds were then at a distinct disadvantage because it was harder for them to crack the seeds. The distribution of individuals within the population changed during the drought because finches with deeper beaks were more likely to survive than were finches with shallow beaks (**Figure 1.9b**). The shaded portion of the histogram in Figure 1.9a shows what the distribution of beak depths would have been like among the survivors. Because many birds died, there were fewer remaining in each category. However, mortality was not random. The proportion of shallow-beaked birds that died greatly exceeded the proportion of deep-beaked birds that died. As a result, the shaded portion of the histogram shows a shift to the right, which means that the average beak depth in the population increased. Thus, the average beak depth among the survivors of the drought was greater than the average beak depth in the same population before the drought.

FIGURE 1.8

During the two-year drought, the size and hardness of seeds available on Daphne Major increased because birds consumed all of the desirable small, soft seeds, leaving mainly larger and harder seeds. Each point on this plot represents an index of seed size and hardness at a given time.



Third, parents and offspring had similar beak depths. The Grants discovered this by capturing and banding nestlings and recording the identity of the nestlings' parents. When the nestlings became adults, the Grants recaptured and measured them. The Grants found that, on average, parents with deep beaks produced offspring with deep beaks (**Figure 1.10**). Because parents were drawn from the pool of individuals that survived the drought, their beaks were, on average, deeper than those of the original residents of the island, and because offspring resemble their parents, the average beak depth of the survivors' offspring was greater than the average beak depth before the drought.

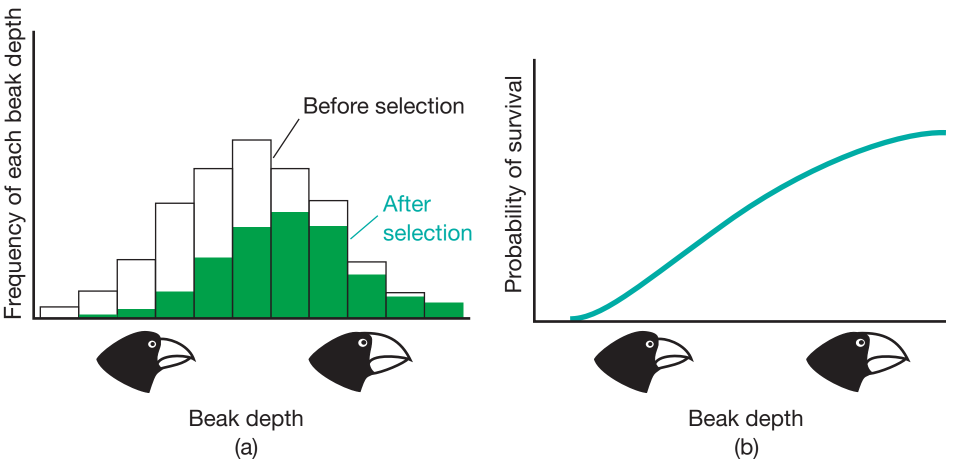


FIGURE 1.9

How directional selection increased mean beak depth among medium ground finches on Daphne Major. (a) The heights of the bars represent the numbers of birds whose beak depths fall within each of the intervals plotted on the *x* axis, with beak depth increasing to the right. The open bars show the distribution of beak depths before the drought began. The shaded bars show the distribution of beak depths after a year of drought. Notice that the number of birds in each category has decreased. Because birds with deep beaks were less likely to die than birds with shallow beaks, the peak of the distribution shifted to the right, indicating that the mean beak depth had increased. (b) The probability of survival for birds of different beak depths is plotted. Birds with shallow beaks are less likely to survive than are birds with deep beaks.

This means that, through natural selection, the average **morphology** (an organism's size, shape, and composition) of the bird population changed so that birds became better adapted to their environment. This process, operating over approximately two years, led to a 4% increase in the mean beak depth in this population (**Figure 1.11**).

Selection preserves the status quo when the most common type is the best adapted.

So far, we have seen how natural selection led to adaptation as the population of finches on Daphne Major evolved in response to changes in their environment. Will this process continue forever? If it did, eventually all the finches would have deep enough beaks to efficiently process the largest seeds available. However, large beaks have disadvantages as well as benefits. The Grants showed, for instance, that birds with large beaks are less likely to survive the juvenile period than are birds with small beaks, probably because large-beaked birds require more food (**Figure 1.12**). Evolutionary theory predicts that, over time, selection will increase the average beak depth in the population until the costs of larger-than-average beak size exceed the benefits. At this point, finches with the average beak size in the population will be the most likely to survive and reproduce, and finches with deeper or shallower beaks than the new average will be at a disadvantage. When this is true, beak size does not change, and we say that an **equilibrium** exists in the population in regard to beak size. The process that produces this equilibrium state is called **stabilizing selection**. Notice that even though the average characteristics of the beak in the population will not change in this situation, selection is still going on. Selection is required to change a population, and selection is also required to keep a population the same.

FIGURE 1.10

Parents with deeper-than-average beaks tend to have offspring with deeper-than-average beaks. Each point represents one offspring. Offspring beak depth is plotted on the vertical axis (deeper beaks farther up the axis), and the average of the two parents' beak depths is plotted on the horizontal axis (deeper beaks farther to the right).