HOW HUMANS EVOLVED

ROBERT BOYD
JOAN B. SILK

SIXTH EDITION

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Robert Boyd • Joan B. Silk

University of California, Los Angeles

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For Sam and Ruby

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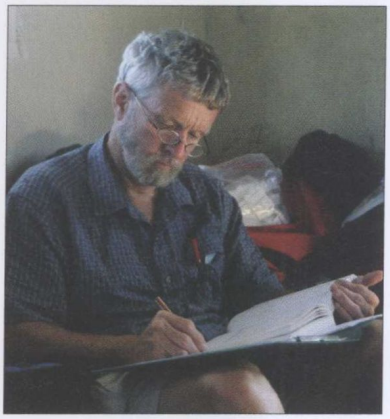

ROBERT BOYD has written widely on evolutionary theory, focusing especially on the evolution of cooperation and the role of culture in human evolution. His book *Culture and the Evolutionary Process* received the J. I. Staley Prize. He has also published numerous articles in scientific journals and has edited volumes. He is currently Professor of Anthropology at the University of California, Los Angeles.

JOAN B. SILK has conducted extensive research on the social lives of monkeys and apes, including extended fieldwork on chimpanzees at Gombe Stream Reserve in Tanzania and on baboons in Kenya and Botswana. She is also interested in the application of evolutionary thinking to human behavior. She has published numerous articles in scientific journals and edited volumes. She is currently Professor of Anthropology and the Center for Society and Genetics at the University of California, Los Angeles.

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*. As evolutionary biologists, we study how evolution works. 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. We try to give life to the creatures that left the bones and made the artifacts that paleontologists and archaeologists painstakingly excavate, by focusing on the processes that generate change, create adaptations, and shape bodies and behavior. 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 openly and clearly. Positive responses to the first five 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 the adaptive significance of infanticide and the effects of dominance rank on reproductive performance; paleontologists disagree about the taxonomic relationships among early hominin species and the emergence of modern humans; and those 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 many 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 different 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.

New in the Sixth 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. These kinds of discoveries include the spectacular fossil finds that reveal new chapters in human ancestry, new data that alter our interpretation of the behavioral strategies of primates, and experimental studies that reveal cross-cultural regularities in mating preferences. New developments in human evolutionary studies require regular updates of the textbook. Although we have made a number of 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 Two, "Primate Ecology and Behavior," and Part Three, "The History of the Human Lineage."

In Part Two, we made a number of changes to Chapter 5, which introduces readers to the primate order. First, we shifted from a cladistic taxonomy to an evolutionary taxonomy, and now group the tarsiers in the suborder Haplorrhini along with the monkeys and apes. Second, we provided a more complete introduction to the diversity of living primate species. Third, we extended and updated our discussion of primate conservation.

Nearly all the chapters in Part Three have been extensively revised. In Chapter 9, we added a description of the newly discovered Eocene primate, *Darwinius masilae,* and thoroughly revised our discussion of the Miocene apes, adding descriptions of several late Miocene apes, and concluding with a discussion of the diversity of the locomotor adaptations of the Miocene hominoids. This material provides a useful foundation for interpreting the newly published trove of information about *Ardipithecus ramidus,* which receives greatly expanded coverage in Chapter 10. In Chapter 10, we also describe new discoveries from Woranso-Mille in Ethiopia which are relevant to understanding the relationship between *Au. anamensis* and *Au. afarensis,* and introduce the new australopith, *Au. sediba* from South Africa. We have shifted material on *Homo habilis* to Chapter 12. Material on the lives of the australopiths has been folded into Chapter 11, in which we focus on the life history and behavioral adaptations of the Oldowan hominins. Chapter 11 has been revised to incorporate new findings about the antiquity of hominin tool use and the lively debate about the taphonomic evidence for hunting versus scavenging at Olduvai sites. In addition to introducing the earliest members of the genus *Homo* in Chapter 12, we have thoroughly revised the chapter to reflect our growing appreciation of the great complexity of middle Pleistocene hominin evolution. Much of this knowledge is derived from analyses of DNA extracted from fossil specimens, and as molecular genetics comes to play a bigger role in our understanding of human origins, discussion of these techniques come to play a larger role in our story. We discuss the implications of the results of genetic analyses of DNA from Neanderthals and the newly discovered bones from the Denisova cave in Chapters 12 and 13. In Chapter 13, we have also included new material on archaeological discoveries at Blombos Cave and Pinnacle Point that suggest the presence of complex modern behavior in southern African by at least 90 kya.

In Part Four, we added a discussion of how genome-wide association studies have allowed the identification of genes affecting polygenic characters such as stature, and the striking confirmation that such characters are influenced by many genes, each with a small phenotypic effect.

We wrote this book with undergraduates in mind, and have designed a number of features to help students use the book effectively. We have retained the "key idea" statements (now printed in blue type), and we recommend that students use these key ideas to keep track of important concepts and facts, and to structure their reviews of the material. Important terms that may be unfamiliar are set in boldfaced 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 to 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 chimpanee 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 is portrayed graphically than to recall verbal descriptions of results.

Ancillary Materials for Teaching and Learning

For Instructors

The Norton Physical Anthropology in Action DVD features over 80 film clips from across the discipline with an emphasis on paleoanthropology and primatology. Perfect for classroom use, these videos help students see and think like anthropologists and make it easy for instructors to illustrate key concepts and spark classroom discussion. Each DVD contains a reference booklet with clip descriptions written by Tracy K. Betsinger of the State University of New York, Oneonta.

Instructor's Resource Disc

This visually dynamic Instructor's Resource Disc, authored by Jeremy DeSilva of Boston University, includes:

- PowerPoint slides with a suggested classroom lecture script in the notes field;
- Clicker questions for each chapter ready for classroom incorporation;
- All the art from the text in both PowerPoint and JPEG formats.

Instructor's Manual and Test Bank (by Elizabeth Erhart, Texas State University; updated by Christina Grassi, Skidmore College; with contributions by Tracy Betsinger, SUNY, Oneonta)

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 Sixth Edition Instructor's Manual includes a revised suggested video and Web resources list, and activities to accompany the new Physical Anthropology in Action DVD. Available in print paperback and for download.

The Test Bank offers teachers over 90 multiple-choice, true/false, and essay questions (organized by difficulty level and topic) for each chapter. New to the edition are new questions in every chapter, knowledge types and page references for every question, and sample answers to the essay questions. Available in print paperback, Exam View Assessment Suite (CD-ROM and downloadable), and for download as a PDF and Word file.

Coursepacks

Available at no cost to professors or students, Norton coursepacks for online or hybrid courses are available in a variety of formats, including all versions of Blackboard and WebCT. With just a simple download from our instructor's Web site, instructors can bring high-quality Norton digital media into a new or existing online course (no extra student passwords required), and it's theirs to keep forever. Content includes

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For Students

StudySpace: Your Place for a Better Grade wwnorton.com/studyspace, authored by Kristina Killgrove, University of North Carolina, Chapel Hill

StudySpace tells students what they know, shows them what they still need to review, and then gives them an organized study plan to master the material. This free and easy-to-navigate Web site offers students an impressive range of exercises, interactive learning tools, assessment, and review materials, all without passwords or hidden costs:

- **NEW! Quiz+ Chapter Review Quizzes** don't just tell students how they did; they show them how they can do better. Quiz+ gives students a targeted study plan that offers specific page references and links to the ebook and other online learning tools. This allows students to instantly access the resources they need, when they need them most.
- **AnthroTours:** Google Earth flyovers of key locations discussed in the book bring the dig to the classroom.
- **Flashcards** for every chapter help students review key concepts before exams. Many of the flashcards will contain images so students can test their knowledge of important fossils.
- **Chapter outlines** and new **learning objectives** help students organize their study and review.

Ebook and Chapter Select Ebook

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An affordable and convenient alternative, Norton ebooks retain the content and design of the print book and allow students to highlight and take notes with ease, print chapters as needed, and search the text. With Chapter Select ebooks, instructors can create a custom ebook that contains only the chapters they want to assign. For *How Humans Evolved,* Sixth Edition, chapters cost $4.

Acknowledgments

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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, which granted us permission to use images of the Laetoli conservation project for the cover of the Second Edition.

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We also acknowledge the thousands of students and dozens of teaching assistants at 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 four 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 outstanding editors Leo Wiegman, Pete Lesser, Aaron Javsicas, and Eric Svendsen. We are also grateful to our excellent editorial assistant, Cait Callahan. We would also like to thank all of those who saw the book through the production process, including Eric Pier-Hocking, Melissa Atkin, and Laura Musich. And special thanks to Elizabeth Erhart at Texas State University, San Marcos, Christina Grassi of Skidmore College, and Tracy Betsinger of SUNY, Oneonta, for preparing the revised Instructor's Manual and Test Bank; Jeremy DeSilva of Boston University for creating the Intructor's Resource Disc; Kristina Killgrove of the University of North Carolina, Chapel Hill, for preparing the revised StudySpace review materials; and Sara Simon of the University of North Carolina, Chapel Hill, for creating the audio pronunciation guide and AnthroTours.

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 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 2) argued that human populations invariably grow until they are limited by starvation, poverty, and death. 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.

Figure 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 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.

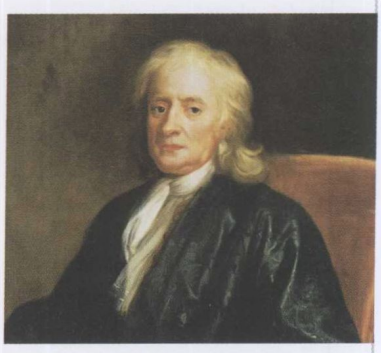

Figure 3 Sir Isaac Newton discovered the laws of celestial mechanics, a body of theory that resolved age-old mysteries about the movements of the planets.

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 of 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 of the intricacies in the dance of the planets could be explained by the action of a few simple processes (Figure 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 of 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 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 look so different around the world? As you will see, evolutionary theory provides answers or insights about all of 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.

All of 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 of 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 like toy guns and violent TV programs (Figure 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, while others adopt and lovingly raise children who are not their own?

Figure 4 A strong appetite for sugar, fat, and salt may have been adaptive for our ancestors, who had little access to sweet, fatty, and salty foods. We have inherited these appetites and have easy access to these foods. As a consequence, many of us suffer from obesity, high blood pressure, diabetes, and heart disease.

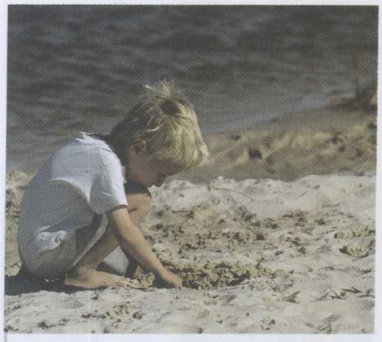

Figure 5 One of the great debates in Western thought focuses on the essential elements of human nature. Are people basically moral beings corrupted by society or fundamentally amoral creatures socialized by cultural conventions, social strictures, and religious beliefs?

Understanding human evolution does not reveal the answers to all of 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 tall grasses of the African savanna 3 million years ago (mya); to a monkey-like animal that clambered through the canopy of great tropical forests covering much of the world 35 mya; and, finally, to a small, egg-laying, insect-eating mammal that scurried about at night during the age of the dinosaurs, 100 mya. 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, in order 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

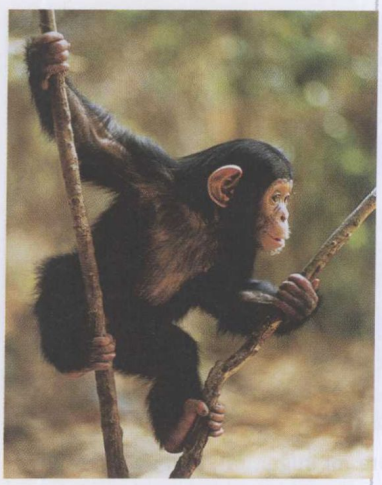

Figure 6 We will draw on information about the behavior of living primates, such as this chimpanzee, to understand how behavior is molded by evolutionary processes, to interpret the hominin fossil record, and to draw insights about the behavior of contemporary humans.

Figure 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 a number of apelike species that walked bipedally but still had ape-sized brains and apelike developmental patterns. These are the fossilized remains of *Homo habilis*, a species that some think is ancestral to modern humans.

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.

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 6).

Part Three: The History of the Human Lineage

General theoretical principles are not sufficient 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 link 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 7).

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 the 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 questions like these.

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.

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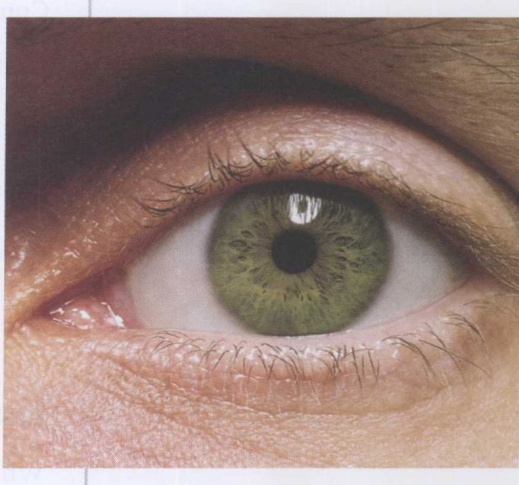

Part Two • Primate Ecology and Behavior