DAVID M. BUSS

EVOLUTIONARY PSYCHOLOGY

THE NEW SCIENCE OF THE MIND

FIFTH EDITION

FIFTH EDITION

Evolutionary Psychology

The New Science of the Mind

David M. Buss
The University of Texas at Austin

Routledge
Taylor & Francis Group
LONDON AND NEW YORK

First published 2015, 2012, 2008 by Pearson Education, Inc.

Published 2016 by Routledge
2 Park Square, Milton Park, Abingdon, Oxon OX14 4RN
711 Third Avenue, New York, NY 10017, USA

Routledge is an imprint of the Taylor & Francis Group, an informa business

Credits and acknowledgments borrowed from other sources and reproduced, with permission, in this textbook appear on appropriate page within the text or on page 463.

ISBN: 9780205992126 (hbk)

Cover Design: Lumina Datamatics

Library of Congress Cataloging-in-Publication Data
Buss, David M.
Evolutionary psychology : the new science of the mind/David M. Buss, The University of Texas at Austin.—Fifth edition.
pages cm.
Includes bibliographical references and index.
ISBN 978-0-205-99212-6 (alk. paper)—ISBN 0-205-99212-9 (alk. paper) 1. Evolutionary psychology—Textbooks. 2. Human evolution—Textbooks. I. Title.
BF698.95.B87 2015
155.7—dc23

2014025568

This book is dedicated to:
Charles Darwin
Francis Galton
Gregor Mendel
R. A. Fisher
W. D. Hamilton
George C. Williams
John Maynard Smith
Robert Trivers
E. O. Wilson
Richard Dawkins
Donald Symons
Martin Daly
Margo Wilson
Leda Cosmides
John Tooby
And to all students of evolutionary psychology,
past, present, and future

About the Author

David M. Buss received his Ph.D. from the University of California at Berkeley. He began his career in academics at Harvard, later moving to the University of Michigan before accepting his current position as professor of psychology at the University of Texas. His primary research interests include human sexuality, mating strategies, conflict between the sexes, homicide, stalking, and sexual victimization. The author of more than 300 scientific articles and 6 books, Buss has won numerous awards including the *American Psychological Association (APA) Distinguished Scientific Award for Early Career Contribution to Psychology*, the *APA G. Stanley Hall Lectureship*, the *APA Distinguished Scientist Lecturer Award*, and a *Robert W. Hamilton Book Award* for the first edition of *Evolutionary Psychology: The New Science of the Mind*. He is also the editor of the first comprehensive *Handbook of Evolutionary Psychology* (Wiley) and co-editor (with Patricia Hawley) of *The Evolution of Personality and Individual Differences*. In 2013, he was named one of the 30 most influential living psychologists in the world. He enjoys extensive cross-cultural research collaborations and lectures widely within the United States and abroad. His hobbies include tennis, squash, and disc golf, and he is an avid film buff.

Contents

PART 2: PROBLEMS OF SURVIVAL

PART 3: CHALLENGES OF SEX AND MATING

PART 4: CHALLENGES OF PARENTING AND KINSHIP

PART 5: PROBLEMS OF GROUP LIVING

Preface

It is especially exciting to be an evolutionary psychologist during this time in the history of science. Most scientists operate within long-established paradigms. Evolutionary psychology, in contrast, is a revolutionary new science, a true synthesis of modern principles of psychology and evolutionary biology. By taking stock of the field at this time, I hope this book contributes in some modest measure to the fulfillment of a scientific revolution that will provide the foundation for psychology in the future. Since the publication of the award-winning first edition of *Evolutionary Psychology: The New Science of the Mind*, there has been an explosion of new research within the field. New journals in evolutionary psychology have been started, and the volume of evolutionary publications in mainstream psychology journals has steadily increased. New courses in evolutionary psychology are being taught in colleges and universities throughout the world. Many gaps in scientific knowledge remain, and each new discovery brings fresh questions and new domains to explore. The field of evolutionary psychology is vibrant, exciting, and brimming with empirical discoveries and theoretical innovations. Indeed, as Harvard professor Steven Pinker notes, "In the study of humans, there are major spheres of human experience—beauty, motherhood, kinship, morality, cooperation, sexuality, violence—in which evolutionary psychology provides the only coherent theory" (Pinker, 2002, p. 135).

Charles Darwin must be considered the first evolutionary psychologist for this prophesy at the end of his classic treatise *On the Origin of Species* (1859): "In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation." More than 150 years later, after some false starts and halting steps, the science of evolutionary psychology is finally emerging. The purpose of this book is to showcase the foundations of this new science and the fascinating discoveries of its practitioners.

When I first started to conduct research in evolutionary psychology as an assistant professor at Harvard University in 1981, evolutionary speculations about humans abounded, but practically no empirical research had been conducted to back them up. Part of the problem was that scientists who were interested in evolutionary questions could not bridge the gap between the grand evolutionary theories and the actual scientific study of human behavior. Today that gap has closed considerably, because of both conceptual breakthroughs and an avalanche of hard-won empirical achievements. Many exciting questions still cry out for empirical scrutiny, of course, but the existing base of findings is currently so large that the problem I faced was how to keep this book to a reasonable length while still doing justice to the dazzling array of theoretical and empirical insights. Although it is written with undergraduates in mind, it is also designed to appeal to a wider audience of laypersons, graduate students, and professionals who seek an up-to-date overview of evolutionary psychology.

I wrote the first edition of this book with another purpose as well—frankly, a revolutionary one. I wrote it so that the hundreds of professors at colleges and universities throughout the world who have been thinking and writing about evolution and human

behavior would be motivated to teach formal courses in evolutionary psychology and get those courses established as part of required psychology curricula. Already evolutionary psychology is attracting the best and the brightest young minds. I hope that this book helps to accelerate the trend and in some small way contributes to the fulfillment of Darwin's prophesy.

NEW TO THIS EDITION

In revising the book for this edition, I had two goals in mind. First, I sought to provide a major update of new discoveries. Toward this end, roughly 300 new references have been added to this edition. Second, I sought to fill in important omissions, based on an explosion of new theories and research:

- Expanded coverage of cognitive psychology, including cognitive mechanisms that interfere with understanding evolutionary processes and deep time.
- New studies on evidence for a small amount of interbreeding between modern humans and Neanderthals.
- Meta-analysis on ovulation effects on women's mate preferences.
- Discussion of evolutionary hypotheses that have been empirically disconfirmed.
- New discussion of the emotion of "disgust" as central to the behavioral immune system; and "sexual disgust" as a specific evolved defense.
- Raft of new studies on spatial navigation abilities of women and men.
- New findings on the emotion of "sexual regret" and gender differences therein.
- Context effects on women's mate preferences, including prevailing health status within the culture.
- Discoveries of new cues to attractiveness, such as the white sclera of the eyes.
- "The lipstick effect" and other contextual shifts in women's mating tactics.
- New research testing different theories of homosexuality.
- Cross-cultural studies in France and Denmark on sex differences in consenting to sex with strangers.
- Women's "nesting" behavior when pregnant.
- "The Baby Effect" and other predictable shifts in men's and women's parenting psychology.
- Sibling competition as a function of magnitude of parental resources.
- Food sharing in Nicaragua, Tanzania, Indonesia, the Saami, and Norwegian reindeer herders.
- The importance of kin contact after marriage among Himba nomadic African pastoralists.
- Effects of grandmothers on grandchild survival.
- "Walk away" rule and its effect on cooperation strategies.
- The "newcomer effect."
- Effect of free-riding on reputation among the Turkana.
- Friends as potential mate poachers.
- Competitive altruism.
- Morphological cues to "design for combat" in men.
- Empirical tests of the "Crazy Bastard Hypothesis."
- Predictors of female–female aggression among the Tsimane of Bolivia.

- New section on the puzzle of suicide terrorism.
- New section on sexual exploitation and cues to sexual exploitability.
- Studies of sexual jealousy in a small-group society, the Himba of Namibia.
- Predictors of men's violence against women in the Tsimane of Bolivia.
- Added section on the "service for prestige" theory of leadership and followership.
- New box on Tactics of Hierarchy Negotiation.
- Eye tracking findings of attentional biases toward infants.
- New studies on "successful psychopaths."
- A large new section titled "The Evolutionary Psychology of Religion."

I have received many inspiring letters and e-mails from teachers and students who have used previous editions of *Evolutionary Psychology* and hope that future readers will also share their enthusiasm. The quest for understanding the human mind is a noble undertaking. As the field of evolutionary psychology matures, we are beginning to gain answers to the mysteries that have probably intrigued humans for hundreds of thousands of years: Where did we come from? What is our connection with other life forms? And what are the mechanisms of mind that define what it means to be a human being?

Supplements

Please visit the companion website at www.routledge.com/9780205992126

Acknowledgments

The acknowledgments for this book must include not only colleagues who have directly commented on its contents, but also those who have influenced my personal evolutionary odyssey, which has spanned more than twenty-five years. My interest in evolution began in an undergraduate geology class in the mid-1970s, when I first realized that there were theories designed specifically to explain the origins of things. My first evolutionary groping was a term paper for a course in 1975 in which I speculated, drawing on now-laughable primate comparisons, that the main reason men have evolved a status-striving motive is higher status produced increased sexual opportunities.

My interest in evolution and human behavior grew when I was in graduate school at the University of California at Berkeley, but I found the most fertile evolutionary soil at Harvard University, which offered me a position as assistant professor of psychology. There I began teaching a course on human motivation using evolutionary principles, although the text scarcely mentioned evolution. My lectures were based on the works of Charles Darwin, W. D. Hamilton, Robert Trivers, and Don Symons. I started corresponding with Don Symons, whose 1979 book is considered by many the first modern treatise on human evolutionary psychology. I owe Don special thanks; his friendship and insightful commentary have informed practically everything that I've written on the subject of evolutionary psychology. Influenced by Don's ideas, I designed my first evolutionary research project on human mating, which eventually mushroomed into a cross-cultural study of 10,047 participants from thirty-seven cultures around the world.

After word got around about my evolutionary interests, a brilliant young Harvard graduate student named Leda Cosmides rapped on my office door and introduced herself. We had the first of many discussions (actually arguments) about evolution and human behavior. Leda introduced me to her equally brilliant husband and collaborator John Tooby, and together they tried to correct some of the more egregious errors in my thinking—something they continue to do to this day. Through Leda and John, I met Irv DeVore, a prominent Harvard anthropologist who conducted "simian seminars" at his Cambridge home, and Martin Daly and Margo Wilson, who came to Harvard on sabbatical. At that point, the early to mid-1980s, Leda and John had not yet published anything on evolutionary psychology, and no one was called an evolutionary psychologist.

The next pivotal event in my evolutionary quest occurred when I was elected to be a fellow at the Center for Advanced Study in the Behavioral Sciences in Palo Alto. Thanks to the encouragement of Director Gardner Lindzey, I proposed a special center project entitled "Foundations of Evolutionary Psychology." The acceptance of this proposal led Leda Cosmides, John Tooby, Martin Daly, Margo Wilson, and me to spend 1989 and 1990 at the center working on the foundations of evolutionary psychology, even through the earthquake that rocked the Bay area. In writing this book, I owe the greatest intellectual debt to Leda Cosmides, John Tooby, Don Symons, Martin Daly, and Margo Wilson, pioneers and founders of the emerging field of evolutionary psychology.

Harvard on one coast and the Center for Advanced Study on the other provided a bounty for budding evolutionary scholars, but I must also thank two other institutions and their inhabitants. First, the University of Michigan supported the evolution and human behavior group between 1986 and 1994. I owe special thanks to Al Cain, Richard Nisbett, Richard Alexander, Robert Axelrod, Barb Smuts, Randolph Nesse, Richard Wrangham, Bobbi Low, Kim Hill, Warren Holmes, Laura Betzig, Paul Turke, Eugene Burnstein, and John Mitani for playing key roles at Michigan. Second, I thank the Department of Psychology at the University of Texas at Austin, which had the prescience to form one of the first graduate programs in evolutionary psychology in the world under the heading of Individual Differences and Evolutionary Psychology. Special thanks go to Joe Horn, Dev Singh, Del Thiessen, Lee Willerman, Peter MacNeilage, David Cohen, and the department chairs Randy Diehl, Mike Domjan, and Jamie Pennebaker for their roles at UT.

I owe tremendous thanks to friends and colleagues who have contributed to the ideas in this book in one form or another: Dick Alexander, Bob Axelrod, Robin Baker, Jerry Barkow, Jay Belsky, Laura Betzig, George Bittner, Don Brown, Eugene Burnstein, Arnold Buss, Bram Buunk, Liz Cashdan, Nap Chagnon, Jim Chisholm, Helena Cronin, Michael Cunningham, Richard Dawkins, Irv DeVore, Frans de Waal, Mike Domjan, Paul Ekman, Steve Emlen, Mark Flinn, Robin Fox, Robert Frank, Steve Gangestad, Karl Grammer, W. D. Hamilton, Kim Hill, Warren Holmes, Sarah Hrdy, Bill Jankowiak, Doug Jones, Doug Kenrick, Lee Kirkpatrick, Judy Langlois, Bobbi Low, Kevin MacDonald, Neil Malamuth, Janet Mann, Linda Mealey, Geoffrey Miller, Randolph Nesse, Dick Nisbett, Steve Pinker, David Rowe, Paul Rozin, Joanna Scheib, Paul Sherman, Irwin Silverman, Jeff Simpson, Dev Singh, Barb Smuts, Michael Studd, Frank Sulloway, Del Thiessen, Nancy Thornhill, Randy Thornhill, Lionel Tiger, Bill Tooke, John Townsend, Robert Trivers, Jerry Wakefield, Lee Willerman, George Williams, D. S. Wilson, E. O. Wilson, and Richard Wrangham.

I would like to thank the following reviewers for their feedback on the first edition: Clifford R. Mynatt, Bowling Green State University; Richard C. Keefe, Scottsdale College; Paul M. Bronstein, University of Michigan-Flint; Margo Wilson, McMaster University; W. Jake Jacobs, University of Arizona; and A. J. Figueredo, University of Arizona; as well as the reviewers for the second edition: John A. Johnson, Penn State, DuBois; Kevin MacDonald, California State University, Long Beach; and Todd K. Shackelford, Florida Atlantic University. Also, a special thank you to the third edition reviewers: Brad Duchaine, Harvard University; Heide Island, University of Central Arkansas; Angelina Mackewn, University of Tennessee at Martin; Roger Mellgren, University of Texas at Arlington; Amy R. Pearce, Arkansas State University; and Thomas Sawyer, North Central College.

The creation of the second edition benefited from the exceptionally thoughtful comments and suggestions by, and discussions with, a number of friends and colleagues: Petr Bakalar, Clark Barrett, Leda Cosmides, Martin Daly, Richard Dawkins, Todd DeKay, Josh Duntley, Mark Flinn, Barry Friedman, Steve Gangestad, Joonghwan Jeon, Doug Kenrick, Martie Haselton, Bill von Hippel, Rob Kurzban, Peter MacNeilage, Geoffrey Miller, Steve Pinker, David Rakison, Kern Reeve, Paul Sherman, Valerie Stone, Larry Sugiyama, Candace Taylor, John Tooby, Glenn Weisfeld, and Margo Wilson. Josh Duntley must be singled out for sharing his encyclopedic knowledge and keen insights. I would also like to thank Carolyn Merrill of Allyn & Bacon for wise counsel, persistence, and prescience.

I would like to thank the following individuals for help making additions and improvements to the third edition: Leda Cosmides, Josh Duntley, Ernst Fehr, Herbert

Gintis, Anne Gordon, Ed Hagen, Martie Haselton, Joe Henrich, Joonghwan Jeon, Mark Flinn, Barry X. Kuhle, Rob Kurzban, Dan O'Connell, John Patton, Steve Pinker, David Rakison, Pete Richardson, Andy Thompson, and Wade Rowatt. I would like to thank the following individuals for insightful comments and suggestions on the fourth edition: Alice Andrews, Ayla Arslan, Sean Bocklebank, Joseph Carroll, Elizabeth Cashdan, Lee Cronk, John Edlund, Bruce Ellis, A. J. Figueredo, Aaron Goetz, Joe Henrich, Sarah Hill, Russell Jackson, Peter Karl Jonason, Jeremy Koster, Barry Kuhle, David Lewis, Frank McAndrew, David McCord, Geoffrey Miller, David Rakison, Brad Sagarin, David Schmitt, Todd Shackelford, Candace Taylor, and Gregory Webster. I would also like to thank my wonderful editor, Susan Hartman, who provided support and enthusiasm throughout several editions of this book, and my superb and meticulous production editors, Aparna Yellai and Revathi Viswanathan.

ACKNOWLEDGMENTS FOR THE FIFTH EDITION

The fifth edition benefitted from discussions with Alice Andrews, Harald Euler, Lee Kirkpatrick, Cristine Legare, Stacey Lynn, Ara Norenzyan, David Rakison, and Andy Thompson.

Thanks go to my students past and present who have made major contributions to the field of evolutionary psychology: Laith Al-Shawaf, Kelly Asao, April Bleske, Mike Botwin, Jaime Confer, Sean Conlan, Dan Conroy-Beam, Todd DeKay, Josh Duntley, Judith Easton, Bruce Ellis, Diana Fleischman, Cari Goetz, Aaron Goetz, Heidi Greiling, Arlette Greer, Martie Haselton, Sarah Hill, Russell Jackson, Joonghwan Jeon, Barry Kuhle, Liisa Kyl-Heku, David Lewis, Anne McGuire, Carin Perilloux, David Schmitt, and Todd Shackelford. Special thanks also to Kevin Daly, Todd DeKay, Josh Duntley, A. J. Figueredo, Barry Kuhle, Martie Haselton, Rebecca Sage, Todd Shackelford, and W. Jake Jacobs for generously providing detailed comments on the entire book.

PART 1

FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

Two chapters introduce the foundations of evolutionary psychology. Chapter 1 traces the scientific movements leading to evolutionary psychology. First, we describe the landmarks in the history of evolutionary theory, starting with theories of evolution developed before Charles Darwin and ending with modern formulations of evolutionary theory widely accepted in the biological sciences today. Next, we examine three common misunderstandings about evolutionary theory. Finally, we trace landmarks in the field of psychology, starting with the influence Darwin had on the psychoanalytic theories of Sigmund Freud and ending with modern formulations of cognitive psychology.

Chapter 2 provides the conceptual foundations of modern evolutionary psychology and introduces the scientific tools used to test evolutionary psychological hypotheses. The first section examines theories about the origins of human nature. Then we turn to a definition of the core concept of an evolved psychological mechanism and outline the properties of these mechanisms. The middle portion of Chapter 2 describes the major methods used to test evolutionary psychological hypotheses and the sources of evidence on which these tests are based. Because the remainder of the book is organized around human adaptive problems, the end of Chapter 2 focuses on the tools evolutionary psychologists use to identify adaptive problems, starting with survival and ending with the problems of group living.

1

The Scientific Movements Leading to Evolutionary Psychology

LEARNING OBJECTIVES

After studying this chapter, the reader will be able to:

- Identify the three essential ingredients of natural selection.
- Define particulate inheritance.
- List three common misunderstandings about evolutionary theory.
- Identify when Neanderthals went extinct.
- Explain why radical behaviorism went into scientific decline.

In the distant future I see open fields for more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation.

—Charles Darwin, 1859

As the archeologist dusted off the dirt and debris from the skeleton, she noticed something strange: The left side of the skull had a large dent, apparently from a ferocious blow, and the rib cage—also on the left side—had the head of a spear lodged in it. Back in the laboratory, scientists determined that the skeleton was that of a Neanderthal man who had died roughly 50,000 years ago, the earliest known homicide victim. His killer, judging from the damage to the skull and rib cage, bore the lethal weapon in his right hand.

The fossil record of injuries to bones reveals two strikingly common patterns (Jurmain et al., 2009; Trinkaus & Zimmerman, 1982; Walker, 1995). First, the skeletons of men contain far more fractures and dents than do the skeletons of women. Second, the injuries are located mainly on the left frontal sides of the skulls and skeletons, suggesting mostly right-handed attackers. The bone record alone cannot tell us with certainty that combat among men was a central

feature of human ancestral life. Nor can it tell us with certainty that men evolved to be the more physically aggressive sex. But skeletal remains provide clues that yield a fascinating piece of the puzzle of where we came from, the forces that shaped who we are, and the nature of our minds today.

The huge human brain, approximately 1,350 cubic centimeters, is the most complex organic structure in the known world. Understanding the human mind/brain mechanisms in evolutionary perspective is the goal of the new scientific discipline called *evolutionary psychology.* Evolutionary psychology focuses on four key questions: (1) *Why* is the mind designed the way it is—that is, what causal processes created, fashioned, or shaped the human mind into its current form? (2) *How* is the human mind designed—what are its mechanisms or component parts, and how are they organized? (3) *What are the functions* of the component parts and their organized structure—that is, what is the mind designed to do? (4) *How* does input from the current environment interact with the design of the human mind to produce observable behavior?

Contemplating the mysteries of the human mind is not new. Ancient Greeks such as Aristotle and Plato wrote manifestos on the subject. More recently, theories of the human mind such as the Freudian theory of psychoanalysis, the Skinnerian theory of reinforcement, and connectionism have vied for the attention of psychologists.

Only within the past few decades have we acquired the conceptual tools to synthesize our understanding of the human mind under one unifying theoretical framework—that of evolutionary psychology. This discipline pulls together findings from all disciplines of the mind, including those of brain imaging; learning and memory; attention, emotion, and passion; attraction, jealousy, and sex; self-esteem, status, and self-sacrifice; parenting, persuasion, and perception; kinship, warfare, and aggression; cooperation, altruism, and helping; ethics, morality, religion, and medicine; and commitment, culture, and consciousness. This book offers an introduction to evolutionary psychology and provides a road map to this new science of the mind.

This chapter starts by tracing the major landmarks in the history of evolutionary biology that were critical to the emergence of evolutionary psychology. Then we turn to the history of the field of psychology and show the progression of accomplishments that led to the need for integrating evolutionary theory with modern psychology.

LANDMARKS IN THE HISTORY OF EVOLUTIONARY THINKING

We begin our examination of the history of evolutionary thinking well before the contributions of Charles Darwin and then consider the various milestones in its development through the end of the twentieth century.

Evolution before Darwin

Evolution refers to change over time. Change in life forms was postulated by scientists to have occurred long before Darwin published his classic 1859 book *On the Origin of Species* (see Glass, Temekin, & Straus, 1959; and Harris, 1992, for historical treatments).

Jean Baptiste Lamarck (1744–1829) was one of the first scientists to use the word *biologie*, which recognized the study of life as a distinct science. Lamarck believed in two major causes of species change: first, a natural tendency for each species to progress toward

a higher form and, second, the inheritance of acquired characteristics. Lamarck proposed that animals must struggle to survive and this struggle causes their nerves to secrete a fluid that enlarges the organs involved in the struggle. Giraffes evolved long necks, he thought, through their attempts to eat from higher and higher leaves (recent evidence suggests that long necks may also play a role in mate competition through physical battles). Lamarck believed that the neck changes that came about from these strivings were passed down to succeeding generations of giraffes, hence the phrase "the inheritance of acquired characteristics." Another theory of change in life forms was developed by Baron Georges Léopold Chrétien Frédérick Dagobert Cuvier (1769–1832). Cuvier proposed a theory called *catastrophism*, according to which species are extinguished periodically by sudden catastrophes, such as meteorites, and then replaced by different species.

Biologists before Darwin also noticed the bewildering variety of species, some with astonishing structural similarities. Humans, chimpanzees, and orangutans, for example, all have exactly five digits on each hand and foot. The wings of birds are similar to the flippers of seals, perhaps suggesting that one was modified from the other (Daly & Wilson, 1983). Comparisons among these species suggested that life was not static, as some scientists and theologians had argued. Further evidence suggesting change over time also came from the fossil record. Bones from older geological strata were not the same as bones from more recent geological strata. These bones would not be different, scientists reasoned, unless there had been a change in organic structure over time.

Another source of evidence came from comparing the embryological development of different species (Mayr, 1982). Biologists noticed that such development was strikingly similar in species that otherwise seemed very different from one another. An unusual loop-like pattern of arteries close to the bronchial slits characterizes the embryos of mammals, birds, and frogs. This evidence suggested, perhaps, that these species might have come from the same ancestors millions of years ago. All these pieces of evidence, present before 1859, suggested that life was not fixed or unchanging. The biologists who believed that life forms changed over time called themselves evolutionists.

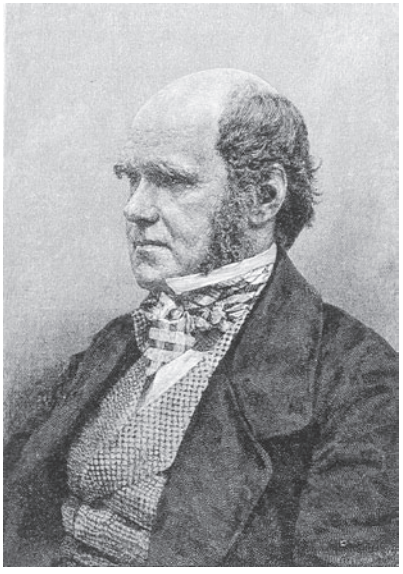
Another key observation had been made by evolutionists before Darwin: Many species possess characteristics that seem to have a purpose. The porcupine's quills help it fend off predators. The turtle's shell helps to protect its tender organs from the hostile forces of nature. The beaks of many birds are designed to aid in cracking nuts. This apparent functionality, so abundant in nature, required an explanation.

Missing from the evolutionists' accounts before Darwin, however, was a theory to explain how change might take place over time and how such seemingly purposeful structures such as the giraffe's long neck and the porcupine's sharp quills could have come about. A causal process to explain these biological phenomena was needed. Charles Darwin provided the theory of just such a process.

Darwin's Theory of Natural Selection

Darwin's task was more difficult than it might at first appear. He wanted not only to explain *why* change takes place over time in life forms, but also to account for the particular ways it proceeds. He wanted to determine how new species emerge (hence the title of his book *On the Origin of Species*), as well as why others vanish or go extinct. Darwin wanted to explain why the component parts of animals—the long necks of giraffes, the wings of birds, and the trunks of elephants—existed in those particular forms. And he wanted to explain the apparent purposive quality of those forms, or why they seem to function to help organisms accomplish specific tasks.

The answers to these puzzles can be traced to a voyage Darwin took after graduating from Cambridge University. He traveled the world as a naturalist on a ship, the *Beagle*, for a five-year period, from 1831 to 1836. During this voyage, he collected dozens of samples of birds and other animals from the Galápagos Islands in the Pacific Ocean. On returning from his voyage, he discovered that the Galápagos finches, which he had presumed were all of the same species, actually varied so much that they constituted different species. Indeed, each island in the Galápagos had a distinct species of finch. Darwin determined that these different finches had a common ancestor but had become different from each other because of the local ecological conditions on each island. This geographic variation was pivotal to Darwin's conclusion that species are not immutable but can change over time.



Charles Darwin created a scientific revolution in biology with his theory of natural selection. His book On the Origin of Species *(1859) is packed with theoretical arguments and detailed empirical data that he amassed over the twenty-five years prior to the book's publication.*

What could account for why species change? Darwin struggled with several different theories of the origins of change, but rejected all of them because they failed to explain a critical fact: the existence of adaptations. Darwin wanted to account for change, of course, but he also wanted to account for why organisms appeared so well designed for their local environments.

> It was . . . evident that [these other theories] could [not] account for the innumerable cases in which organisms of every kind are beautifully adapted to their habits of life—for instance, a woodpecker or tree-frog to climb trees, or a seed for dispersal by hooks and plumes. I had always been much struck by such adaptations, and until these could be explained it seemed to me almost useless to endeavour to prove by indirect evidence that species have been modified. (Darwin, from his autobiography; cited in Ridley, 1996, p. 9)

Darwin unearthed a key to the puzzle of adaptations in Thomas Malthus's *An Essay on the Principle of Population* (published in 1798), which introduced Darwin to the notion that organisms exist in numbers far greater than can survive and reproduce. The result must be a "struggle for existence," in which favorable variations tend to be preserved and unfavorable ones tend to die out. When this process is repeated generation after generation, the end result is the formation of new adaptation.

More formally, Darwin's answer to all these puzzles of life was the theory of *natural selection* and its three essential ingredients: *variation, inheritance,* and *differential reproductive success.*[1] First, organisms vary in all sorts of ways, such as in wing length, trunk strength, bone mass, cell structure, fighting ability, defensive ability, and social cunning. Variation is essential for the process of evolution to operate—it provides the "raw materials" for evolution.

Second, only some of these variations are inherited—that is, passed down reliably from parents to their offspring, who then pass them on to their offspring down through the generations. Other variations, such as a wing deformity caused by an environmental accident, are not inherited by offspring. Only those variations that are inherited play a role in the evolutionary process.

The third critical ingredient of Darwin's theory is selection. Organisms with some heritable variants leave more offspring *because* those attributes help with the tasks of *survival* or *reproduction*. In an environment in which the primary food source might be nut-bearing trees or bushes, some finches with a particular shape of beak, for example,

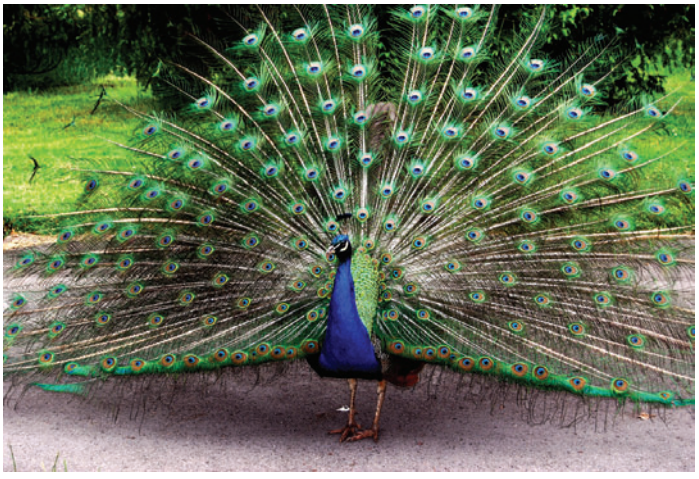
[1] The theory of natural selection was discovered independently by Alfred Russel Wallace (Wallace, 1858); Darwin and Wallace co-presented the theory at a meeting of the Linnean Society.

might be better able to crack nuts and get at their meat than finches with other shapes of beaks. More finches who have beaks better shaped for nut cracking survive than those with beaks poorly shaped for nut cracking.

An organism can survive for many years, however, and still not pass on its inherited qualities to future generations. To pass its inherited qualities to future generations, it must reproduce. Thus, *differential reproductive success*, brought about by the possession of heritable variants that increase or decrease an individual's chances of surviving and reproducing, is the "bottom line" of evolution by natural selection. Differential reproductive success or failure is defined by reproductive success relative to others. The characteristics of organisms that reproduce more than others, therefore, get passed down to future generations at a relatively greater frequency. Because survival is usually necessary for reproduction, it took on a critical role in Darwin's theory of natural selection.

Darwin's Theory of Sexual Selection

Darwin had a wonderful scientific habit of noticing facts that seemed inconsistent with his theories. He observed several that seemed to contradict his theory of natural selection, which he sometimes referred to as the theory of "survival selection." First, he noticed weird structures that seemed to have absolutely nothing to do with survival; the brilliant plumage of peacocks was a prime example. How could this strange luminescent structure possibly have evolved? The plumage is obviously metabolically costly to the peacock. Furthermore, it seems like an open invitation to predators. Darwin became so obsessed with this apparent anomaly that he once commented, "The sight of a feather in a peacock's tail, whenever I gaze at it makes me sick!" (quoted in Cronin, 1991, p. 113). Darwin also observed that in some species, the sexes differed dramatically in size and structure. Why would the sexes differ so much, Darwin wondered, when both males and female confront essentially the same problems of survival, such as eating, fending off predators, and combating diseases?



Darwin got sick at the sight of a peacock because, initially, the brilliant plumage seemed to have no obvious survival value and hence could not be explained by his original theory of natural selection. He eventually developed the theory of sexual selection, which could explain the peacock's plumage, and presumably he stopped getting sick when he witnessed one.

Darwin's answer to these apparent contradictions to the theory of natural selection was to devise a second evolutionary theory: the theory of *sexual selection*. In contrast to the theory of natural selection, which focused on adaptations that have arisen as a consequence of successful survival, the theory of sexual selection focused on adaptations that arose as a consequence of successful mating. Darwin proposed two primary means by which sexual selection could operate. The first is *intrasexual competition*—competition between members of one sex, the outcomes of which contributed to mating access to the other sex. The prototype of intrasexual competition is two stags locking horns in combat. The victor gains sexual access to a female either directly or through controlling territory or resources desired by the female. The loser typically fails to mate. Whatever qualities lead to success in the same-sex contests, such as greater size, strength, or athletic ability, will be passed on to the next generation because of the mating success of the victors. Qualities that are linked with losing fail to get passed on. So evolution—change over time—can occur simply as a consequence of intrasexual competition.

The second means by which sexual selection could operate is *intersexual selection*, or preferential mate choice. If members of one sex have some consensus about the qualities that are desired in members of the opposite sex, then individuals of the opposite sex who possess those qualities will be preferentially chosen as mates. Those who lack the desired qualities fail to get mates. In this case, evolutionary change occurs simply because the qualities that are desired in a mate increase in frequency with the passing of each generation. If females prefer to mate with males who give them gifts of food, for example, then males with qualities that lead to success in acquiring food gifts will increase in frequency over time. Darwin called the process of intersexual selection *female choice* because he observed that throughout the animal world, females of many species were discriminating or choosy about whom they mated with.

Stags locking horns in combat is a form of sexual selection called intrasexual competition. The qualities that lead to success in these same-sex combats get passed on in greater numbers to succeeding generations because the victors gain increased mating access to members of the opposite sex.

Darwin's theory of sexual selection succeeded in explaining the anomalies that worried him. The peacock's tail, for example, evolved because of the process of intersexual selection: Peahens prefer to mate with males who have the most brilliant and luminescent plumage. Males are often larger than females in species in which males engage in physical combat with other males for sexual access to females—a sex difference caused by the process of intrasexual competition.

The Role of Natural Selection and Sexual Selection in Evolutionary Theory

Darwin's theories of natural and sexual selection are relatively simple to describe, but many sources of confusion surround them even to this day. This section clarifies some important aspects of selection and its place in understanding evolution.

First, natural selection and sexual selection are not the only causes of evolutionary change. Some changes, for example, can occur because of a process called *genetic drift*, which is defined as random changes in the genetic makeup of a population. Random changes come about through several processes, including mutation (a random hereditary change in the DNA), founder effects, and genetic bottlenecks. *Founder effects* occur when a small portion of a population establishes a new colony and the founders of the new colony are not genetically representative of the original population. Imagine, for example, that the 200 colonizers who migrate to a new island happen by chance to include an unusually large number of redheads. As the population on the island grows, say, to 2,000 people, it will contain a larger proportion of redheads than did the original population from which the colonizers came. Thus, founder effects can produce evolutionary change—in this example, an increase in genes coding for red hair. A similar random change can occur through genetic bottlenecks, which happen when a population shrinks, perhaps owing to a random catastrophe such as an earthquake. The survivors of the random catastrophe carry only a subset of the genes of the original population. In sum, although natural selection is the *primary* cause of evolutionary change and the only known cause of adaptations, it is not the only cause of evolutionary change. Genetic drift—through mutations, founder effects, and genetic bottlenecks—can also produce change in the genetic makeup of a population.

Second, evolution by natural selection is not forward-looking and is not "intentional." The giraffe does not spy the juicy leaves stirring high in the tree and "evolve" a longer neck. Rather, those giraffes that, owing to an inherited variant, happen to have longer necks have an advantage over other giraffes in getting to those leaves. Hence they have a greater chance of surviving and thus of passing on their slightly longer necks to their offspring. Natural selection merely acts on variants that happen to exist. Evolution is not intentional and cannot look into the future and foresee distant needs.

Another critical feature of selection is that it is *gradual*, at least when evaluated relative to the human life span. The short-necked ancestors of giraffes did not evolve long necks overnight or even over the course of a few generations. It has taken dozens, hundreds, thousands, and in some cases millions of generations for the process of selection to gradually shape the organic mechanisms we see today. Of course, some changes occur extremely slowly, others more rapidly. And there can be long periods of no change, followed by a relatively sudden change, a phenomenon known as "punctuated equilibrium" (Gould & Eldredge, 1977). But even these "rapid" changes occur in tiny increments in each generation and take hundreds or thousands of generations to occur.

Darwin's theory of natural selection offered a powerful explanation for many baffling aspects of life. It explained the origin of new species (although Darwin failed to recognize the full importance of geographic isolation as a precursor to natural selection in the formation of new species; see Cronin, 1991). It accounted for the modification of organic structures over time. It accounted for the apparent purposive quality of the component parts of those structures—that is, they seemed "designed" to serve particular functions that contributed to survival or reproduction.

Perhaps most astonishing to some (but upsetting to others), in 1859 Darwin's natural selection united all species into one grand tree of descent in one bold stroke. For the first time in recorded history, each species was viewed as being connected with all other species through a common ancestry. Human beings and chimpanzees, for example, share more than 98 percent of each other's DNA and shared a common ancestor roughly 6 or 7 million years ago (Wrangham & Peterson, 1996). Even more startling is the fact that many human genes turn out to have counterpart genes in a transparent worm called *Caenorhabditis elegans*. They are highly similar in chemical structure, suggesting that humans and this worm evolved from a distant common ancestor (Wade, 1997). In short, Darwin's theory made it possible to locate humans in the grand tree of life, showing their place in nature and their links with all other living creatures.

Darwin's theory of natural selection created a storm of controversy. Lady Ashley, a contemporary of Darwin, remarked on hearing his theory that human beings descended from apes: "Let's hope it's not true; but if it is true, let's hope that it does not become widely known." In a famous debate at Oxford University, Bishop Wilberforce bitingly asked his rival debater Thomas Huxley whether the "ape" from which Huxley descended was on his grandmother's or his grandfather's side.

Even biologists at the time were highly skeptical of Darwin's theory of natural selection. One objection was that Darwinian evolution lacked a coherent theory of inheritance. Darwin himself preferred a "blending" theory of inheritance, in which offspring are mixtures of their parents, much like pink paint is a mixture of red paint and white paint. This theory of inheritance is now known to be wrong, so early critics were correct in the objection that the theory of natural selection lacked a solid theory of heredity.

Another objection was that some biologists could not imagine how the early stages of the evolution of an adaptation could be useful to an organism. How could a partial

wing help a bird, if a partial wing is insufficient for flight? How could a partial eye help a reptile, if a partial eye is insufficient for sight? Darwin's theory of natural selection requires that each and every step in the gradual evolution of an adaptation be advantageous in the currency of reproduction. Thus, partial wings and eyes must yield an adaptive advantage, even before they evolve into fully developed wings and eyes. For now, it is sufficient to note that partial forms can indeed offer adaptive advantages; partial wings, for example, can keep a bird warm and aid in mobility for catching prey or avoiding predators, even if they don't afford full flight. This objection to Darwin's theory is therefore surmountable (Dawkins, 1986). Further, it is important to stress that just because biologists or other scientists have difficulty imagining certain forms of evolution, such as how a partial wing might be useful, that is not a good argument against such forms having evolved. This "argument from ignorance," or as Dawkins (1982) calls it, "the argument from personal incredulity," is not good science, however intuitively compelling it might sound. Indeed, most people find evolution by natural selection and evolutionary time scales extremely difficult to conceptualize (Rodeheffer, Daugherty, & Brase, 2011).

A third objection came from religious creationists, many of whom viewed species as immutable (unchanging) and created by a deity rather than by the gradual process of evolution by selection. Furthermore, Darwin's theory implied that the emergence of humans and other species was "blind," resulting from the slow, unplanned, cumulative process of selection. This contrasted with the view that creationists held of humans (and other species) as part of God's grand plan or intentional design. Darwin had anticipated this reaction, and apparently delayed the publication of his theory in part because he was worried about upsetting his wife, Emma, who was deeply religious.

The controversy continues to this day. Although Darwin's theory of evolution, with some important modifications, is the unifying and nearly universally accepted theory within the biological sciences, its application to humans, which Darwin clearly envisioned, still meets some resistance. But humans are not exempt from the evolutionary process. We finally have the conceptual tools to complete Darwin's revolution and forge an evolutionary psychology of the human species.

Evolutionary psychology is able to take advantage of key theoretical insights and scientific discoveries that were not known in Darwin's day. The first among these is the physical basis of inheritance—the gene.

The Modern Synthesis: Genes and Particulate Inheritance

When Darwin published *On the Origin of Species*, he did not know the nature of the mechanism by which inheritance occurred. An Austrian monk named Gregor Mendel showed that inheritance was "particulate," and not blended. That is, the qualities of the parents are not blended with each other, but rather are passed on intact to their offspring in distinct packets called *genes*. Furthermore, parents must be born with the genes they pass on; genes cannot be acquired by experience.

Mendel's discovery that inheritance is particulate, which he demonstrated by cross-breeding different strains of pea plants, remained unknown to most of the scientific community for some thirty years. Mendel had sent Darwin copies of his papers, but either they remained unread or Darwin did not recognize their significance.

A *gene* is defined as the smallest discrete unit that is inherited by offspring intact, without being broken up or blended—this was Mendel's critical insight. *Genotypes*, in contrast, refer to the entire collection of genes within an individual. Genotypes, unlike