



DAVID M. BUSS

# EVOLUTIONARY PSYCHOLOGY

The New Science of the Mind

SIXTH EDITION



# Evolutionary Psychology

Where did we come from? What is our connection with other life forms? What are the mechanisms of mind that define what it means to be a human being? Evolutionary psychology is a revolutionary new science, a true synthesis of modern principles of psychology and evolutionary biology.

Since the publication of the award-winning first edition of *Evolutionary Psychology*, there has been an explosion of research within the field. In this book, David M. Buss examines human behavior from an evolutionary perspective, providing students with the conceptual tools needed to study evolutionary psychology and apply them to empirical research on the human mind. This edition contains expanded coverage of cultural evolution, with a new section on culture–gene co-evolution, additional studies discussing interbreeding between modern humans and Neanderthals, expanded discussions of evolutionary hypotheses that have been empirically disconfirmed, and much more!

*Evolutionary Psychology* features a wealth of student-friendly pedagogy including critical-thinking questions and case study boxes designed to show how to apply evolutionary psychology to real-life situations. It is also accompanied by a thoroughly updated companion website featuring PowerPoints for each chapter, test bank questions, and links to web resources and videos.

*Evolutionary Psychology* is an invaluable resource for undergraduates studying psychology, biology, and anthropology.

**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 six 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.





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# **Evolutionary Psychology**

The New Science of the Mind

Sixth Edition

David M. Buss

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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



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# 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 200 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 cultural evolution, with a new section on culture–gene co-evolution.
- New studies on evidence for a small amount of interbreeding between modern humans and Neanderthals.
- New large-scale studies on ovulation effects on women’s mate preferences.
- Expanded discussion of evolutionary hypotheses that have been empirically disconfirmed.
- Expanded discussion of the emotion of “disgust” as central to the behavioral immune system and “sexual disgust” as a specific evolved defense and links to preferred mating strategy.
- Discovery of a new cue to physical attractiveness—lumbar curvature.
- New findings on the emotion of *sexual regret* and gender differences therein from the highly gender-egalitarian country of Norway.
- Mate preferences among the semi-nomadic Himba of Namibia.
- Discoveries of the effects of marriage on longevity.
- Discussion of “mismatches” between ancestral and modern environments.
- Expanded discussion of theories and empirical tests of homosexuality, bisexuality, and other sexual orientations.
- Use of modern apps, such as Snapchat, to seek mating opportunities.
- New discussion of the method of evolutionary computer simulations and agent-based modeling.
- Effects of physical and behavioral resemblance of child to father on paternal investment.
- New work on food aversions in pregnant women.
- Eye-tracking studies showing that dangerous predators capture our visual attention, even in the face of visual distractions.
- Study of 53 cultures reveals an effect of “burdensomeness to kin” on suicidal ideation and suicide.
- New section on accidental death.
- Influence tactics children and parents use on each other.
- Effects of genetic relatedness, such as full versus half-siblings, on kin investment.
- Evidence from Icelandic Vikings on causes of Viking raids and evidence that kin protect against getting killed in raids.
- Empirical refutation of a kin-based hypothesis about sexual infidelity.
- New section on need-based transfers, risk pooling, and social insurance.
- Use of social media and cyber-bullying in intrasexual competition.
- Eye-tracking studies reveal spontaneous assessment of physical formidability in others.
- Individual difference predictors of the sexual over-perception bias.
- “Dark Triad” personality traits predict sexual deception and sexual harassment.
- Massive study of 63,000 people reveals strong gender differences in upset over sexual versus emotional infidelity among heterosexuals, but not among those with other sexual orientations.
- New study of sexual jealousy among women in Mozambique.
- Women’s resistance tactics to male mate guarding.
- “Death before dishonor”—the tremendous importance of social reputation.
- New study of 33 non-industrial populations reveals effects of men’s status on a variety of reproductive outcomes.
- New research on the emotions of pride and shame in status and reputation.
- New research on the importance of physical formidability in modern status hierarchies.
- Expanded section on the evolutionary psychology of religion and the role of “Big Gods” in large-scale cooperation.

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/cw/Buss](http://www.routledge.com/cw/Buss).

# 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 25 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 37 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.

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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.





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# 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 20th 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 Frédéric 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.

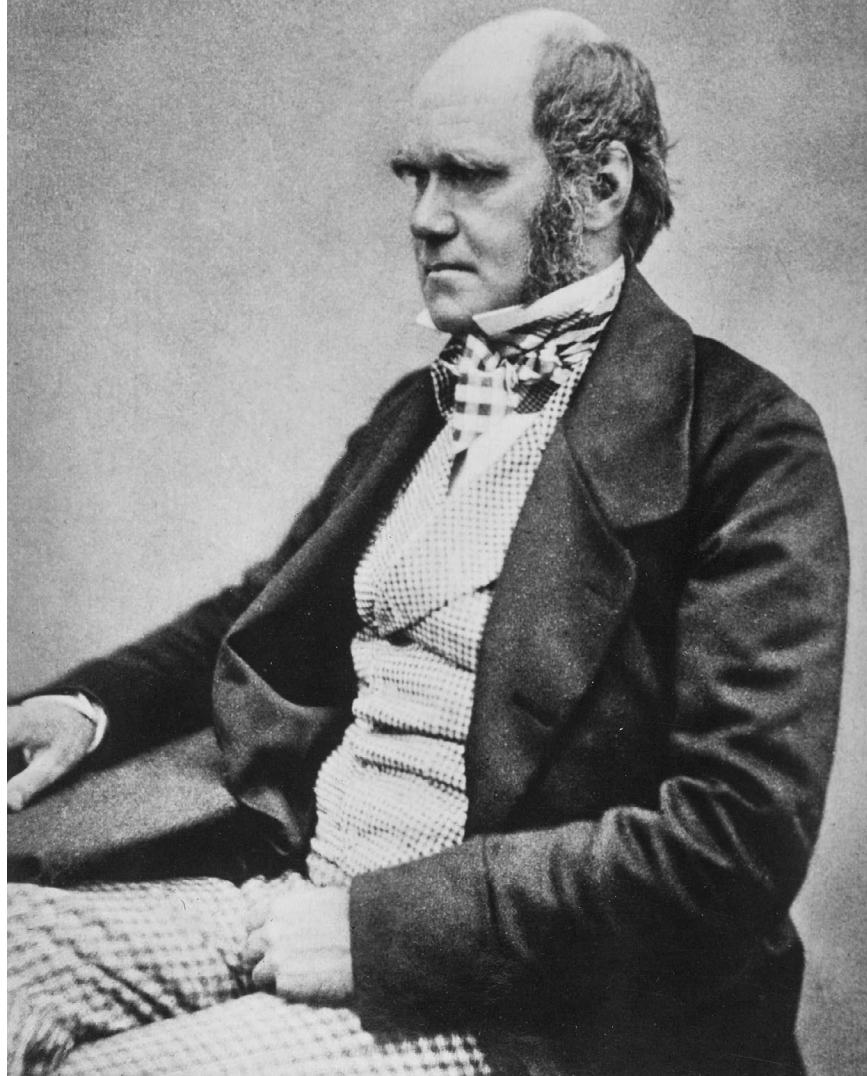
Missing from the evolutionists' accounts before Darwin, however, was a theory to explain how change might take place over time and how such seemingly purposeful structures such as the giraffe's long neck and the porcupine's sharp quills could have come about. A causal process to explain these biological 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 5-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.

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.



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 25 years prior to the book's publication.

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*.<sup>1</sup>

<sup>1</sup> 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.

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, 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 females 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.



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.

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.

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

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 dozens, 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