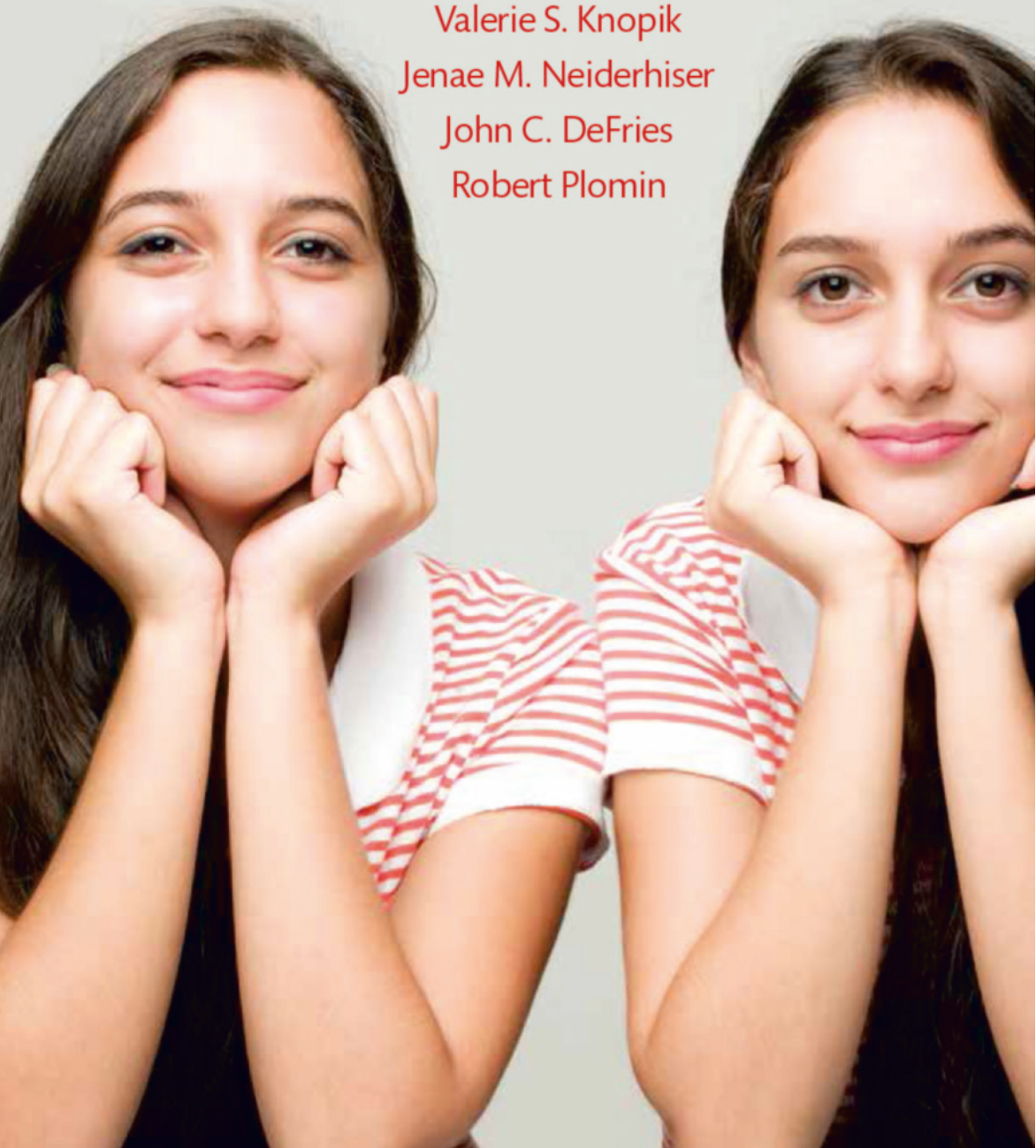
Seventh Edition

BEHAVIORAL GENETICS

Valerie S. Knopik
Jenae M. Neiderhiser
John C. DeFries
Robert Plomin



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Contents

CHAPTER SEVEN

CHAPTER EIGHT

CHAPTER NINE

CHAPTER SEVENTEEN

CHAPTER EIGHTEEN

CHAPTER NINETEEN

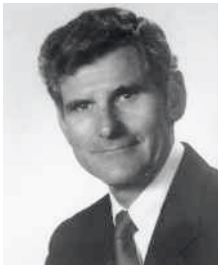
About the Authors

Bethany O Photography

VALERIE S. KNOPIK is Director of the Division of Behavioral Genetics at Rhode Island Hospital and a professor in the Departments of Psychiatry & Human Behavior and Behavioral & Social Sciences at the Warren Alpert School of Medicine at Brown University. She received her doctorate in psychology from the University of Colorado, Boulder, in 2000, where she worked with John DeFries and conducted research in the Colorado Learning Disabilities Research Center. She subsequently completed a fellowship in psychiatric genetics and genetic epidemiology at Washington University School of Medicine in St. Louis from 2000 to 2002 and continued as junior faculty for two years. She joined the faculty at Brown University in 2004 and holds an adjunct associate professor appointment at Washington University School of Medicine in St. Louis. Knopik's primary area of interest is the joint effect of genetic and environmental (specifically prenatal and early postnatal) risk factors on child and adolescent externalizing behavior, associated learning and cognitive deficits, and later substance use. She is currently conducting a family study, the Missouri Mothers and Their Children Study, that is designed to disentangle prenatal environmental effects from genetic effects on child and adolescent behavior. Her work has been recognized by the Research Society for Alcoholism; the NIDA Genetics Workgroup; and the Behavior Genetics Association, from whom she received the Fuller and Scott Early Career Award in 2007. She was the secretary of the Behavior Genetics Association (2013–2016), currently serves as an associate editor of *Behavior Genetics*, and is on the editorial board of *Psychological Medicine*.

Photo by Tracy Tomei

JENAE M. NEIDERHISER is Liberal Arts Research Professor of Psychology at Penn State University. After receiving her PhD in Human Development and Family Studies from Penn State University in 1994, she joined the faculty of the Center for Family Research, Department of Psychiatry and Behavioral Science, at The George Washington University in Washington, DC, advancing from assistant research professor to professor from 1994 to 2007. In 2007 she joined the Department of Psychology at Penn State University, and she also holds the appointment of Professor of Human Development and Family Studies and is co-director of the Gene and Environment Research Initiative at Penn State University. Neiderhiser's work has focused on how genes and environments work together throughout the life span. She has had a particular focus on genotype-environment correlation and how individuals shape their own environments, especially within the family. In her pursuit of this question she has collaborated on developing a number of novel or underutilized research designs, including the extended children of twins design and an ongoing prospective adoption study, the Early Growth and Development Study. Neiderhiser is an associate editor for *Frontiers in Behavioral and Psychiatric Genetics* and is on the editorial board of several developmental psychology journals.



Jerry Avery/Avery Portrait Studios

JOHN C. DEFRIES is a faculty fellow, Institute for Behavioral Genetics, and professor emeritus, Department of Psychology and Neuroscience, University of Colorado, Boulder. After receiving his doctorate in agriculture (with specialty training in quantitative genetics) from the University of Illinois in 1961, he remained on the faculty of the University of Illinois for six years. In 1962, he began research on mouse behavioral genetics, and the following year he was a research fellow in genetics at the University of California, Berkeley. After returning to Illinois in 1964, DeFries initiated an extensive genetic analysis of open-field behavior in laboratory mice. Three years later, he joined the Institute for Behavioral Genetics, and he served as its director from 1981 to 2001. DeFries and Steve G. Vandenberg founded the journal *Behavior Genetics* in 1970, and DeFries and Robert Plomin founded the Colorado Adoption Project in 1975. For over three decades, DeFries' major research interest has concerned the genetics of reading disabilities, and he founded the Colorado Learning Disabilities Research Center with Richard K. Olson in 1990. He served as president of the Behavior Genetics Association in 1982 and 1983, receiving the association's Th. Dobzhansky Award for Outstanding Research in 1992, and he became a fellow of the American Association for the Advancement of Science (Section J, Psychology) in 1994 and the Association for Psychological Science in 2009.

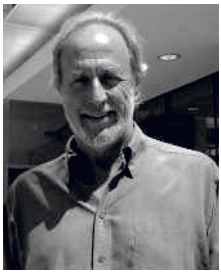


Photo by Emily Smith-Woolley

ROBERT PLOMIN is MRC Research Professor of Behavioral Genetics at the Social, Genetic and Developmental Psychiatry Centre at the Institute of Psychiatry, Psychology and Neuroscience in London. He received his doctorate in psychology from the University of Texas, Austin, in 1974, one of the few graduate programs in psychology that offered a specialty in behavioral genetics at that time. He then joined the faculty of the Institute for Behavioral Genetics at the University of Colorado, Boulder, where he began working with John DeFries. Together, they created the longitudinal Colorado Adoption Project of behavioral development, which has continued for more than 30 years. Plomin worked at Penn State University from 1986 until 1994, when he moved to the Institute of Psychiatry, Psychology and Neuroscience in London to help launch the Social, Genetic and Developmental Psychiatry Centre. The goal of his research is to bring together genetic and environmental research strategies to investigate behavioral development. Plomin launched a study of all twins born in England during 1994 to 1996, focusing on developmental delays in childhood. He served as secretary (1983–1986) and president (1989–1990) of the Behavior Genetics Association, and has received lifetime achievement awards from the Behavior Genetics Association (2002), American Psychological Society (2005), the Society for Research in Child Development (2005), and the International Society for Intelligence Research (2011).

Preface

Some of the most important scientific accomplishments of the twentieth century occurred in the field of genetics, beginning with the rediscovery of Mendel's laws of heredity and ending with the first draft of the complete DNA sequence of the human genome. The pace of discoveries has continued to accelerate in the first part of the twenty-first century. One of the most dramatic developments in the behavioral sciences during the past few decades is the increasing recognition and appreciation of the important contribution of genetic factors to behavior. Genetics is not a neighbor chatting over the fence with some helpful hints—it is central to the behavioral sciences. In fact, genetics is central to all the life sciences and gives the behavioral sciences a place in the biological sciences. Genetic research includes diverse strategies, such as twin and adoption studies (called quantitative genetics), which investigate the influence of genetic and environmental factors, as well as strategies to identify specific genes (called molecular genetics). Behavioral geneticists apply these research strategies to the study of behavior in biopsychology, clinical psychology, cognitive psychology, developmental psychology, educational psychology, neuroscience, psychopharmacology, and social psychology, and increasingly in other areas of the social sciences such as behavioral economics and political science.

The goal of this book is to share with you our excitement about behavioral genetics, a field in which we believe some of the most important discoveries in the behavioral sciences have been made in recent years. This seventh edition continues to emphasize what we know about genetics in the behavioral sciences rather than how we know it. Its goal is not to train students to become behavioral geneticists but rather to introduce students in the behavioral, social, and life sciences to the field of behavioral genetics.

This seventh edition represents a passing of the baton to the next generation. Two new and younger authors (Knopik and Neiderhiser) have joined forces with two authors from the previous editions (Plomin and DeFries), which has brought new energy and ideas that help to capture developments in this fast-moving and highly interdisciplinary field. In addition to updating research with more than 600 new references, this edition represents a substantial reorganization. One feature of this edition is that it continues to highlight the value of behavioral genetics for understanding the environment (Chapter 7) and its interplay with genetics (Chapter 8). At first, chapters on the environment might seem odd in a textbook on genetics, but in fact the environment is crucial at every step in the pathways between genes, brain, and behavior. One of the oldest controversies in the behavioral sciences, the so-called nature (genetics) versus nurture (environment) controversy, has given way to a view that both nature and nurture are important for complex behavioral traits. Moreover, genetic research has made important discoveries about how the environment affects behavioral development.

We have also expanded our coverage of genomewide sequencing, gene expression, and especially epigenetics as pathways between genes and behavior (Chapter 10). Our review of cognitive abilities includes a new section on neurocognitive measures (Chapter 11). Coverage of psychopathology and substance abuse has been expanded (Chapters 13, 14, 15, and 17), a new section on obesity and the microbiome has been included (Chapter 18), and a new chapter on aging has been added (Chapter 19), reflecting the enormous growth of genetic research in these areas. We have also reorganized the presentation of the history of the field of behavioral genetics (Chapter 2).

We begin with an introductory chapter that will, we hope, whet your appetite for learning about genetics in the behavioral sciences. The next few chapters present historical perspectives, the basic rules of heredity, its DNA basis, and the methods used to find genetic influence and to identify specific genes. The rest of the book highlights what is known about genetics in the behavioral sciences. The areas about which the most is known are cognitive abilities and disabilities, psychopathology, personality, and substance abuse. We also consider areas of behavioral sciences that were introduced to genetics more recently, such as health psychology and aging. Throughout these chapters, quantitative genetics and molecular genetics are interwoven. One of the most exciting developments in behavioral genetics is the use of molecular genetics to assess the substantial genetic influence on behavioral traits. The final chapter looks to the future of behavioral genetics.

Because behavioral genetics is an interdisciplinary field that combines genetics and the behavioral sciences, it is complex. We have tried to write about it as simply as possible without sacrificing honesty of presentation. Although our coverage is representative, it is by no means exhaustive or encyclopedic. History and methodology are relegated to boxes and an appendix to keep the focus on what we now know about genetics and behavior. The appendix, by Shaun Purcell, presents an overview of statistics, quantitative genetic theory, and a type of quantitative genetic analysis called

model fitting. In this edition we have retained an interactive website that brings the appendix to life with demonstrations: http://pngu.mgh.harvard.edu/purcell/bgim/. The website was designed and written by Shaun Purcell. A list of other useful websites, including those of relevant associations, databases, and other resources, is included after the appendix. Following the websites list is a glossary; the first time each glossary entry appears in the text it is shown in boldface type.

We thank the following individuals, who gave us their very helpful advice for this new edition: Avshalom Caspi, *Duke University;* Thalia Eley, *King's College London;* John McGeary, *Providence VA Medical Center;* Rohan Palmer, *Rhode Island Hospital and Brown University;* Nancy Pedersen, *Karolinska Institute;* Chandra Reynolds, *University of California, Riverside;* Helen Tam, *Pennsylvania State University.*

We also gratefully acknowledge the important contributions of the coauthors of the previous editions of this book: Gerald E. McClearn, Michael Rutter, and Peter McGuffin. We especially wish to thank Ashten Bartz, who helped us organize the revision and references and prepare the final manuscript. Finally, we thank our editors at Worth Publishers, Sarah Berger and Christine M. Cardone, our Worth editorial assistant, Melissa Rostek, and the Senior Project Editor, Liz Geller, who helped support our efforts in this new edition.

CHAPTER **ONE**

Overview

Some of the most important recent discoveries about behavior involve genetics. For example, autism (Chapter 15) is a severe disorder beginning early in childhood in which children withdraw socially, not engaging in eye contact or physical contact, with marked communication deficits and stereotyped behavior. Until the 1980s, autism was thought to be environmentally caused by cold, rejecting parents or by brain damage. But genetic studies comparing the risk for identical twins, who are identical genetically (like clones), and fraternal twins, who are only 50 percent similar genetically, indicate substantial genetic influence. If one member of an identical twin pair is autistic, the risk that the other twin is also autistic is very high, about 60 percent. In contrast, for fraternal twins, the risk is low. Molecular genetic studies are attempting to identify the **genes*** that contribute to the genetic susceptibility to autism.

Later in childhood, a very common concern, especially in boys, is a cluster of attention-deficit and disruptive behavior problems called attention-deficit / hyperactivity disorder (ADHD) (Chapter 15). Results obtained from numerous twin studies have shown that ADHD is highly heritable (genetically influenced). ADHD is one of the first behavioral areas in which specific genes have been identified. Although many other areas of childhood psychopathology show genetic influence, none are as heritable as autism and ADHD. Some behavior problems, such as childhood anxiety and depression, are only moderately heritable, and others, such as antisocial behavior in adolescence, show little genetic influence.

More relevant to college students are personality traits such as risk-taking (often called sensation seeking) (Chapter 16), drug use and abuse (Chapter 17), and learning abilities (Chapters 11). All these domains have consistently shown substantial genetic

** Boldface indicates the first appearance in the text of a word or phrase that is in the Glossary.*

influence in twin studies and have recently begun to yield clues concerning individual genes that contribute to their **heritability.** These domains are also examples of an important general principle: Not only do genes contribute to disorders such as autism and ADHD, they also play an important role in normal variation. For example, you might be surprised to learn that differences in weight are almost as heritable as differences in height (Chapter 18). Even though we can control how much we eat and are free to go on crash diets, differences among us in weight are much more a matter of nature (genetics) than nurture (environment). Moreover, normal variation in weight is as highly heritable as overweight or obesity. The same story can be told for behavior. Genetic differences do not just make some of us abnormal; they contribute to differences among all of us in normal variation for mental health, personality, and cognitive abilities.

One of the greatest genetic success stories involves the most common behavioral disorder in later life, the terrible memory loss and confusion of Alzheimer disease, which strikes as many as one in five individuals in their eighties (Chapter 19). Although Alzheimer disease rarely occurs before the age of 65, some early-onset cases of dementia run in families in a simple manner that suggests the influence of single genes. Three genes have been found to be responsible for many of these rare early-onset cases.

These genes for early-onset Alzheimer disease are not responsible for the much more common form of Alzheimer disease that occurs after 65 years of age. Like most behavioral disorders, late-onset Alzheimer disease is not caused by just a few genes. Still, twin studies indicate genetic influence. If you have a twin who has late-onset Alzheimer disease, your risk of developing it is twice as great if you are an identical twin rather than a fraternal twin. These findings suggest genetic influence.

Even for complex disorders like late-onset Alzheimer disease, it is now possible to identify genes that contribute to the risk for the disorder. For example, a gene has been identified that predicts risk for late-onset Alzheimer disease far better than any other known risk factor. If you inherit one copy of a particular form (**allele**) of the gene, your risk for Alzheimer disease is about four times greater than if you have another allele. If you inherit two copies of this allele (one from each of your parents), your risk is much greater. Finding these genes for early-onset and late-onset Alzheimer disease has greatly increased our understanding of the brain processes that lead to dementia.

Another example of recent genetic discoveries involves intellectual disability (Chapter 12). The single most important cause of intellectual disability is the inheritance of an entire extra **chromosome** 21. (Our **DNA**, the basic hereditary molecule, is packaged as 23 pairs of chromosomes, as explained in Chapter 4.) Instead of inheriting only one pair of chromosomes 21, one from the mother and one from the father, an entire extra chromosome is inherited, usually from the mother. Often called Down syndrome, trisomy-21 is one of the major reasons why women worry about pregnancy later in life. Down syndrome occurs much more frequently when mothers are over 40 years old. The extra chromosome can be detected early

in pregnancy by a variety of procedures, including **amniocentesis,** chorionic villus sampling, and newer noninvasive methods that examine fetal DNA in the maternal bloodstream (Wagner, Mitchell, & Tomita-Mitchell, 2014).

Another gene has been identified that is the second most common cause of intellectual disability, called ***fragile X syndrome.*** The gene that causes the disorder is on the X chromosome. Fragile X syndrome occurs nearly twice as often in males as in females because males have only one X chromosome. If a boy has the fragile X allele on his X chromosome, he will develop the disorder. Females have two X chromosomes, and it is necessary to inherit the fragile X allele on both X chromosomes in order to develop the disorder. However, females with one fragile X allele can also be affected to some extent. The fragile X gene is especially interesting because it involves a type of genetic defect in which a short sequence of DNA mistakenly repeats hundreds of times. This type of genetic defect is now also known to be responsible for several other previously puzzling diseases (Chapter 12).

Genetic research on behavior goes beyond just demonstrating the importance of genetics to the behavioral sciences and allows us to ask questions about how genes influence behavior. For example, does genetic influence change during development? Consider cognitive ability, for example; you might think that as time goes by we increasingly accumulate the effects of Shakespeare's "slings and arrows of outrageous fortune." That is, environmental differences might become increasingly important during one's life span, whereas genetic differences might become less important. However, genetic research shows just the opposite: Genetic influence on cognitive ability increases throughout the individual's life span, reaching levels later in life that are nearly as great as the genetic influence on height (Chapter 11). This finding is an example of developmental behavioral genetic research.

School achievement and the results of tests you took to apply to college are influenced almost as much by genetics as are the results of tests of cognitive abilities such as intelligence (IQ) tests (Chapter 11). Even more interesting, the substantial overlap between such achievement and the ability to perform well on tests is nearly all genetic in origin. This finding is an example of what is called **multivariate genetic analysis.**

Genetic research is also changing the way we think about environment (Chapters 7 and 8). For example, we used to think that growing up in the same family makes brothers and sisters similar psychologically. However, for most behavioral dimensions and disorders, it is genetics that accounts for similarity among siblings. Although the environment is important, environmental influences can make siblings growing up in the same family different, not similar. This genetic research has fostered environmental research looking for the environmental reasons why siblings in the same family are so different.

Recent genetic research has also shown a surprising result that emphasizes the need to take genetics into account when studying environment: Many environmental measures used in the behavioral sciences show genetic influence! For example, research in developmental psychology often involves measures of parenting that are, reasonably

enough, assumed to be measures of the family environment. However, genetic research has convincingly shown genetic influence on parenting measures. How can this be? One way is that genetic differences among parents influence their behavior toward their children. Genetic differences among children can also make a contribution. For example, parents who have more books in their home have children who do better in school, but this **correlation** does not necessarily mean that having more books in the home is an environmental cause for children performing well in school. Genetic factors could affect parental traits that relate both to the number of books parents have in their home and to their children's achievement at school. Genetic involvement has also been found for many other ostensible measures of the environment, including childhood accidents, life events, and social support. To some extent, people create their own experiences for genetic reasons (Chapter 8).

These are examples of what you will learn about in this book. The simple message is that genetics plays a major role in behavior. Genetics integrates the behavioral sciences into the life sciences. Although research in behavioral genetics has been conducted for many years, the field-defining text was published only in 1960 (Fuller & Thompson, 1960). Since that date, discoveries in behavioral genetics have grown at a rate that few other fields in the behavioral sciences can match. This growth is accelerating following the sequencing of the human **genome,** that is, identifying each of the more than 3 billion steps in the spiral staircase that is DNA, leading to the identification of the DNA differences among us that are responsible for the heritability of normal and abnormal behavior.

Recognition of the importance of genetics is one of the most dramatic changes in the behavioral sciences during the past several decades. Over 80 years ago, Watson's (1930) behaviorism detached the behavioral sciences from their budding interest in heredity. A preoccupation with the environmental determinants of behavior continued until the 1970s, when a shift began toward the more balanced contemporary view that recognizes genetic as well as environmental influences. This shift toward genetics in the behavioral sciences can be seen in the increasing number of publications on behavioral genetics. As shown in Figure 1.1, the increase in human behavioral genetic publications has been meteoric, with the numbers of publications doubling on average every five years since the 1990s. During the last five years, more than 2000 papers were published each year.

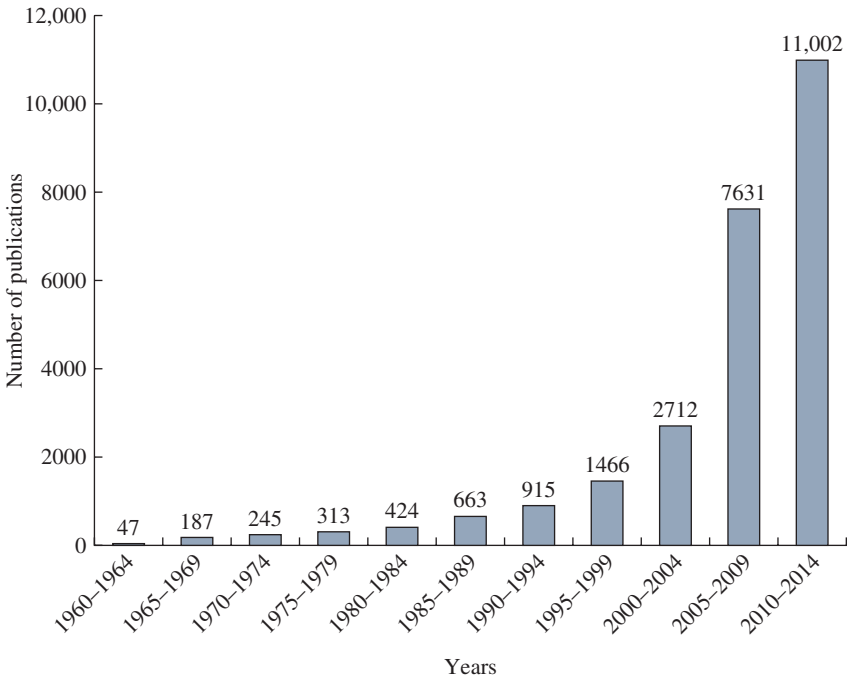


FIGURE 1.1 Numbers of human behavioral genetic papers published in five-year intervals since the field-defining textbook on behavioral genetics in 1960. Data from a resource of behavioral genetic papers (Ayorech et al., 2016).

CHAPTER **TWO**

Historical Perspective

Everyone can cite some examples in which some degree of talent, quality of temper, or other trait is characteristic of a family. Phrases like "a chip off the old block" and "it runs in the family" indicate a notion that behavioral traits, like physiological ones, can be inherited. The concept that "like begets like" has had great practical importance in the development of domesticated animals, which have been bred for behavioral as well as morphological characteristics (see Chapter 5). The notion of inheritance, including inheritance of behavioral traits, appeared in human thought tens of thousands of years ago, when the domestication of the dog began.

Biological thought during recorded history was dominated by Aristotle in the fourth century BC, and by the teachings of Galen, a Roman, concerning anatomy in the second century AD. Progress in understanding biological phenomena virtually halted during the Middle Ages from the fifth to the fifteenth century. Then came the Renaissance and Leonardo da Vinci's study of anatomy in connection with art. Leonardo's work characterized the far-ranging inquisitiveness of Renaissance scholars. However, it was the exhaustive work of Andreas Vesalius on human anatomy, published in 1543, and the discovery of the circulation of blood by William Harvey in 1628 that opened the doors to experimentation on the phenomena of life.

THE ERA OF DARWIN

After Harvey's discovery, the pace of biological research quickened and many fundamental developments in technique and theory ensued in the following century. One of the cornerstones of biology was laid by the Swede Karl von Linne (better known as Linneaus), who, in 1735, published *Systema Naturae,* in which he established a system of taxonomic classification of all known living things. In so doing, Linneaus emphasized the separateness and distinctness of species. As a result, the view that species

were fixed and unchanging became the prevailing one. This was a view that fit the biblical account of creation. However, this was not the only perspective. For example, in the latter part of the eighteenth century the Englishman Erasmus Darwin suggested that plant and animal species appear capable of improvement, although he believed that God had so designed life. Another view was promoted by the Frenchman Jean Baptiste Lamarck, who argued that the deliberate efforts of an animal could result in modifications of the body parts involved, and that the modifications so acquired could be transmitted to the animal's offspring. Changes of this sort could accumulate, so that eventually the characteristics of the species would change. While Lamarck was not the first to assume that changes acquired in this manner could be transmitted to the next generation, he crystallized the notion. This view became known as Lamarckism, or the law of use and disuse. As we shall see, this is an incorrect view of evolution, but it was significant in that it questioned the prevailing view that species do not change.

Charles Darwin

One of the most influential books ever written, the 1859 *On the Origin of Species,* was authored by Erasmus Darwin's grandson, Charles Darwin (Figure 2.1). Darwin's famous 1831–1836 voyage around the world on the *Beagle* led him to observe the remarkable adaptations of species to their environments. For example, he made particularly compelling observations about 14 species of finches found in a small area on the Galápagos Islands. The principal differences among these finches were in their beaks, and each beak was exactly appropriate for the particular eating habits of the species (Figure 2.2).

FIGURE 2.1 Charles Darwin as a young man. (Fine Art/Corbis.)

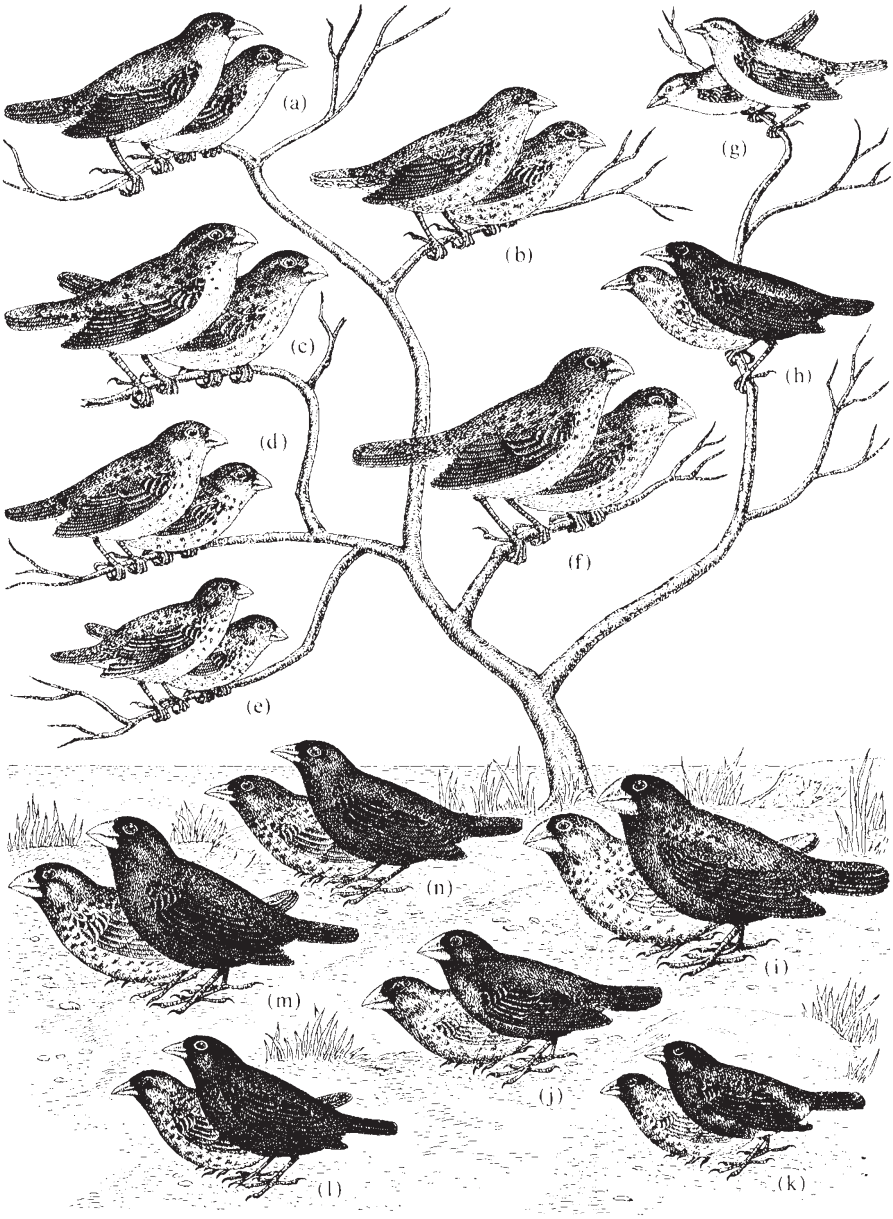


FIGURE 2.2 The 14 species of finches in the Galápagos Islands and Cocos Island. (a) A woodpecker-like finch that uses a twig or cactus spine instead of its tongue to dislodge insects from tree-bark crevices. (b–e) Insect eaters. (f, g) Vegetarians. (h) The Cocos Island finch. (i–n) The birds on the ground eat seeds. Note the powerful beak of (i), which lives on hard seeds. (Reproduced with permission. Copyright © 1953 Scientific American, a division of Nature America, Inc. All rights reserved.)

Theology of the time proposed an "argument from design," which viewed the adaptation of animals and plants to the circumstances of their lives as evidence of the Creator's wisdom. Such exquisite design, so the argument went, implied a "Designer." Darwin was asked to serve as a naturalist on the surveying voyage of the *Beagle* in order to provide more examples for the "argument from design." However, during his voyage, Darwin began to realize that species, such as the Galápagos finches, were not designed once and for all. This realization led to his heretical theory that species evolve one from another: "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends" (Darwin, 1896, p. 380). For over 20 years after his voyage, Darwin gradually and systematically marshaled evidence for his theory of evolution.

Darwin's theory of evolution begins with variation within a population. Variation exists among individuals in a population due, at least in part, to heredity. If the likelihood of surviving to maturity and reproducing is influenced even to a slight degree by a particular trait, offspring of the survivors will show more of the trait than their parents' generation. In this way, generation after generation, the characteristics of a population can gradually change. Over a sufficiently long period, the cumulative changes can be so great that populations become different species, no longer capable of interbreeding successfully.

For example, the different species of finches that Darwin saw on the Galápagos Islands may have evolved because individuals in a progenitor species differed slightly in the size and shape of their beaks. Certain individuals with slightly more powerful beaks may have been more able to break open hard seeds. Such individuals could survive and reproduce when seeds were the main source of food. The beaks of other individuals may have been better at catching insects, and this shape gave those individuals a selective advantage at certain times. Generation after generation, these slight differences led to other differences, such as different habitats. For instance, seed eaters made their living on the ground and insect eaters lived in the trees. Eventually, the differences became so great that offspring of the seed eaters and insect eaters rarely interbred. Different species were born. A Pulitzer Prize–winning account of 25 years of repeated observations of Darwin's finches, *The Beak of the Finch* (Weiner, 1994), shows **natural selection** in action (see "Galapagos Finch Evolution": https://www.youtube.com/watch?v=mcM23M-CCog).

Although this is the way the story is usually told, another possibility is that behavioral differences in habitat preference led the way to the evolution of beaks rather than the other way around. That is, heritable individual differences in habitat preference may have existed that led some finches to prefer life on the ground and others to prefer life in the trees. The other differences, such as beak size and shape, may have been secondary to these habitat differences. Although this proposal may seem to be splitting hairs, this alternative story makes two points. First, it is difficult to know the mechanisms driving evolutionary change. Second, although behavior is