



The Biological Bases of Behavior

Although we've always known that behavior and thought are products of the brain, over the past several decades it has become increasingly clear that understanding the mind and behavior requires an understanding of biology. Genes, of course, influence the development and functioning of the brain, each of which have been shaped by millions of years of evolution, adapting us to the general conditions of human life on earth. In this unit, Chapter 3 examines the role of genes and evolution in the underlying mechanisms of behavior; Chapter 4 examines the structure of the nervous system and its principles of operation; and Chapter 5 is concerned with the neural and hormonal mechanisms underlying motivation and emotion.

Genetics and Evolutionary Foundations of Behavior

LEARNING OUTCOMES

After studying this chapter, you should be able to:

- Identify some basic genetic mechanisms and describe how they work.
- Describe the influence of heredity on behavioral traits.
- Explain the theory of evolution by natural selection.
- Describe the functionalist approach to explaining behavior.
- Explain how natural selection relates to species-typical behaviors.
- Explain how patterns of mating, hurting, and helping can be understood in the context of evolution.

Have you ever spent time watching chimpanzees in their enclosure at a zoo? If not, we recommend seizing the next opportunity to do so, as the experience will undoubtedly convey a strong sense of the animal's kinship to us. Its facial expressions, its curiosity, even its sense of humor, are so like ours that we intuitively see it as a hairy, long-armed cousin. Indeed, the chimpanzee *is* our cousin. Along with the bonobo, a chimp-like ape discussed later in this chapter, it is one of our two closest animal relatives. Geneticists have lined up the DNA molecules of chimpanzees against those of humans and found that they match at 98.8% of their individual base units (The Chimpanzee Sequencing and Analysis Consortium, 2005). In genetic material, we are just 1.2% different from a chimpanzee. Humans' language and culture, and the knowledge these have given us, have in some ways separated us markedly from our non-human cousins. But in our genes—and in our basic drives, emotions, perceptual processes, and ways of learning—we are kin not just to chimpanzees, but in varying degrees to all of the mammals, and in lesser degrees to other animals as well.

More than 150 years ago, in *The Origin of Species*, Charles Darwin (1859/1963) presented a theory of evolution that explains both the similarities and the differences among the animal species. According to Darwin, all species are similar to one another because of common ancestry, and all species are unique because natural selection has adapted each species to the aspects peculiar to the environment in which it lives and reproduces. Darwin presented massive amounts of evidence for his theory, and essentially everything that scientists have learned since, about our own and other species, is consistent with it.

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CHAPTER OUTLINE

[Review of Basic Genetic Mechanisms](#)

[Inheritance of Behavioral Traits](#)

[Evolution by Natural Selection](#)

[Natural Selection as a Foundation for Functionalism](#)

[Natural Selection as a Foundation for Understanding Species-Typical Behaviors](#)

[Evolutionary Analyses of Mating, Aggression, and Helping](#)

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This chapter is primarily about the application of evolutionary theory to the behavior of humans and other animals. **Evolution** is the long-term adaptive process, spanning generations, that equips each species for life in its ever-changing natural habitat.

Darwin developed his theory of evolution before genes were discovered, but the theory is best understood today in the light of our knowledge of genes. This chapter begins by discussing genetic mechanisms and their implications for the inheritance of behavioral characteristics. The rest of the chapter is concerned with the evolution of behavior and how we can learn about our own behavior by comparing it to that of our animal relatives. Among other things, we examine patterns of mating, aggression, and helping, in our species and in others, from an evolutionary perspective.

Review of Basic Genetic Mechanisms

You have probably studied the mechanisms of gene action and reproduction in a biology course, but we will review them briefly here, focusing on their implications for psychology.



FOCUS 1

How can genes affect behavioral traits through their role in protein synthesis?

How Genes Affect Behavior

Researchers sometimes use a sort of shorthand, speaking of genes “for” particular behavioral traits. For example, they might speak of genes *for* singing ability, *for* aggression, or *for* cooperation. However, it is important to realize that genes never produce or control behavior directly; more accurately, genes are *associated* with behavior. All the effects that genes have on behavior occur through their role in building and modifying the physical structures of the body. Those structures, interacting with the environment, produce behavior. Thus, a gene might influence singing ability by promoting the development of a brain system that analyzes sounds, or by promoting certain physical aspects of the vocal cords. Similarly, a gene might affect aggressiveness by fostering the growth of brain systems that organize aggressive behavior in response to irritating stimuli. In a sense, all genes that contribute to the body’s development are “for” behavior, since all parts of the body are involved in behavior. Especially relevant for behavior, however, are genes that contribute to the development of sensory systems, motor systems (muscles and other organs involved in movement), and, most especially, the nervous system (which includes the brain).

Genes Provide the Codes for Proteins

Genes affect the body’s development through their influence on the production of protein molecules. Biologically speaking, we are what we are because of our proteins. A class of proteins called *structural proteins* forms the structure of every cell of the body. Another, much larger class called *enzymes* controls the rate of every chemical reaction in every cell.

Physically, **genes** are components of extremely long molecules of a substance called **DNA** (deoxyribonucleic acid). These molecules exist in the egg and sperm cells that join to form a new individual, and they replicate themselves during each cell division in the course of the body’s growth and development. A replica of your whole unique set of DNA molecules exists in the nucleus of each of your body’s cells, where it serves to code for and regulate the production of protein molecules.

Each protein molecule consists of a long chain of smaller molecules called amino acids. A single protein molecule may contain anywhere from several hundred up to many thousand amino acids in its chain. There are a total of 20 distinct amino acids in every form of life on earth, and they can be arranged in countless sequences to form different protein molecules. Some portions of the DNA in your cells serve as templates (molds or patterns) for producing another molecular substance called

RNA (ribonucleic acid), which in turn serves as a template for producing protein molecules. Scientists often describe a gene as a segment of a DNA molecule that contains the code that dictates the particular sequence of amino acids for a single type of protein. With that definition, geneticists have determined that human beings (and also chimpanzees and mice) have about 20,000 genes (International Human Genome Sequencing Consortium, 2004).

Recent molecular work has led many geneticists to change their definition of a gene, so that it includes portions of DNA that have other functions, not just the coding of protein molecules (ENCODE Project Consortium, 2012). Most of the DNA in human cells does not code for proteins. Although much of this noncoding DNA was once called “junk DNA” because scientists believed it had no purpose, recent evidence indicates that about 80% of DNA serves some function, such as regulating the activity of the coding DNA (ENCODE Project Consortium, 2012). Geneticists now distinguish between *coding genes*, which code for unique protein molecules, and *regulatory genes*, which work through various biological means to help activate or suppress specific coding genes and thereby influence the body's development. Recent research comparing human and chimpanzee DNA suggests that the biggest genetic differences between the two species lie in certain regulatory genes that affect the development of the brain (Prabhakar et al., 2006; McClean et al., 2011).

Genes Work Only Through Interaction With the Environment

At every level, from biochemical to behavioral, the effects of genes and environment are entwined. *Environment*, as used in this context, refers to every aspect of an individual and his or her surroundings except the genes themselves. It includes the nourishing womb and maternal bloodstream before birth; the internal chemical environment of the individual; and all the events, objects, and other individuals encountered after birth. Foods—a part of the environment—supply genes with amino acids, which are needed to manufacture proteins. Environmental effects also help to turn genes “on” and “off,” resulting in bodily changes that alter the individual's behavioral capacity. Such changes can occur in adulthood as well as earlier in development. For example, physical exercise modifies the chemical environment of muscle cells, activating genes that promote further growth of the muscle. One's body and behavioral capacities result from a continuous, complex interplay between genes and environment (see **Figure 3.1**). One is no more basic than the other—genes are always expressed in a context.

The world of reptiles provides a fascinating example of the role of context in gene expression. In mammals, being male or female is a matter of genes, but this is not the case for many reptiles. Sex in many turtles, alligators, and crocodiles is determined not by differences in genes but by differences in the temperature at

FOCUS 2

What does it mean to say that genes can influence behavioral traits only through interaction with the environment? How are genes involved in long-term behavioral changes derived from experience?

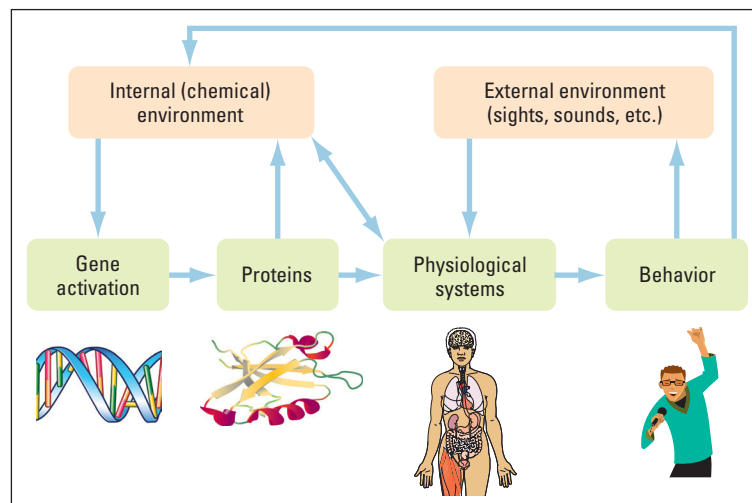


FIGURE 3.1 Route through which genes affect behavior Genes build proteins, which form or alter the body's physiological systems (including brain systems), which, in turn, produce behavior. Each step in this process involves interaction with the environment. Aspects of the internal environment control gene activation, and aspects of both the internal and the external environments act on physiological systems to control behavior. Behavior, in turn, can affect gene activation through direct and indirect effects on the internal environment.



"So, how do you want to play this?
Nature, nurture, or a bit of both?"

which the eggs are incubated. Theoretically, we could have genetically identical twin reptiles, one male and one female. Genes still provide the critical instructions for developing into a male or female animal, but the context in which the genes are expressed (a warm versus a cool temperature) determines the sex that will form. A tour guide in the Galápagos Islands (about 600 miles off the coast of Ecuador) told how he remembered which temperature produces which sex for the Galápagos giant tortoises: "Hot chicks and cool dudes."

Researchers have studied specific mechanisms through which experiences can activate genes and thereby alter the individual's brain and behavior. For example, adult mice and rats that have not given birth will normally avoid newborns of their species that are placed in their cage. However, if exposed to newborns continuously for several hours or more, they gradually begin to care for them. Why? The sight, sound, or smell of newborns activates a particular gene. The activated gene produces a protein molecule that stimulates activity in a specific cluster of brain cells that are known to

be crucial for the motivation and organization of such behaviors as retrieving young to a nest and hovering over them. The result is that a mouse or rat that previously did not take care of young is transformed into a mouse or rat that does. This type of behavior change is known as environmental induction of gene activity (Brown et al., 1996; Numan, 2007).

There is good reason to believe that prolonged behavioral effects that derive from experience, including those that we call "learning," involve the activation of genes (Spencer et al., 2009). Experiences activate genes, which produce proteins, which in turn alter the function of some of the neural circuits in the brain and thereby change the individual's behavior.



FOCUS 3

How can the same genotype produce various phenotypes?

FIGURE 3.2 Identical twins These 13-year-old girls have the same genotype, but they obviously differ in at least one aspect of their phenotype. It is uncertain what caused this difference. It may have derived from their occupying different positions in the womb such that one received more early nutrition than the other, which activated genes promoting more growth.



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Distinction Between Genotype and Phenotype

The term **genotype** refers to the set of genes that the individual inherits, whereas the term **phenotype** refers to the observable properties of the body and behavioral traits. The same genes can have different effects, depending on the environment and the mix of other genes. Two individuals with the same genotype can be quite different in phenotype as a result of differences in their environments. Genetically identical rats will differ phenotypically in their behavior toward infant rats if one has been previously exposed to infant rats and the other has not. Genetically identical human twins will differ in size if they have been exposed differently

to growth-promoting factors in their environments (see **Figure 3.2**), and they will differ in behavior if they have been subjected to different learning experiences.

How Genes Are Passed Along in Sexual Reproduction

Genes not only provide the codes for building proteins; they also serve as the biological units of heredity. They are replicated and passed along from parents to offspring.

To understand how genes are passed along in sexual reproduction, it is useful to know how they are arranged within cells. The genetic material (DNA) exists in each cell in structures called **chromosomes**, which are usually dispersed throughout the cell nucleus. Just prior to cell division, however, the chromosomes condense into compact forms that can be stained, viewed through a microscope, and photographed. The normal human cell has 23 pairs of chromosomes. Twenty-two of these are true pairs in both the male and the female, in the sense that each chromosome looks like its mate and contains similar genes.

The remaining pair is made up of the sex chromosomes. In the normal human male cell, that “pair” consists of a large chromosome labeled X and a small chromosome labeled Y (see **Figure 3.3**). Genetically, the only difference between the sexes is that females have two X chromosomes (XX—a true pair) rather than the XY of the male.

The Production of Genetically Diverse Egg and Sperm Cells

When cells divide to produce new cells *other than egg or sperm cells*, they do so by a process called **mitosis**. In mitosis, each chromosome precisely replicates itself and then the cell divides, with one copy of each chromosome moving into each of the two cell nuclei thus formed. Because of the faithful copying of genetic material in mitosis, all your body's cells, except your egg or sperm cells, are genetically identical to one another. The differences among cells in your body—such as muscle cells and skin cells—arise from the differential activation of their genes, not from different gene content.

When cells divide to produce egg or sperm cells, they do so by a different process, called **meiosis**, which results in cells that are not genetically alike (see **Figure 3.4**). During meiosis, each chromosome replicates itself once, but then the cell divides twice. Before the first cell division, the chromosomes of each pair line up next to one another and exchange genetic material in a random manner. Although the chromosomes in each pair look the same, they do not contain precisely the same genes. The result of this random exchange of genetic material and of the subsequent cell divisions is that each egg or sperm cell produced is genetically different from any other egg or sperm cell and contains only half of the full number of chromosomes (one member of each of the 23 pairs).

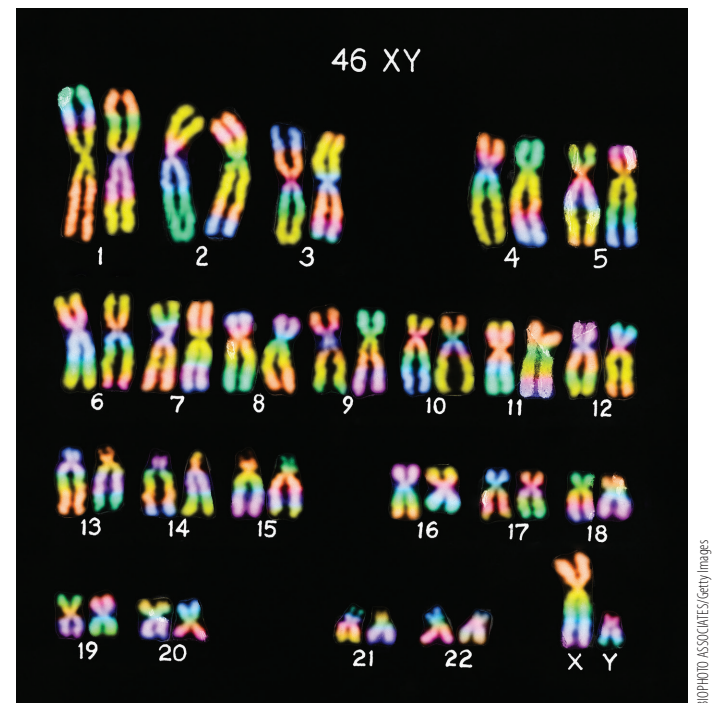


FIGURE 3.3 Chromosomes of a normal human male cell The 22 numbered pairs of chromosomes are the same in a normal female cell as they are in a normal male cell. The remaining two, labeled X and Y, are the sex chromosomes. The normal human female cell (not shown) has a second X chromosome instead of a Y.

FOCUS 4

How does meiosis produce egg or sperm cells that are all genetically different from one another?

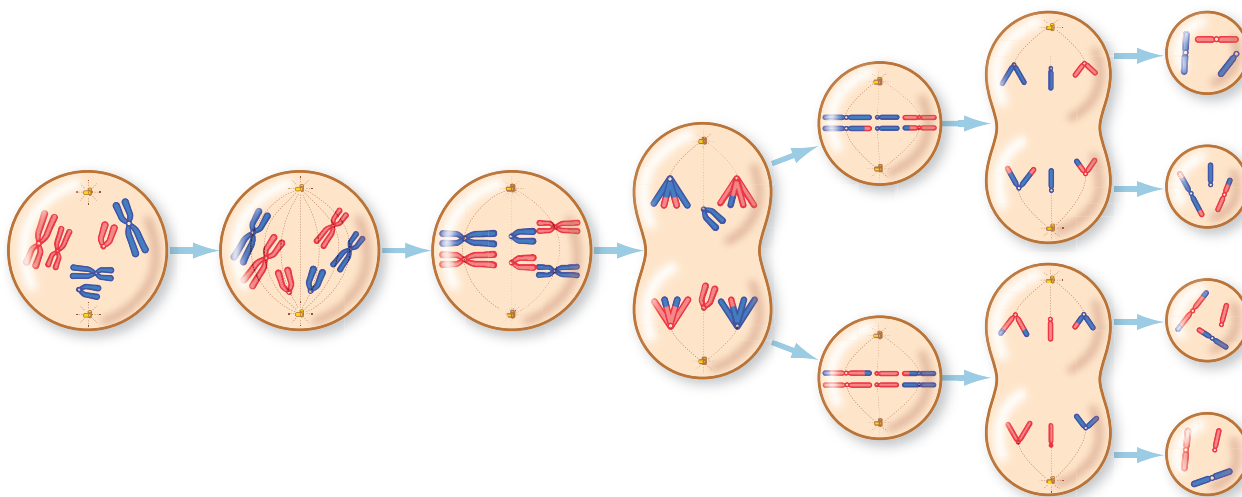


FIGURE 3.4 Schematic illustration of meiosis in sperm production This illustration is for a creature that has only three pairs of chromosomes rather than the 23 pairs that humans have. At the beginning (left), each chromosome has already replicated itself and remains attached to its replica. The pairs of replicated chromosomes (one blue and one red in each pair in the diagram) then line up next to one another and exchange genetic material through a process called *crossing over*. The cell then divides twice, resulting in four sperm cells, each with just one member of each pair of chromosomes. Notice that each sperm cell is genetically different from the others, having a different mix of the original (blue and red) material from the parental pairs of chromosomes. The diagram greatly oversimplifies the effects of crossing over. In fact, each chromosome would cross over many times with its paired mate, resulting in a random mixing of genetic material. Meiosis in egg production is similar to that in sperm production, but only one of the two cells produced at each division survives.

**FOCUS 5**

What is the advantage of producing genetically diverse offspring?

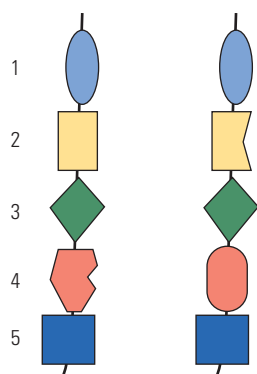


FIGURE 3.5 Schematic illustration of gene loci on a pair of chromosomes

Successive genes are depicted here as beads on a string. This pair of chromosomes is *homozygous* at loci 1, 3, and 5 (the paired genes there are identical to each other) and *heterozygous* at loci 2 and 4 (the paired genes there are not identical to each other). Nonidentical genes that can occupy the same locus on a pair of chromosomes are referred to as *alleles* of each other. Thus the two genes at locus 2 are alleles, as are the two at locus 4.

**FOCUS 6**

What is the difference between a dominant and a recessive gene (or allele)?

The Genetic Diversity of Offspring

It may seem ironic that the very cells you use for “reproduction” are the only cells in your body that cannot, in theory, reproduce you. They are the only cells in your body that do not have all your genes. In sexual reproduction you are, of course, not really reproducing yourself. Rather, you are creating a genetically unique individual who has half of your genes and half of your partner’s genes. When a sperm and an egg unite, the result is a single new cell, the **zygote**, which contains the full complement of 23 paired chromosomes. One member of each of these pairs comes from each parent. The zygote then grows, through mitosis, into a new person. Because each sperm or egg is different from any other sperm or egg (even from the same parent), each zygote is unique.

The value of sex, as opposed to simple cloning (the asexual production of genetically identical offspring), lies in the production of genetically diverse offspring. In a continually changing environment, genes have a better chance of surviving if they are rearranged at each generation in many different ways, to produce different kinds of bodies, than if they are all put into the same kind of body—an almost literal example of the old saying, “Don’t put all your eggs in one basket.” By producing diverse offspring, parents reduce the risk that all of their offspring will die as a result of some unforeseen change in the environment.

There are, however, people who are genetically identical to each other: **identical twins**. They are formed when two bundles of cells separate from each other during the early mitotic divisions following the formation of a zygote. Because they originate from one zygote, identical twins are also known as *monozygotic twins*. **Fraternal twins**, or *dizygotic twins*, originate from two zygotes, each formed from different egg and sperm cells. Fraternal twins have the same degree of genetic similarity as any two non-twin siblings. In later chapters, you will see how psychologists make use of twins in research to understand how much of the variability in certain psychological traits results from differences in people’s genes, as opposed to differences in their environments.

Consequences of the Fact That Genes Come in Pairs

You have seen that genes exist on long DNA strands in chromosomes, rather like beads on a string, and that chromosomes come in pairs. The two genes that occupy the same *locus* (location; plural *loci*) on a pair of chromosomes are sometimes identical to each other and sometimes not. When they are identical, the individual is said to be *homozygous* [**home**-oh-**zai**-gus] at that locus, and when they are not identical, the individual is said to be *heterozygous* [**het**-er-oh-**zai**-gus] at that locus (see **Figure 3.5**). Different genes that can occupy the same locus, and thus can potentially pair with each other, are called **alleles**.

For example, a gene for a straight hairline and a gene for a widow’s peak in humans are alleles because they can occupy the same locus. If you are homozygous for a widow’s peak, you have two copies of a gene that manufactures an enzyme that makes your hairline dip in the middle of your forehead. What if you were heterozygous for hairline, with one copy of the allele for a widow’s peak and one copy for a straight hairline? In this case, you would have a widow’s peak, just as if you were homozygous for this trait. This is because the allele for a widow’s peak is *dominant* and the one for a straight hairline is *recessive*. A **dominant** gene (or allele) will produce its observable effects in either the homozygous or the heterozygous condition, and a **recessive** gene (or allele) will produce its effects only in the homozygous condition. But not all pairs of alleles manifest dominance or recessiveness. Some pairs blend their effects. For example, if you cross red snapdragons (a kind of flower) with white snapdragons, the offspring will have pink flowers, because neither the red nor the white allele is dominant over the other.

Mendelian Pattern of Heredity

The idea that the units of heredity come in pairs and that one member of a pair can be dominant over the other was developed in the mid-nineteenth century by

an Austrian monk named Gregor Mendel. In a typical experiment, Mendel would start with two purebred strains of pea plants that differed in one or more easily observed traits. He could cross-pollinate them to observe the traits of the offspring, called the *F1* (first filial) generation. Then he would pollinate the *F1* peas with pollen from other *F1* peas to produce the *F2* (second filial) generation.

In one experiment, for example, Mendel cross-pollinated a strain of pea plants that regularly produced round seeds with a strain that regularly produced wrinkled seeds. His famous findings were that (a) all of the *F1* generation had round seeds and (b) three-fourths of the *F2* generation had round seeds and one-fourth had wrinkled seeds.

Mendel's findings make perfect sense if we assume that seed texture is controlled by a single pair of genes, with the allele for round dominant over that for wrinkled. To illustrate this, let us use the capital letter *R* to stand for the dominant, round-producing allele, and the small letter *r* for the recessive, wrinkle-producing allele. The purebred round strain is homozygous for the "round" allele (*RR*), and the purebred wrinkled strain is homozygous for the "wrinkled" allele (*rr*). (Purebred strains are homozygous for all traits.) Because one allele must come from each parent, the only possible result for the *F1* generation, produced by crossing the two purebred strains, is the heterozygous condition (*Rr*). This explains why all the *F1* peas in Mendel's experiment were round. At the next step, when *Rr* peas receive pollen from other *Rr* peas to produce the *F2* generation, four equally likely combinations can occur: (1) an *R* from each parent (*RR*), (2) an *R* from the female parent and an *r* from the male (*Rr*), (3) an *r* from the female parent and an *R* from the male (*rR*), and (4) an *r* from each parent (*rr*). (See **Figure 3.6**.) Since only one of these possible outcomes (*rr*) is wrinkled, the expectation is that one-fourth of the *F2* generation will be wrinkled and the other three-fourths round. This is just what Mendel found.

Whenever a trait is inherited in a pattern like that observed by Mendel, we can assume that the trait results from variation in alleles at a single gene locus that interact in a dominant-recessive manner.

The Double-Edged Sword of Sickle-Cell Anemia

A few hereditary diseases are caused by a single pair of recessive genes that lead to an early death (or were deadly before the advent of modern medicine). Among these is *sickle-cell anemia*, a disease that interferes with the transport of oxygen in the blood. In healthy individuals, the red blood cells that carry the oxygen are usually disk shaped. In patients with sickle-cell anemia, the blood cells are distorted, shaped like a sickle, or crescent moon. Because of their shape, the sickled cells tend to pile up and block small blood vessels, resulting in pain and destruction of tissue, as well as other complications that can be fatal. Given that natural selection is supposed to favor characteristics that enhance the chances of an individual surviving, and that genes that essentially kill their host do not get passed on to future generations, why haven't sickle-cell-anemia genes been eliminated?

The answer is that although having two recessive genes for sickled cells was often a death sentence before the advent of modern medicine, having just one recessive gene and one normal, dominant gene (that is, being heterozygous at that locus) provided some benefit. The genes associated with sickle-cell anemia originated in areas of the globe where malaria was common, chiefly in Africa. People with a single sickle-cell gene are less likely to die of malaria because their red blood cells are poor at supporting the growth of the malaria parasite. People who have one recessive gene (carriers) living in these areas are thus more likely to live to reproduce than noncarriers, keeping the recessive and potentially deadly gene in the gene pool. The benefit is not to those who have the disease, but to those who are carriers (Desai & Dhanani, 2004).

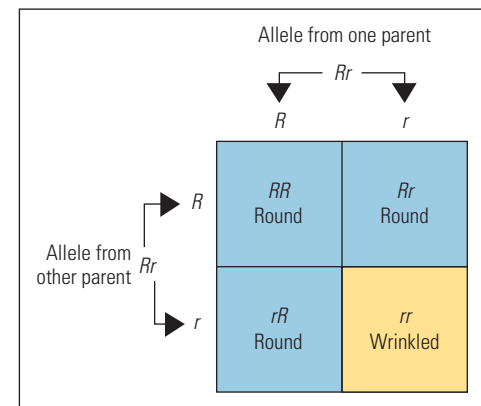


FIGURE 3.6 Explanation of Mendel's 3:1 ratio When a pea plant that is heterozygous for round versus wrinkled seeds is pollinated by another pea plant that is similarly heterozygous, four possible gene combinations occur in the offspring. Here *R* stands for the dominant, round-producing allele, and *r* for the recessive, wrinkle-producing allele. The phenotype of three of the offspring will be round and that of one wrinkled. This 3:1 ratio was Mendel's famous finding.

FOCUS 7

Why do three-fourths of the offspring of two heterozygous parents show the dominant trait and one-fourth show the recessive trait?

FOCUS 8

Why might a disease caused by two recessive genes persist in the gene pool?

SECTION REVIEW

Genes affect behavior by affecting the bodily structures involved in behavior.

Nature of Genetic Influence <ul style="list-style-type: none">■ Through their influence on protein synthesis, genes affect bodily structures and behavior.■ Genes act in concert with the environment, not in isolation. For example, environmental cues can activate genes that make rats or mice nurturant to newborns.	Meiosis and Sexual Reproduction <ul style="list-style-type: none">■ Meiosis results in egg and sperm cells that are genetically unique and contain only half the full number of chromosomes.■ Meiosis involves random assortment of paired genes.■ Genetic diversity produced by sexual reproduction promotes survival of genes by reducing the chance that all offspring will die.	Gene Pairing <ul style="list-style-type: none">■ Paired genes, which occupy the same locus (location) on a pair of chromosomes, may be identical (homozygous) or different (heterozygous). Gene variations that can occupy the same locus are called alleles.■ Mendel's discovery of consistent ratios of traits in offspring of cross-pollinated strains of peas led to the gene concept and to the concepts of dominance and recessiveness.■ Some genetic conditions, such as sickle-cell anemia, carry both risks and benefits for the individuals born with them.
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Inheritance of Behavioral Traits


Variation in genes contributes to variation in behavior. Some behavioral characteristics are inherited in accordance with the same pattern that Mendel observed in plants, indicative of control by a single pair of genes. Most behavioral characteristics, however, depend on many genes. In this section, we look first at two examples of single-gene traits and then at traits that are affected by many genes.

Examples of Single-Gene (Mendelian) Behavioral Traits

Mendelian Inheritance of Fearfulness in Dogs

One of the first demonstrations of single-gene control of a behavioral trait in dogs was published more than 50 years ago. In pioneering research on the role of genes in behavior, John Paul Scott and John Fuller (1965) studied the behavior of basenji hounds, cocker spaniels, and their mixed-breed offspring. Basenjis are timid dogs, showing fear of people until they have received much gentle handling. Cockers, in contrast, show little fear under normal rearing conditions. In a standard test with 5-week-old puppies, Scott and Fuller found that all the basenji puppies yelped and/or ran away when approached by a stranger, whereas only a few of the cocker puppies showed these reactions. When cockers and basenjis were crossbred, the offspring (*F1* hybrids) were like basenjis in this test: All showed signs of fear when approached. Since this was as true of hybrids raised by cocker mothers as of those raised by basenji mothers, Scott and Fuller concluded that the effect stemmed from the hybrid dogs' genes and not from anything they learned from their mothers.

The fact that the *F1* hybrids were as fearful as the purebred basenjis suggested to Scott and Fuller that the difference in fearfulness between the two purebred strains might be controlled by a single gene locus, with the allele promoting fear dominant over that promoting confidence. If this were so, then mating *F1* hybrids with each other should produce a group of offspring (*F2* generation) in which three-fourths would show basenji-like fear and one-fourth would show cocker-like confidence—the same ratios that Mendel had found with seed texture in pea plants. Scott and

**FOCUS 9**

How did Scott and Fuller show that the difference in fearfulness between cocker spaniels and basenji hounds is controlled by a single gene locus, with the “fear” allele dominant over the “non-fear” allele?

Fuller did this experiment and, indeed, found ratios very close to those predicted. As additional evidence, they also mated *F1* hybrids with purebred cockers. About half the offspring of those backcrosses were basenji-like in fear, and the other half were cocker-like in confidence—just as can be expected if the “fear” allele is dominant over the “non-fear” allele. (see **Figure 3.7**)

From this research, can we conclude that fear in all its various forms is controlled by a single gene? No. Scott and Fuller’s work demonstrates only that the difference between cocker spaniels and basenji hounds in a particular test of fear is controlled by a single gene. In a broader context, many different genes must contribute to building the complex neural structure needed to experience fear and express it in behavior. Recognize also that Scott and Fuller could detect the effect of a specific gene pair because they raised all the dogs in similar environments; their studies do not diminish the role of environmental influences. In other research, Scott (1963) showed that any puppy isolated from people for the first 4 months of life will be fearful of humans. Had Scott and Fuller isolated the cockers from all human contact and given the basenjis lots of kind handling before the behavioral test, they might well have found the cockers to be more fearful than the basenjis, despite the genetic predispositions toward the opposite behavior.

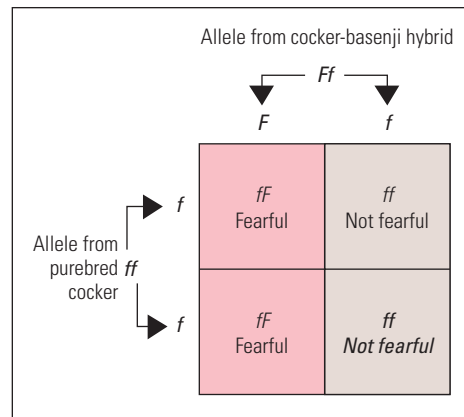


FIGURE 3.7 Explanation of Scott and Fuller’s results of mating basenji-cocker hybrids with purebred cockers

The finding that half the offspring were fearful and half were not makes sense if fearfulness results from a dominant allele (*F*) and lack of fearfulness results from a recessive allele (*f*). Because half the offspring receive *F* from their hybrid parent and all receive *f* from the purebred parent, half the offspring will be *Ff* (phenotypically fearful) and the other half *ff* (not fearful).

FOCUS 10

Why would it be a mistake to conclude, from Scott and Fuller’s work, that fear in dogs is caused just by one gene or that it is caused just by genes and not by the environment?

FOCUS 11

How do genes and the environment interact to affect individuals with PKU?

FOCUS 12

How does the distribution of scores for a polygenic trait differ from that usually obtained for a single-gene trait?

Mendelian Inheritance and Expression of Genetic Disorders

Most of the behaviorally relevant traits in humans that derive from alteration at a single gene locus are brain disorders, caused by relatively rare, mutant, malfunctioning genes passed from generation to generation. For example, in *phenylketonuria*, or *PKU*, infants inherit two recessive genes involved in the processing of the amino acid phenylalanine. The presence of these genes causes the amino acid to accumulate in the brain, resulting in intellectual disorders. However, PKU only has its detrimental effects if the person consumes foods that contain phenylalanine. (Phenylalanine is found in many foods and is a principal ingredient in some artificial sweeteners made with Aspartame®.) Newborns are routinely screened for the ability to process phenylalanine, and when babies who have the PKU genes are placed on a phenylalanine-free diet they develop normally. Moreover, by adulthood, people with PKU can consume phenylalanine without any negative consequences. Genes themselves, then, do not “cause” PKU – excessive phenylalanine in the diet does. However, the inability to process phenylalanine is “caused” by defective genes. Thus, even in this prototypical case of a genetic disease, genes and environment clearly interact (Widaman, 2009).

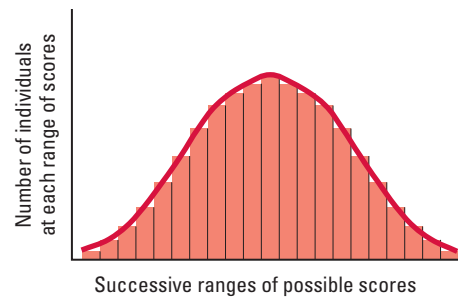
Polygenic Characteristics and Selective Breeding

Characteristics that derive from variation at a single gene locus are typically *categorical* in nature. That is, they are characteristics that sharply differentiate one group from another. Peas are either round or wrinkled; mixed-breed basenji-cockers differ so sharply from one another in fearfulness that they can be categorized into two distinct groups; newborn babies either have or do not have PKU (none of them “sort of have it”).

But most anatomical and behavioral differences among individuals of any species are measurable in degree, not type. They are *continuous* rather than categorical. That is, the measures taken from individuals do not fall into two or more distinct groups but can lie anywhere within the observed range of scores. Most often, the set of

FIGURE 3.8 Normal distribution

When many individuals are tested for a polygenic characteristic, the majority usually fall in the middle of the range of scores and the frequency tapers off toward zero at the extremes. Mathematically, this defines a normal curve. (For a more complete description, see the *Statistical Appendix* at the end of the book.)



scores obtained on such measures approximate a **normal distribution**, meaning that most scores fall near the middle of the range and the frequency tapers off toward the two extremes (see **Figure 3.8**). Measures of aggressiveness in mice, of maze learning in rats, and of conscientiousness in people are just a few of the behavioral measures that are consistently found to fit a normal distribution.

Characteristics that vary in a continuous way are generally affected by many genes and are therefore called **polygenic characteristics** (the prefix *poly-* means “many”). Of course, these traits are also influenced by variation in the environment, so the variability observed in a graph such as Figure 3.8 results from a combination of genetic differences at many gene loci and environmental differences. In animals the role of genes in polygenic traits is studied through the procedure of selective breeding.

**FOCUS 13**

How are the characteristics of animals shaped through selective breeding?

Selective Breeding for Behavioral Characteristics in Animals

To the degree that individuals within a species differ in any measurable characteristic because of differences in their genes, that characteristic can be modified over successive generations through **selective breeding**. This procedure involves the mating of individuals that lie toward the same extreme on the measure in question. For single-gene characteristics the effects of selective breeding are immediate, but for polygenic characteristics the effects are gradual and cumulative over generations.

The basic procedure of selective breeding is by no means new. For thousands of years, plant and animal breeders have used selective breeding to produce new and better strains of every sort of domesticated species. Grains were bred for plumper seeds; cows, for docility and greater milk production; horses, along separate lines for working and racing; canaries, for their song; and dogs, along dozens of different lines for such purposes as following a trail, herding sheep, and guarding property.

The procedure in every case was essentially the same: The members of each generation that best approximated the desired type were mated to produce the next generation, resulting in a continuous genetic molding toward the varieties we see today.

Under controlled laboratory conditions, researchers have used selective breeding to produce many behaviorally specialized strains of animals, usually to better understand the biological foundations of the behaviors in question. Fruit flies have been bred to move either toward or away from a source of light, mice to be either more or less inclined to fight, rats to either prefer or not prefer alcohol over water, and foxes to be either highly aggressive or extraordinarily docile and friendly toward humans (Kukekova et al., 2008; Wimer & Wimer, 1985). It should come as no surprise that selective breeding can influence essentially any behavioral trait: Behaviors depend on particular sensory, motor, and neural structures, all of which are built from proteins whose production depends on genes.



RIA Novosti/Science Source

■ **A fox bred for tameness** Since 1959, researchers in Russia have been selectively breeding silver foxes for tameness. At each generation, only those foxes that show the least fear and aggression and the most affection to humans have been bred. The result, after more than 30 generations, is a breed of foxes that are as friendly to humans as are dogs (Kukekova et al., 2008; Trut, 1999).

Selective Breeding for Maze Learning: Tryon's Classic Research

The first long-term, systematic study of selective breeding in psychology was begun in the 1920s by Robert Tryon (1942). Tryon wanted to demonstrate that a type of behavior frequently studied by psychologists could be strongly influenced by variation in genes.

Tryon began by testing a genetically diverse group of rats for their ability to learn a particular maze. Then he mated the males and females that had made the fewest errors in the maze to begin what he called the “maze bright” strain and those that had made the most errors to begin the “maze dull” strain. When the offspring of succeeding generations reached adulthood, he tested them in the same maze and mated the best-performing members of the bright strain, and the worst-performing members of the dull strain, to continue the two lines.

Some of his results are shown in **Figure 3.9**. With each generation the two strains became increasingly distinct, until by the seventh there was almost no overlap between them. Almost all seventh-generation bright rats made fewer errors in the maze than even the best dull rats. To control for the possibility that the offspring were somehow learning to be bright or dull from their mothers, Tryon cross-fostered the rats so that some of the offspring from each strain were raised by mothers in the other strain. He found that rats in the bright strain were equally good in the maze, and those in the dull strain equally poor, regardless of which mothers raised them.

Once a strain has been bred to show some behavioral characteristic, the question arises as to what other behavioral or physiological changes accompany it. Tryon referred to his two strains of rats as “bright” and “dull,” but all he had measured was their performance in a particular type of maze. Performance in the maze no doubt depended on many sensory, motor, motivational, and learning processes, and specific changes in any of them could in theory have mediated the effects that Tryon

FOCUS 14

How did Tryon produce “maze bright” and “maze dull” strains of rats? How did he show that the difference was the result of genes, not rearing?

FOCUS 15

Why is the strain difference produced by Tryon not properly characterized in terms of “brightness” or “dullness”?



FIGURE 3.9 Selective breeding for “maze brightness” and “maze dullness” in rats The top graph shows, for the original parent stock, the distribution of rats according to the number of errors they made in the maze. Subsequent graphs show this distribution separately for the rats bred to be “bright” or “dull.” With successive generations of selective breeding, an increasing percentage in the “bright” strain made few errors and an increasing percentage in the “dull” strain made many errors. (Data from Tryon, 1942.)

observed. In theory, Tryon's "dull" rats could simply have been those that had less acute vision, or were less interested in the variety of food used as a reward, or were more interested in exploring the maze's blind alleys.

In later studies, another researcher found that Tryon's "dull" rats were as good as the "bright" ones, and sometimes even better, at other learning tasks (Searle, 1949). We do not know what underlying abilities or dispositions changed in Tryon's two strains of rats to produce their difference in maze performance, but the change was apparently not one of general learning ability. This problem still occurs in modern behavioral genetics research, in which new strains of animals (usually mice) are created by adding, deleting, or modifying known genes using sophisticated genetic-engineering methods. The behavioral differences between two strains found in one laboratory often fail to occur in another laboratory, apparently because of subtle differences in the way the animals are housed or tested (Cabib et al., 2000; Crabbe et al., 1999).

Polygenic Behavioral Characteristics in Humans

Most of the measures of human traits that interest psychologists—such as scores on personality tests—are continuous and normally distributed, and are affected by many genes as well as by environmental variables. Some psychologists are interested in the degree to which the differences in such scores, for a particular group of people, are the result of differences in their genes or differences in their environmental experiences. Of course, psychologists can't perform selective breeding studies with humans, but they have developed other methods to estimate that degree. Those methods involve comparing the average difference in test scores for people who are closely related to one another with that for people who are less closely related, using people who are chosen in such a way that the environments of the closely related people are no more similar to one another than are those of the less closely related people. Comparisons of identical twins with fraternal twins, and of biologically related siblings with adoptive siblings, have proven particularly useful. In later chapters you will read about such methods as they apply to a variety of psychological topics including intelligence tests, personality tests, and predisposition to various mental disorders.



FOCUS 16

How might a better understanding of epigenetics change the way we view genetic inheritance?

Epigenetics: How Genes Really Get Turned On and Off

It was not long after the publication of the first "complete" drafts of the human genome in February 2001 (International Human Genome Sequencing Consortium, 2001; Venter et al., 2001) that biologists realized that genes are only part of the story. Identical twins, and even cloned animals, are different from one another at birth, and these differences cannot be attributed to genes. Instead, they have been attributed to epigenetic effects. **Epigenetics** is defined as "changes in gene function that do not alter its underlying structure of DNA but result in genes being switched on or off in a reversible way" (Puumala & Hoyme, 2015, p. 15), or, as David Moore describes it, "how genetic material is activated or deactivated—that is, expressed—in different contexts" (Moore, 2015, p. 14). We inherit from our parents not only DNA but also a variety of chemical markers that regulate genes, turning them on at certain times, off at others, and determining how much protein they produce. Recall that every cell in your body has the same DNA, but only some of it is active at any one time. Although each cell possesses the genetic information to grow an eye, for example, eyes do not grow from your liver or on your elbows. Epigenetic mechanisms are responsible for this.

The best understood mechanism for epigenetic effects is that of *DNA methylation*. The DNA of all plants, vertebrates, and many invertebrates has chemicals from the methyl group (written CH₃ by chemists) attached to some of its nucleic acids. Methylation does not alter the protein that a gene will produce, but rather influences whether the genes will produce the protein at all. Most highly methylated genes do not produce their proteins; that is, they are "shut off" (Moore, 2015). **Figure 3.10** shows a sketch of a strand of DNA and where methylation takes place. (Also shown

in the figure is another epigenetic mechanism, *histone modification*, which typically results in activating DNA.)

Processes of DNA methylation seem highly regulated and similar across individuals. For example, in early development, genes that govern the building of an eye become methylated and “turn off” in all tissues except those that will eventually develop into eyes. However, DNA methylation can also be influenced by experience; indeed, it seems to be the primary mechanism by which experience modifies gene action and thus behavior. And these effects can last for years. For example, researchers in Canada assessed pregnant women’s experience of hardship as a result of a major ice storm in Quebec in 1998. Thirteen years later they looked for epigenetic effects in immune-system cells of the children born of these pregnancies. They reported that mothers’ ratings of hardship during pregnancy were related to subsequent levels of DNA methylation in their children’s genes associated with the immune system (Cao-Lei et al., 2014). In other research, 11- to 14-year-old children who had been exposed to physical maltreatment showed greater methylation to a gene associated with stress regulation and to a gene associated with nerve growth factor than nonmaltreated children (Romens et al., 2015). Recent research using placental blood (Kertes, et al., 2016) or saliva (Parades et al., 2016) has shown that early stress is related to the methylation of genes associated with the expression of the stress hormone cortisol and related to subsequent internalizing behavior. Whether these effects help children better adapt to difficult environments or contribute to mental and physical disorders is debatable, but they do clearly demonstrate a chemical mechanism for how experience affects gene expression.

Some of the epigenetic markers created by methylation can be inherited, along with the behavior they influence, as shown in the following example. Mother rats groom their infant pups, mostly by licking them. Pups that have “high-licking mothers” grow up to be less vulnerable to stress than pups with “low-licking mothers.” When the female pups mature and become mothers themselves, they show the same licking pattern as their mothers. This is true even when the pups are cross-fostered (that is, when a pup born to a low-licking mother is raised by a high-licking mother or vice versa). As adults, they show the pattern of their foster mother, not their genetic mother, and this pattern continues for at least several generations (Francis et al., 1999; Meaney, 2010, 2013). Michael Meaney and his colleagues documented the biochemical mechanisms responsible for these transgenerational effects, showing how early experience can alter behavior and be transmitted to future generations, all without any changes in the genes themselves.

Something similar seems to happen in humans. For example, excessive childhood stress in the form of abuse or neglect is associated with poor mental health in later life including personality disorders, depression, anxiety disorders, and substance abuse (Cicchetti & Toth, 2006). The hormone cortisol is associated with such stress, and complex interactions between cortisol, brain activity, and experience over the course of development are related to how people respond to stress (Carpenter et al., 2004; Lee et al., 2005). Discerning the chemical causes of behavior is difficult in humans (few people allow the chemicals in their brains to be assayed while they are still alive). However, research with nonhuman animals suggests that the way the human brain “learns” to react to stress through the production and processing of the hormone cortisol is likely governed by epigenetic mechanisms (Moore, 2015).

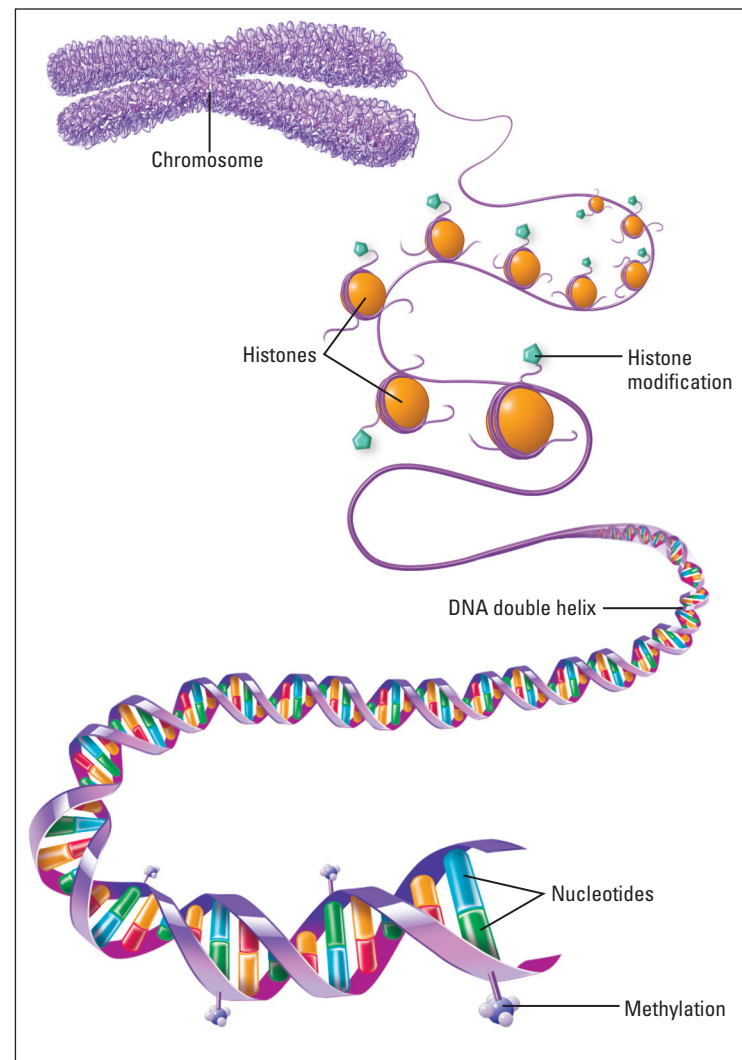


FIGURE 3.10 A schematic diagram of DNA pulled from a chromosome, showing nucleotide bases, the double helix wrapped around histones, and some epigenetic modifications to the DNA.

Although we know of no studies showing the transmission of behavior across generations in humans via epigenetic mechanisms, there is such evidence in the realm of physical development from survivors of the Dutch Hunger Winter. During World War II, parts of the Netherlands experienced extreme famine. For women who were pregnant during this time, not only they but their unborn children were severely deprived of calories. The Dutch government followed these children who were conceived during the famine, as well as the next generation. When women suffered malnutrition during their first three months of pregnancy, their babies were born with normal weight but were at high risk for obesity as adults. Moreover, when these female babies became mothers themselves, their offspring were heavier than average. That is, experiences of the grandmother while pregnant influenced the development of her *grandchildren* (Lumey, 1998). A similar phenomenon has been reported on the effects of malnutrition on the subsequent growth rate and health (susceptibility to cardiovascular disease) for a sample of Swedish *men* (Kaati et al., 2002).

The field of epigenetics is just coming into its own, but new discoveries promise to shed light on the biological basis of inheritance, including ways in which a person's lifetime experiences might influence the phenotype of his or her grandchildren, as well as defining more clearly the nature of gene-environment interactions.

SECTION REVIEW


Hereditary effects on behavioral traits can involve just one gene, but usually involve many.		
<p>Single-Gene Traits</p> <ul style="list-style-type: none">■ Single-gene traits (controlled by one pair of genes) are categorical (all or none) in nature.■ Mendelian patterns of inheritance indicate single-gene control.■ Examples are breed differences in fearfulness in dogs and the human hereditary disorder phenylketonuria (PKU).	<p>Polygenic Traits</p> <ul style="list-style-type: none">■ Polygenic traits (influenced by many gene pairs) are continuous (present in varying degrees) and often fit a normal distribution.■ Through selective breeding, a trait can be strengthened or weakened gradually over generations.■ Examples include Tryon's breeding of rats for maze ability and the Russian program of breeding foxes for tameness.	<p>Epigenetics</p> <ul style="list-style-type: none">■ Experiences cause biochemical changes that affect the activation of genes.■ The best understood mechanism for epigenetic effects is that of DNA methylation.■ Experiences early in life can produce effects that persist years later.■ In some situations, epigenetic effects can be transmitted to children and grandchildren without any changes in the genes themselves.

Evolution by Natural Selection

Lady Ashley, a pillar of London society in the 1850s, is purported to have said upon hearing Darwin's ideas that humans evolved from apes, "Let's hope it's not true; but if it is true, let's hope that it does not become widely known." Lady Ashley's wish did not come true, as Darwin's theory is widely known today and serves as the foundation for modern biology and is also of central importance for understanding human psychology.

Darwin's Insight: Selective Breeding Occurs in Nature

In the first chapter of *The Origin of Species*, Darwin (1859/1963) used the term **artificial selection** to refer to human-controlled selective breeding, and he reminded readers of the enormously diverse varieties of plants and animals that had been produced through that procedure. He then pointed out—and this was his true, original insight—that breeding in nature is also selective and can also produce changes in living things over generations.



FOCUS 17

What insight led Darwin to his theory of evolution? How is natural selection similar to and different from artificial selection?

Selective breeding in nature, which Darwin labeled **natural selection**, is dictated not by the needs and whims of humans but by the obstacles to survival and reproduction that are imposed by the natural environment. Those obstacles include predators, limited food supplies, temperature extremes, difficulty in finding and attracting mates for sexual reproduction—anything that can cut life short or otherwise prevent an organism from producing offspring. Animals and plants that have characteristics that help them overcome such obstacles are, by definition, more likely to have offspring than those that lack such characteristics.

Darwin's concept of natural selection is a simple one, having four core concepts (see **Table 3.1**). First, more individuals are born in a generation than will survive. Second, not all members of a generation are the same—there is *variation* in features or traits. Third, these individual differences are inherited, passed from one generation to the next. Fourth, individuals with collections of traits that fit well with the local environment are more apt to survive and have more offspring than individuals whose traits do not fit as well with the local environment. Any inherited trait that increases the number of offspring an individual produces is automatically “selected for,” as the trait is passed on to those offspring. Conversely, any inherited trait that decreases the number of one's offspring is automatically “selected against,” appearing in fewer members of the next generation. Thus, as long as inheritable differences exist among individuals in an interbreeding population, and as long as some of those differences affect survival and reproduction, evolution will occur.

TABLE 3.1 Core concepts of Darwin's theory of natural selection

- There is overproduction of offspring in each generation.
- There is *variation* in features or traits within members of a generation.
- Individual differences are inherited from one generation to the next.
- Individuals with collections of traits that fit well with the local environment are more apt to survive and have more offspring than individuals whose traits do not fit as well with the local environment.

Genetic Diversity Provides the Material for Natural Selection

Darwin realized that something, passed along through eggs and sperm, must provide the hereditary foundation for evolution, but he knew nothing of genes. Mendel's work, which was the first step toward our modern knowledge of genes, was unknown to most scientists until about 1900, long after Darwin's death. Today we know that genes are the units of heredity and that evolution entails generational changes in the frequencies of particular genes in an interbreeding population. Genes that improve an individual's ability to survive and reproduce in the existing environment increase from generation to generation, and genes that impede this ability decrease over the generations.

The genetic variability on which natural selection acts has two main sources: (1) the reshuffling of genes that occurs in sexual reproduction (already discussed) and (2) mutations. **Mutations** are errors that occasionally and unpredictably occur during DNA replication, causing the “replica” to be not quite identical to the original. In the long run of evolution, mutation is the ultimate source of all genetic variation.



FOCUS 18

How are genes involved in evolution? What are the sources of genetic diversity on which natural selection acts?

New mutations are more often harmful than helpful, and natural selection usually weeds them out. But occasionally a mutation is useful, producing a protein that affects the organism's development in a way that increases its ability to reproduce. Because of its effect on reproduction, the gene arising from such a mutation increases in frequency from generation to generation. At the level of the gene, this is evolution.

Prior to the modern understanding of genes, many people believed that changes in an individual that stem from practice or experience could be inherited and therefore provide a basis for evolution. For example, some argued that early giraffes, by frequently stretching their necks to reach leaves in trees, slightly elongated their necks in the course of their lives and that this change was passed on to their offspring—resulting, over many generations, in the long-necked giraffes we see today. That idea, referred to as the inheritance of acquired characteristics, is most often attributed to Jean-Baptiste de Lamarck (1744–1829), although many other evolutionists, both before and after Lamarck, held the same view (Futuyma, 1997). Even Darwin did not reject that idea, but he added to it the concepts of random variation and natural selection.

The biologist August Weismann established that what happens to the body cells during the life of an animal does not affect that animal's gametes (egg and sperm), a principle known as the doctrine of the separation of the germ (sex cells) and somatic (body cells) lines. No matter how many generations of mice have their tails snipped off, their offspring continue to be born with tails. Today, evolution is defined as changes in gene frequency between populations of individuals, with changes in genes being the “cause” of forming new species. However, animals inherit more than just their genes. They inherit chemicals within the egg and some cellular machinery, as well as a species-typical environment (a womb in mammals, for example). Although genes remain the focus of evolutionary change, as we saw in the earlier section on epigenetics, experiences within an animal's lifetime can sometimes result in inheritance of features across generations.

Environmental Change Provides the Force for Natural Selection



FOCUS 19

How does change in the environment affect the direction and speed of evolution? How did a study of finches illustrate the role of environmental change in evolution?

Evolution is spurred by changes in the environment: Climates change, sources of food change, predators change, and so on. When the conditions of life change, what was previously a useful characteristic may become harmful, and vice versa.

Darwin viewed evolution as a slow and steady process. But today we know that it can occur rapidly, slowly, or almost not at all, depending on the rate and nature of environmental change and on the degree to which genetic variability already exists in a population (Gould & Eldredge, 1993). Environmental change spurs evolution not by causing the appropriate mutations to occur but by promoting natural selection. Some mutations that previously would not have been advantageous and would have gradually been weeded out by natural selection are advantageous in the new environment, so they are passed along in increasing numbers from generation to generation. Evolution sometimes occurs so quickly that people can see it happen. In fact, scientists since Darwin's time have reported more than a hundred different examples of observed evolution (Endler, 1986).

Some of the best-documented examples of observed evolution come from the work of Peter and Rosemary Grant, who for more than 30 years studied a species of finch, the *medium ground finch*, on one of the Galápagos Islands (Grant & Grant, 2008). The Grants found that the members of this species differ somewhat in the thickness of their beaks, that the variation is inheritable, and that environmental changes can result in rapid evolution toward either thicker or thinner beaks. In the 1970s, a severe drought lasting several years caused most of the finches to die because the plants that produce the seeds they eat failed to grow. The birds that survived and produced offspring were those that happened to have thicker, more powerful beaks—powerful enough to crack open the large, hard-shelled seeds that remained after the smaller seeds had been eaten (see **Figure 3.11**).

Two decades later, another species of ground finch, the *large ground finch*, established a breeding colony on the island and began competing with the medium ground finch for food. The intruders were much better adapted for eating the large, hard-shelled seeds than were the medium ground finches, but they were less well adapted for eating the small seeds. The result, for the medium ground finches, was depletion in the supply of large seeds but not of small seeds. Under this condition, the medium ground finches with thinner bills, better adapted for eating the small seeds, were more likely to survive and produce offspring than were those with thicker bills. Within a few generations under this new set of conditions, the average beak thickness of the medium ground finches declined considerably (Grant & Grant, 2006).

The evolution of simple or small changes, such as in skin pigmentation or in beak thickness, can occur in a few generations when selection conditions are strong, but more complex changes require much more time. The difference between, say, a chimpanzee brain and a human brain could not have come about in a few generations, as it must have involved many mutations, each conveying a slight selective advantage to the chimpanzee (in its environment) or to the human (in our environment). When evolutionists talk about “rapid” evolution of complex changes, they are usually talking about periods measured in hundreds of thousands of years (Gould & Eldredge, 1993). **Figure 3.12** provides a simplified sketch of how evolution by natural selection works to produce new forms and functions.



FIGURE 3.11 Rapid evolution During years of drought, natural selection quickly produced the thicker beak, shown at left, in the medium ground finches studied by Peter and Rosemary Grant. During years of competition with a larger thick-billed species, natural selection quickly produced the thinner beak, shown at the right.

Evolution Has No Foresight

People sometimes mistakenly think of evolution as a mystical force working toward a predetermined end. One manifestation of this belief is the idea that evolution could produce changes for some future purpose, even though they are useless or harmful at the time that the change occurs. But evolution has no foresight. The finches studied by the Grants could not have evolved thicker beaks in anticipation of drought, or thinner ones in anticipation of thick-beaked competitors. Only genetic changes that increase survival and reproduction in the immediate environment can proliferate through natural selection.

Another manifestation of the belief in foresight is the idea that present-day organisms can be ranked according to the distance they have moved along a set evolutionary route, toward some planned end (Gee, 2002). For example, some may think of humans as the “most evolved” creatures, with chimpanzees next and amoebas way down on the list. But evolution has no set route or planned end. Humans, chimps, and amoebas have their different forms and behavioral characteristics because of chance events that resulted in them occupying different niches in the environment, where the selection criteria differed. The present-day amoeba is not an early step toward humans but rather a creature that is at least as well adapted to its environment as we are to ours. The amoeba has no more chance of evolving to become like us than we have of evolving to become like it.

A third manifestation of the belief in foresight is the idea that natural selection is a moral force, that its operation and its products are in some sense right or good. In everyday talk, people sometimes imply that whatever is natural (including natural selection) is good and that evil stems from society or human contrivances that go beyond nature. If natural selection promotes a self-interested struggle among individuals, for example, then selfishness is right. Such equations are logically indefensible because nature itself is neither moral nor immoral except as judged so by us. This is referred to as the *naturalistic fallacy*, and it is precisely that, a fallacy. Nature is neither good nor bad, moral nor immoral. To say that natural selection led to a given characteristic does not lend any moral virtue to that characteristic. Fighting, for example, is as much a product of evolution as is cooperation, but that is no reason to consider them morally equivalent.



FOCUS 20

What are three mistaken beliefs about evolution, all related to the misconception that foresight is involved?

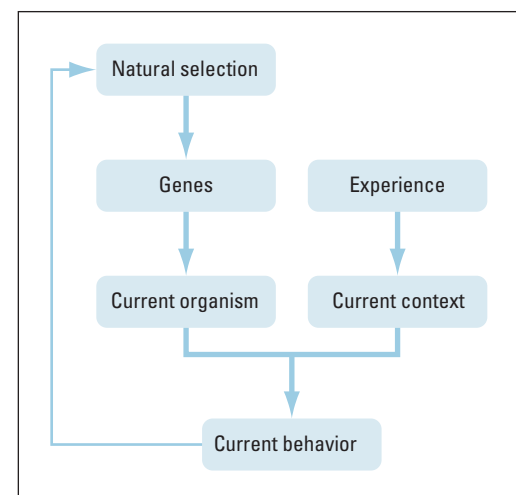



FIGURE 3.12 Natural selection over time Genes and experience combine to produce an animal's current structure and its behavior. That behavior is then the target for natural selection, continuing the cycle.

SECTION REVIEW

Natural selection is the driving force of evolutionary change.

How Natural Selection Works <ul style="list-style-type: none">■ To the degree that a trait enhances survival and reproduction, genes producing that trait are passed on to offspring. The result is that such genes become more frequent over generations.■ Mutations and reshuffling of genes in sexual reproduction provide genetic diversity on which natural selection operates.	Role of Environmental Change <ul style="list-style-type: none">■ The rate and nature of environmental change affect the rate and course of evolution.■ Examples are the effects of drought and of competition from another species on the evolution of beak thickness in finches.■ Complex changes, requiring many mutations, require a long time to evolve.	Evolution Lacks Foresight <ul style="list-style-type: none">■ Natural selection can only lead to changes that are immediately adaptive; it cannot anticipate future needs.■ There is no preset pathway for evolution.■ The naturalistic fallacy is the error of equating “natural” with “moral” or “right.” Natural selection is not a moral force.
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Natural Selection as a Foundation for Functionalism

**FOCUS 21**

How does an understanding of evolution provide a basis for functionalism in psychology?

The mechanisms underlying behavior are products of natural selection; they came about because they promoted survival and reproduction. Just as Tryon used artificial selection to breed rats to be better at learning a particular maze, natural selection automatically breeds animals to be better at doing what they must to survive and reproduce in their natural environments. This idea provides a foundation for the psychological approach known as *functionalism*—the attempt to explain behavior in terms of what it accomplishes for the behaving individual.

The functionalist approach to explaining behavior is essentially the same as the functionalist approach to explaining anatomy: Why do giraffes have long necks? Why do humans lack fur? Why do male songbirds sing in the spring? Why do humans have such an irrepressible ability to learn language? The anatomist trying to answer the first two questions, and the behavioral researcher or psychologist trying to answer the latter two, would look for ways by which each trait helped ancestral members of the species to survive and reproduce.

**FOCUS 22**

How are distal explanations of behavior different from, but complementary to, proximate explanations?

Distal and Proximate Explanations of Behavior

Biologists and psychologists who think in evolutionary terms find it useful to distinguish between two kinds of explanations of behavior—distal and proximate, both of which are needed to properly understand a behavior (Scott-Phillips et al., 2011).

- **Distal explanations** (as in “distant”) are explanations at the evolutionary level. They are statements of the role that the behavior has played in the animal’s survival and reproduction over evolutionary time. Viewed from the vantage point of the gene, they are statements of how the behavior helped the individual’s ancestor’s genes make it into the next generation. Distal causation is sometimes referred to as *ultimate causation*.
- **Proximate explanations** (as in “proximity”) are explanations that deal not with function but with mechanism; they are statements of the immediate conditions, both inside and outside the animal, that elicit the behavior.

Distal and Proximate Explanations Complement Each Other

Consider how distal and proximate explanations might be applied to the question of why male songbirds of many species sing in the spring. A *distal explanation* might

look like this (Koodsma & Byers, 1991): Over the course of evolution, songbirds have adapted to a mating system that takes place in the spring. The male's song serves to attract a female for mating and to warn other males to stay away from the singer's territory in order to avoid a fight. In the evolution of these birds, males whose genes promoted such singing produced more offspring (more copies of their genes) than did males whose genes failed to promote such singing.

A *proximate explanation*, in contrast, might go as follows (Ball & Hulse, 1998): Through the birds' visual system, the increased period of daylight in the spring triggers a physiological mechanism that leads to the increased production of the sex hormone testosterone, which in turn acts on certain areas of the brain (which we might call the "song areas"), promoting the drive to sing.

Notice the complementary nature of these explanations. The distal explanation states the survival or reproductive value of the behavior, and the proximate explanation states the stimuli and physiological mechanisms through which the behavior occurs.

The Search for Distal Explanations in Human Psychology

Evolution by natural selection is the basis of all of the complex biological mechanisms underlying human behavior and experience—including perception, learning, memory, thought, motivation, and emotion. They all came about because each small step in their evolution tended to promote our ancestors' survival and reproduction. Thus, for any basic psychological characteristic that is part of human nature, it is legitimate to ask: How did this characteristic improve the survival and reproductive chances of our ancestors? How did it help our ancestors get their genes into the next generation?

The distal explanations of some human traits (especially those we share with all other mammals) are relatively obvious. We have strong drives to breathe air, drink fluids, and consume foods because our bodies need these things to remain alive. We have strong drives to engage in sex because that is the means by which our genes transfer from one generation to the next. Individuals who lacked such drives are ancestors to nobody today; their genes died with them.

The distal explanations of some other human traits, however, are not so obvious. It is not obvious, for example, why humans everywhere tend to sleep about eight hours each night, or why humans everywhere under certain conditions experience the disturbing emotion of guilt.

Limitations on Functionalist Thinking

Before we go deeper into discussions of distal functions, it is useful to acknowledge the limitations of functionalist thinking. Not every detail of every trait serves a useful function, and some traits that were once functional may not be so today. Here are four reasons why a particular trait or behavior may not be functional.

Some Traits Are Vestigial

Some traits that evolved because they served the needs of our ancestors are no longer functional today, yet they remain. These remnants of our past are called **vestigial characteristics**.

As an example, consider the grasp reflex by which newborn infants close their fingers tightly around objects in their hands. This reflex may well be useful today in the development of the infant's ability to hold and manipulate objects, but that does not explain why prematurely born infants grasp so strongly that they can support their own weight, why they grasp with their toes as well as their hands, and why the best stimulus for eliciting this reflex is a clump of hair (Eibl-Eibesfeldt, 1975). These aspects of the reflex make more sense when we observe them in other primates. To survive, infant monkeys and apes cling tightly with hands and feet to their mother's fur while she swings in trees or goes about her other daily business. In the course of



Anthony Mercical/Science Source

■ **A redwing blackbird at home** This male's singing warns other males of the species to stay away.



FOCUS 23

What are four reasons for the existence of traits or behaviors that do not serve survival and reproductive functions?

our evolution from ape-like ancestors, we lost our fur, so our infants can no longer cling to us in this way, but the reflex remains.

The concept of vestigial traits becomes especially relevant to psychologists when applied to our inherited drives. Because of culture, our habitats and lifestyles have changed dramatically in just a few centuries, a speck on the evolutionary time scale. Essentially all of our evolution as a species occurred in conditions that were quite different from those of today, and some of our inherited tendencies may be harmful, rather than helpful, in the habitat we now occupy. An example is our great appetite for sugar. In the world of our ancestors, sugar was a rare and valuable commodity. It existed primarily in fruits and provided energy needed for vigorous physical activity. But today sugar is readily available in most areas of the world, and life (for many of us) is less physically strenuous. Yet our preference for sugar persists as strong as ever, despite such negative consequences as tooth decay and obesity.

Some Traits Are Side Effects of Natural Selection for Other Traits

Useless changes can come about in evolution as by-products of natural selection for other, useful changes. A simple example in humans is the navel, or belly button (Buss et al., 1998). To the best of anyone's knowledge, the navel serves no function related to survival or reproduction. It is simply a remnant left from the umbilical cord. The umbilical cord, of course, does serve a survival and reproductive function: It conveys nutrients from the mother to the developing fetus. As such, we refer to the umbilical cord as an **adaptation**. It is a universal and reliably developing inherited feature that arose as a result of natural selection and helped to solve some problem of survival. But navels are simply the necessary by-products of umbilical cords and have no function themselves. An anatomist from Mars who observed belly buttons on adult earthlings, but who never observed a fetus or the birth process, would be at a loss to explain why such a structure would have evolved.

It is possible that some human psychological capacities, even some that are so general that we would consider them to be part of human nature, came about as side effects of the evolution of other capacities. For example, are the universal human proclivities for art and music direct effects of natural selection, or side effects? Perhaps these proclivities served to attract mates during much of our evolutionary history (as they seem to today), and were therefore selected for directly, much as song was selected for in birds. Or perhaps they emerged simply as by-products of selection for other proclivities, such as those for planning, constructing tools, and communicating through language. A third possibility, combining the first two, is that proclivities for art and music may have initially emerged as by-products and then been selected for because of their usefulness for attracting mates or other helpers. At present, we do not have evidence to support strongly any of these theories over the others.

Some Traits Result Simply From Chance

Some inheritable characteristics that result from just one or two mutations are inconsequential for survival and reproduction. Different races of people have somewhat differently shaped noses. Maybe that variation is caused by natural selection. Perhaps one shape worked best in one climate and another worked best in another climate, so natural selection molded the noses differently. But we can't assume that. The different shapes might be a result of mutations that didn't matter and therefore were never weeded out by natural selection. Maybe the small group of people who migrated to a specific part of the world, and who were the ancestors of a particular racial group, just happened to carry along genes for a nose shape that was different from the average for the group they left. Such variation, due to chance alone without selection, is called *genetic drift*.

Many years ago, researchers discovered that the incidence of schizophrenia (a serious mental disorder, discussed in Chapter 15) is three times greater among people living in northern Sweden, above the Arctic Circle, than among people in most

other parts of the world (Huxley et al., 1964). There are at least three possible explanations of this observation: (a) Environmental conditions, such as the harsh climate or the isolation it produces, might tend to bring on schizophrenia in people who are prone to it. (b) Natural selection might have increased the frequency of schizophrenia-promoting genes among these people, perhaps because such genes help protect people from harmful effects of physical stressors such as cold climate. (This was the hypothesis suggested by Huxley and his colleagues.) (c) The Arctic population may have been founded by a small group of Swedish migrants who, just by chance, had a higher proportion of schizophrenia-promoting genes than the population at large. This last possibility (also mentioned by Huxley and his colleagues) would be an example of genetic drift. To this day, scientists are unsure which of these theories is correct.

Evolved Mechanisms Cannot Deal Effectively With Every Situation

Our basic drives, emotions, and other behavioral tendencies came about in evolution because, on balance, they promoted survival and reproduction more often than they interfered with survival and reproduction. That does not mean, however, that every instance of activation of such a drive, emotion, or tendency serves survival or reproductive ends. The emotion of guilt serves the distal function of helping us to preserve our relationships with people whose help we need for survival and reproduction. When we hurt someone we depend on, we feel guilty, which motivates us to make amends and patch up the relationship. That does not mean, however, that every manifestation of guilt in every person serves that function. Sometimes guilt can be crippling; our capacity for guilt can be exploited by others for their ends at our expense. The best that natural selection could do was to develop a guilt mechanism that is triggered by certain general conditions. It could not build a mechanism capable of distinguishing every possible condition from every other one and triggering guilt only when it is useful. The same is true for all of our other evolved emotions and drives.

SECTION REVIEW

The concept of natural selection provides a secure footing for functionalism.

<p>The Functionalist Approach</p> <ul style="list-style-type: none">■ Functionalism is an approach to psychology that focuses on the usefulness of a particular behavior to the individual engaging in it.■ Distal explanations are functional explanations, examining the role that specific behaviors play in survival and reproduction.■ Proximate explanations are complementary to distal explanations; they are concerned with mechanisms that bring about behavior.	<p>Limitations of Functionalism</p> <ul style="list-style-type: none">■ Some traits are vestigial; they once served a function but no longer do.■ Some traits, such as the umbilical cord, are adaptations; whereas others, such as the navel, are side effects, or by-products, of other traits that arose through natural selection.■ Some traits are products just of chance, not natural selection.■ Even evolved mechanisms, such as that for guilt, are not useful in every situation in which they are active.
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Natural Selection as a Foundation for Understanding Species-Typical Behaviors

Suppose you saw an animal that looked exactly like a dog, but it meowed, climbed trees, and ignored the mail carrier. Would you call it a dog or a cat? Clearly, we identify animals as much by their behavior as by their anatomy. Every species of animal has certain characteristic ways of behaving. These are commonly called *instincts*,

but a more technical term for them is **species-typical behaviors**. Meowing, tree climbing, and acting aloof are species-typical behaviors of cats. Dam building is species-typical of beavers. Smiling, talking, and two-legged walking are species-typical behaviors of humans.

Many psychologists (particularly developmental psychologists) avoid using the word “instinct” and the related term “innate” for two reasons. First, they imply “no experience necessary” and this is associated with *genetic determinism*, the belief that genes “determine” behavior independent of experience. The mistake here is assuming or implying that genes influence behavior directly, rather than through the indirect means of working with the environment to build or modify biological structures that then, in interplay with the environment, produce behavior. Some popular books on human evolution have exhibited the deterministic fallacy by implying that one form of behavior or another—such as fighting for territories—is unavoidable because it is controlled by our genes. That implication is unreasonable even when applied to nonhuman animals. Territorial birds, for example, defend territories only when the environmental conditions are ripe for them to do so. We humans can control our environment and thereby control ourselves. We can either enhance or reduce the environmental ingredients needed for a particular behavioral tendency to develop and manifest itself.

The second reason psychologists avoid the word “instinct” is because it is not easily defined. And, as Patrick Bateson wrote (2002, p. 2212):

Apart from its colloquial uses, the term instinct has at least nine scientific meanings: present at birth (or at a particular stage of development), not learned, developed before it can be used, unchanged once developed, shared by all members of the species (or at least of the same sex and age), organized into a distinct behavioral system (such as foraging), served by a distinct neural module, adapted during evolution, and differences among individuals that are due to their possession of different genes. One does not necessarily imply another even though people often assume, without evidence, that it does.

For these reasons, we will avoid the term “instinct” in this book, using the more descriptive term “species-typical behaviors.”


Species-Typical Behaviors in Humans

Species-typical behaviors are products of evolution, but that does not mean they are necessarily rigid in form or uninfluenced by learning. To understand more fully the concept of species-typical behaviors, let us examine some examples in human beings.

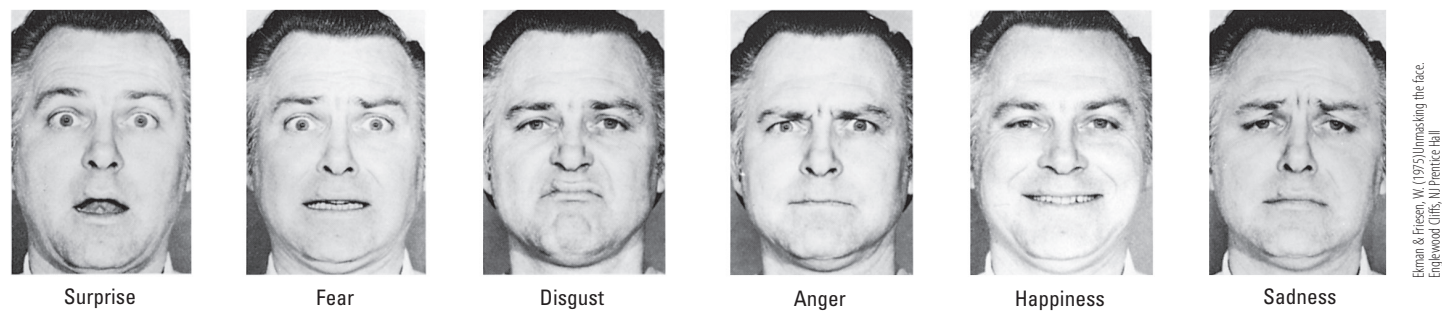
Human Emotional Expressions as Examples of Species-Typical Behaviors

Darwin noted that humans, like other animals, automatically communicate moods and behavioral intentions to one another through body postures, movements, and facial expressions. In his book *The Expression of the Emotions in Man and Animals*, Darwin (1872/1965) argued that specific facial expressions accompany specific emotional states in humans and that these expressions are universal, occurring in people throughout the world and even in people who were born blind and thus could not have learned them through observation.

In an extension of Darwin’s pioneering work, Paul Ekman and Wallace Friesen (1975, 1982) developed an atlas that describes and depicts the exact facial-muscle movements that make up each of six basic emotional expressions in people: surprise, fear, disgust, anger, happiness, and sadness (see **Figure 3.13**). They then showed photographs of each expression to individuals in many different cultures, including members of a preliterate tribe in the highlands of New Guinea who had little previous contact with other cultures. They found that people in every culture described each depicted emotion in a way that was consistent with descriptions in

**FOCUS 24**

What evidence supports the idea that many human emotional expressions are examples of species-typical behaviors?



Ekman & Friesen, W. (1975) Unmasking the face. Englewood Cliffs, NJ: Prentice Hall

the United States (Ekman, 1973; Ekman et al., 1987). In a reversal of this procedure, they also photographed members of the New Guinea tribe who had been asked to act out various emotions and showed the photographs to college students in the United States. The college students were quite accurate in labeling the emotions portrayed by the New Guineans.

In a further extension of Darwin's work, Irenäus Eibl-Eibesfeldt (1989) documented the cross-cultural universality of many nonverbal signals, including one that he labeled the *eyebrow flash*, a momentary raising of the eyebrows lasting about one sixth of a second, usually accompanied by a smile and an upward nod of the head (see **Figure 3.14**). He observed this expression in every culture he studied—including those in New Guinea, Samoa, and various parts of Africa, Asia, South America, and Europe—and concluded that it is a universal sign of greeting among friends. Raised eyebrows are also a component of the emotional expression of surprise (look at Figure 3.13 again), so the eyebrow flash with its accompanying smile might be interpreted as a nonverbal way of saying, "What a happy surprise to see you!"

Eibl-Eibesfeldt (1975) also filmed children who were born blind, or both blind and deaf, and found that they manifest emotions in the same basic ways as sighted children do (see **Figure 3.15**). Such observations provide the most direct evidence that at least some human expressions do not have to be learned through observing them in others or hearing descriptions of them.

Taking all the evidence together, there can be little doubt that we are biologically predisposed to express certain emotions in certain species-typical ways. It is also clear, however, that we can control and modify our emotional expressions and learn new ones. Even researchers who focus on universal expressions are quick to point out cross-cultural differences. For example, Eibl-Eibesfeldt (1975) found that despite its cross-cultural similarity in form and general meaning, large cultural differences exist in the use of the eyebrow flash. The Japanese, who are reserved in social expressions among adults, use it mainly when greeting young children, whereas Samoans greet nearly everyone in this way. More recently, researchers have shown that cultural dialects occur in the emotional expressions that Ekman and Friesen included in their atlas. In general, people can identify each emotion

FIGURE 3.13 Six basic human emotional expressions These expressions, taken from Ekman and Friesen's atlas of emotional expressions, were produced by a model who was asked to move specific facial muscles in specific ways. As you study each figure, try to describe the positions of the facial features for each expression. For example, surprise can be described as follows: The brows are pulled upward, producing horizontal wrinkles across the forehead; the eyes are opened wide, revealing white above the iris; and the lower jaw is dropped, with no tension around the mouth.



FOCUS 25

How do human emotional expressions illustrate the point that species-typical behaviors can be modified by learning?



Eibl-Eibesfeldt (1989). Human ethology. Hawthorne, NY: Walter de Gruyter, Inc.



FIGURE 3.15 Some emotional expressions need not be learned through observation This child, manifesting joy, has been blind and deaf since birth.



FOCUS 26

How do the examples of two-legged walking and language in humans, and singing in white-crowned sparrows, illustrate the point that species-typical behaviors may depend on learning?



FOCUS 27

How is the concept of biological preparedness related to that of species-typical behavior? How do the examples of human walking and talking illustrate biological preparedness?

more easily and accurately when it is expressed by other members of their own culture than when it is expressed by members of a very different culture (Elfenbein & Amady, 2003; Elfenbein et al., 2007).

The Role of Learning in the Development of Species-Typical Behaviors

To say that a behavior is species-typical is not to say that it is unaffected by learning. As we just pointed out, our basic emotional expressions are species-typical, but cultural differences among them are learned. The role of learning is even more obvious in two of our most characteristic species-specific behaviors—our manner of walking and our use of language.

A scientist from Mars would almost certainly point to two-legged walking and use of a grammar-based language as among the defining behavioral characteristics of the human species. These characterize humans everywhere and clearly depend on inherited predispositions, yet their development also clearly depends on learning.

During the peak months of learning to walk (generally during the second year of life), toddlers spend an average of about 6 hours per day practicing balancing and walking and, on a typical day, take about 9,000 walking steps and travel the length of 29 football fields (Adolph et al., 2003). For the most part they are not trying to get to any particular place; they are just walking for the sake of walking. By the time they are proficient walkers, they have spent thousands of hours practicing, on their own initiative. During those same months, infants also, on their own initiative, intensely practice talking. With language, infants do not just learn the motor coordination needed to produce the sounds; they also learn the basic vocabulary and grammar of the language that they hear around them. Talking and two-legged walking are species-typical behaviors in humans, but a human raised in an environment where either of these capacities was impossible to practice would not develop that capacity. Such an inhuman environment would not produce a normal human being.

Learning plays crucial roles in the development of species-specific behaviors in other animals as well. For example, white-crowned sparrows develop the ability to sing their species-typical song only if they are permitted to hear it during the first summer after hatching (Marler, 1970). Indeed, populations of the species living in different areas have somewhat different dialects, and young birds learn to sing the dialect that they hear (Nelson et al., 2004). Yet the range of possible songs that the birds can learn is limited by their biology. No matter what its environmental experiences, a white-crowned sparrow cannot learn to sing like a canary or like any species other than a white-crowned sparrow.

Biological Preparedness as the Basis for Species-Typical Behaviors

The difference between behaviors that we call instinctive, or species-typical, and those that we do not so label has to do with their degree of *biological preparedness*. Natural selection has equipped each species with anatomical structures that ensure that normal individuals of the species, who grow up in a normal environment for that species, will be physically able to perform their species-typical behaviors and will be motivated to learn what they must for adequate performance.

We humans come into the world biologically prepared to learn to walk on two legs. Natural selection has provided us with anatomical features—such as strong hindlimbs with feet, weaker forelimbs without feet, an upwardly tilted pelvis, and a short, stiff neck—that combine to make it more convenient for us to walk upright than on all fours. Moreover, we are born with neural systems in the brain and spinal cord that enable us to move our legs correctly for coordinated two-legged walking and with neural structures that motivate us to practice this behavior at the appropriate stage in our development. Consider the difference between two-legged walking



JennieWoodcock/Reflections Photolibary/Contis/Documentary/Getty Images



© Geri Engberg/The Image Works

■ **Biological preparedness** Infants are born with a “stepping reflex,” which shows that they have, inborn, the neural mechanisms for two-legged walking. Perfecting that behavior, however, requires extensive practice during the toddling stage, when the legs have become strong enough to support the child’s weight.

in humans and in dogs. Dogs are capable of learning to walk on two legs, and much is made of that fact by circus trainers, but they are never very good at it. They do not have the appropriate muscular and skeletal systems to coordinate the behavior properly, and they have no natural impulse to walk in this manner. A dog, unlike a human child, will practice two-legged walking only if it receives immediate rewards, such as food, for doing so. Thus, two-legged walking is not a species-typical behavior in dogs.

The same is true for talking. Humans are born with anatomical structures, including a larynx and a flexible tongue, that can produce a wide range of sounds and with a brain that has special neural centers for understanding and producing language. Infants begin talking at a certain stage even if they receive little encouragement from those around them. Chimpanzees can be taught to simulate some aspects of human language, just as dogs can be taught to walk on their hind legs, but they require lots of encouragement and are never very good at it.

Species-Typical Behavior Is a Relative Concept

Having characterized the concept of species-typical behavior in terms of biological preparedness, we must now add that the concept is relative rather than absolute. No behavior stems just from biological preparedness; some sort of experience with the environment is always involved. Conversely, any behavior that an individual can produce—no matter how artificial it may seem or how much training is required—must make use of the individual’s inherited biological capacities. The concept of species-typical behavior is useful as long as we accept it as relative and do not argue about whether a given behavior really should or should not be called species-typical.

The question to ask when we study a particular behavior is not, Is this a species-typical behavior? Rather, the meaningful questions are these:


- What are the environmental conditions needed for the full development of this behavior?
- What internal mechanisms are involved in producing this behavior?
- What consequences does this behavior have in the individual’s daily life?
- In the course of evolution, why would the genes that make this behavior possible have been favored by natural selection?

These questions can be asked of any behavior, regardless of whether it is thought of as species-typical.



FOCUS 28

Why is the concept of species-typical behavior relative rather than absolute?



FOCUS 29

What is the difference between a homology and an analogy, and how can researchers tell whether a similarity between two species in some trait is one or the other?

The Value of Cross-Species Comparisons of Species-Typical Behaviors

In psychology as well as biology, scientists have learned a lot about our species by comparing us to other animals. The basic rationales for learning about any one species by comparing it with others are found in the principle of evolution by natural selection.

Two Forms of Cross-Species Comparison: Homologies and Analogies

An understanding of evolution makes it clear that two conceptually different classes of similarities exist across species: homologies and analogies.

A **homology** is any similarity that exists because of the different species' common ancestry. All animals originated from a common ancestor, so it is not surprising that some homologies—such as those in the basic structure of DNA molecules and of certain enzymes—can be found between any two species. But the more closely related two species are, the more homologies they show.

Much research has been done contrasting humans with chimpanzees and bonobos. As we noted earlier in this chapter, humans share more than 98% of their DNA with each of these great apes, making them our closest genetic relatives. However, it is *not* the case that humans evolved from chimpanzees or bonobos. Rather, we shared a common ancestor with these animals, which lived in Africa between 5 and 7 million years ago. That ancestor was likely very chimp-like, but over the course of the next several million years evolved into at least three lines that eventually led to modern humans, chimpanzees, and bonobos. **Figure 3.16** shows the evolutionary relationship of humans to the great apes and Old World monkeys.

An **analogy**, in contrast, is any similarity that stems not from common ancestry but from *convergent evolution*. Convergent evolution occurs when different species, because of some similarity in their habitats or lifestyles, independently evolve a common characteristic.

Consider some comparisons among species that can fly. Flying has arisen separately in three taxonomic groups: birds, some insects (such as butterflies), and some mammals (bats). Similarities across these three groups in their flying motions, and in the anatomical structures that permit flight, are examples of analogies because they do not result from common ancestry (see **Figure 3.17**). However, similarities in flight and wings among species within any of these groups, such as between crows and sparrows, are likely to be homologies. The last common ancestor between a crow and a sparrow was itself a bird with wings, but the last common ancestor between a crow and a butterfly, or between a crow and a bat, did not have wings.

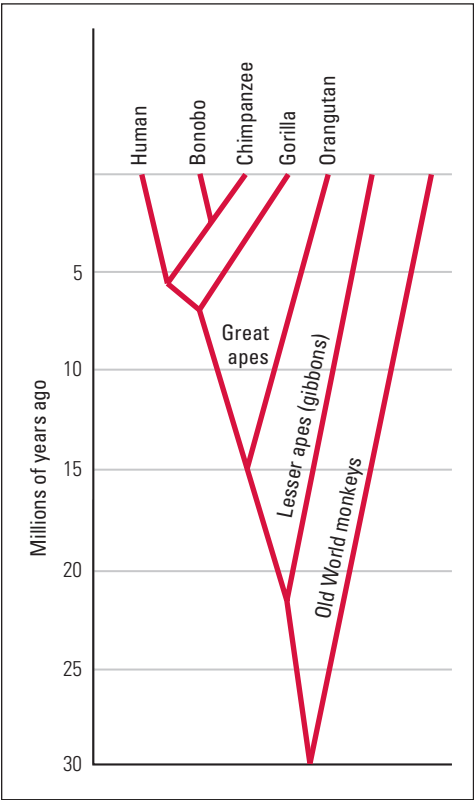


FIGURE 3.16 Relationship of humans to apes and Old World monkeys The ancestral line leading to humans split off from that leading to Old World monkeys 30 million years ago, and it split off from that leading to bonobos and chimpanzees about 6 million years ago. (Data from Corballis, 1999.)



(a)



(b)



(c)

FIGURE 3.17 Analogous wings Similarities in the wings and flying behavior of birds, bats, and butterflies are considered to be analogies, not homologies, because they arose independently in evolution.



FIGURE 3.18 Cells built by honeybees and bumblebees Honeybees build hives with hexagonally shaped cells (a), the optimal shape for storing large amounts of honey and larvae using the least amount of precious wax. To understand how such behavior might have come about through natural selection, Darwin studied homologous but simpler storage structures of related bee species. The simplest, produced by bumblebees (b), consists simply of a cluster of spherical cells, which the bees easily build by sweeping their abdomens compass-like to carve out the spheres. Other species build intermediate structures, with spherical cells that intersect and are patched up with flat wax walls at the places of intersection. Darwin suggested that ancestors of modern honeybees built their hives in a way similar to that of modern bumblebees but, through evolution, began making their cells ever closer together and more regularly spaced and patching up the intersections, resulting eventually in hexagonal cells.

The Value for Psychology of Studying Homologies

Homologies are useful for research on the physiological mechanisms of behavior (that is, research on how the brain and other biological structures operate to produce the behavior being studied). Because convergent evolution can produce similar behaviors that operate through different mechanisms, researchers who seek to understand the physiological mechanism of some behavior in humans through experiments on other species must study species in which the relevant behavior is homologous, not analogous, to that in humans. Many basic mechanisms of learning, motivation (such as hunger), and sensation (such as vision) are homologous across all or at least most species of mammals, and we have learned much about these by studying them in mice, rats, cats, and other laboratory mammals.

Homologies are also useful for inferring the pathways along which species-typical behaviors evolved. By comparing the different forms of a particular species-typical behavior in closely related species, it is often possible to reconstruct how the more complex of these forms evolved through a series of steps from the simpler form. Darwin (1859/1963) himself used this method to figure out the evolutionary steps through which honeybees acquired their marvelous ability to construct complex hives consisting of wax combs of closely fitting hexagonal cells in which to store honey and larvae (see **Figure 3.18**).

Homologies as Clues to the Evolutionary Origins of Two Human Smiles

In research that is more directly relevant to psychology, Darwin also used homologies to understand the origins of species-typical emotional expressions in humans. He watched monkeys and apes at the London Zoo and noted that a number of their expressions seemed to be homologous to human expressions, including the smile (Darwin, 1872/1965). Research following up on Darwin's work has suggested that people may produce two kinds of smiles, which may have separate evolutionary origins.

People smile in two quite different contexts: (1) when genuinely happy and (2) when wishing to show another person that they are favorably disposed toward that person. The latter situation need not entail happiness at all; in fact, people are especially likely to smile at others in potentially tense circumstances, apparently as a



FOCUS 30

How are homologies used for learning about (a) the physiological mechanisms and (b) the evolutionary pathways of species-typical traits?

**FOCUS 31**

How do studies of homologies between humans and other primates support the view that the human greeting smile and the human happy smile have separate evolutionary origins?

FIGURE 3.19 Possible homologues to two types of human smiles The silent bared-teeth display (a) is believed to be homologous to the human greeting smile, and the relaxed open-mouth display (b) is believed to be homologous to the human laugh and happy smile. The animals in both photos are chimpanzees.



(a)



(b)

Nonhuman primates manifest two distinct smile-like displays. The one that seems most clearly to be homologous to the human greeting smile is the *silent bared-teeth display* (see **Figure 3.19a**). This facial expression involves contraction of the same facial muscles as are involved in the human greeting smile (Parr et al., 2007). In macaque monkeys this display seems to have evolved as a means for a more submissive ape to look at a more dominant one without provoking a fight. If it could be translated into words, it might be rendered as, “I’m looking at you but I’m not going to attack, so please don’t attack me.” This type of display takes on a new function in chimpanzees, something more similar to that of the human smile of greeting (van Hooff, 1976). Both the more submissive and the more dominant of two chimpanzees show the display upon meeting, and it usually precedes friendly interaction between them. As used by the more submissive individual, it may retain its original meaning, “Please don’t attack me,” but as used by the more dominant, it may mean, “Rest assured, I won’t attack,” and as used by both it may mean, “Let’s be friends.”

The other primate smile-like expression is the *relaxed open-mouth display*, or *play face* (see **Figure 3.19b**), which occurs mostly in young primates during playful fighting and chasing and is most clearly homologous to human laughter. It involves the same facial muscles as are involved in human laughter (Parr et al., 2007), and in chimpanzees it is often accompanied by a vocalized *ahh ahh ahh*, which sounds like a throaty human laugh. This display apparently originated as a means for young primates to signal to each other that their aggressive-like behavior is not to be taken seriously; nobody will really get hurt. Interestingly, in human children, laughter occurs during playful fighting and chasing more reliably than during any other form of play (Blurton-Jones, 1967). Thus, our laughter is not only similar in form to the relaxed open-mouth display of other primates but also, at least in some cases, seems to serve a similar function.

**FOCUS 32**

How can we use analogies to make inferences about the distal functions of species-typical traits?

The Value for Psychology of Studying Analogies

You have just seen examples of how homologies can be used to make inferences about the evolutionary origins of species-typical behaviors. Analogies, in contrast, are not useful for tracing evolutionary origins, but are useful for making inferences about the distal functions of species-typical behaviors. If different species have independently evolved a particular behavioral trait, then comparing the species may reveal commonalities of habitat and lifestyle that are clues to the distal function of that trait. You will see examples of this use of analogies in the remaining sections of this chapter, as applied to patterns of mating, patterns of aggression, and patterns of helping.

SECTION REVIEW

Species-typical behaviors have come to exist through natural selection.

Species-Typical Behaviors

- Species-typical behaviors are ways of behaving that characterize a species—such as cats meowing and humans walking upright.
- They may be influenced by learning or even require learning, as exemplified by cultural differences in the eyebrow flash, human language learning, and white-crowned sparrows' song development.
- They depend on biological preparedness—that is, having anatomical structures that permit and motivate the behavior.

Homologies and Analogies

- Homologies are similarities due to common ancestry. They are useful for studying underlying mechanisms and for tracing the evolutionary course of species-typical behaviors, exemplified by research on the greeting smile and happy smile in humans.
- Analogies are similarities due to convergent evolution (independent evolution of similar traits). They are useful for inferring distal functions.

Evolutionary Analyses of Mating, Aggression, and Helping

Evolutionary theory is concerned with a handful of core issues including survival, mating, kin, and social relationships. In this section we examine three topics related to some of these issues: mating, aggression, and helping.

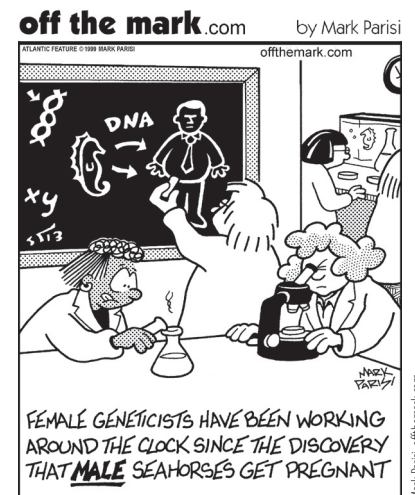
A Theory Relating Mating Patterns to Parental Investment

From an evolutionary perspective, no behavior is more important than mating. Mating is the means by which all sexually reproducing animals get their genes into the next generation. Mating is also the most basic form of social behavior. If females and males did not need to come together to reproduce, members of a species could, in theory, go through life completely oblivious to one another.

Countless varieties of male–female arrangements for sexual reproduction have evolved in different species of animals. One way to classify them is according to the number of partners a male or female typically mates with over a given period of time, such as a breeding season. Four broad classes are generally recognized: **polygyny** [pah-li-ji-nee], in which one male mates with more than one female; **polyandry** [pah-lee-an-dree], in which one female mates with more than one male; **monogamy**, in which one male mates with one female; and **promiscuity**, in which members of a group consisting of more than one male and more than one female mate with one another (Shuster & Wade, 2009). (These terms are easy to remember if you know that *poly-* means “many”; *mono-*, “one”; *-gyn*, “female”; and *-andr*, “male”; for example, polyandry means “many males.”) As illustrated in **Figure 3.20**, a feature of both polygyny and polyandry is that some individuals are necessarily deprived of a mating opportunity—a state of affairs associated with considerable conflict.

In a now-classic article, Robert Trivers (1972) outlined *parental investment theory*. **Parental investment** can be defined roughly as the time, energy, and risk to survival that are involved in producing, feeding, and otherwise caring for each offspring. Trivers proposed that in sexually reproducing species there is a conflict between mating effort (time/effort expended in finding and keeping a mate) and parenting effort (time/effort expended in raising offspring). Trivers proposed that, in general, the sex that invests more in parenting will be more selective in choosing a mate than the less-investing sex, whereas the less-investing sex will compete more vigorously for access to the more investing sex.

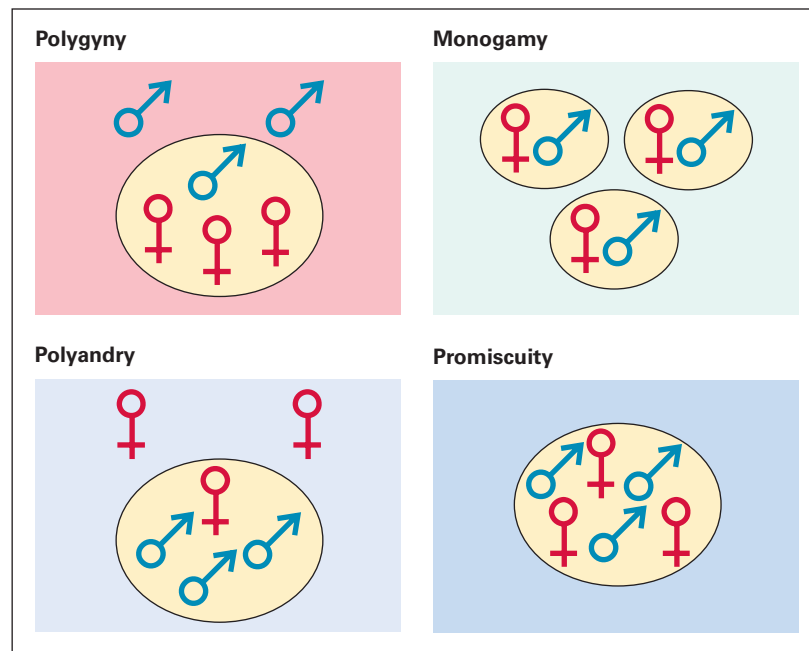
To illustrate and elaborate on this theory—and to see how it is supported by cross-species comparisons focusing on analogies—let us apply it to each of the four general classes of mating patterns.



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What is Trivers's theory of parental investment?

FIGURE 3.20 Four mating systems In a polygynous system (common in mammals), the unmated males are a threat to the mated male, and in a polyandrous system (present in some birds and fishes), the unmated females are a threat to the mated female. Threat is reduced by monogamy and promiscuity because with those systems most individuals find mates.



FOCUS 34

Based on Trivers's theory of parental investment, why does high investment by the female lead to (a) polygyny, (b) large size of males, and (c) high selectivity in the female's choice of mate?

Polygyny Is Related to High Female and Low Male Parental Investment

Most species of mammals are polygynous, and Trivers's theory helps explain why. Mammalian reproductive physiology is such that the female necessarily invests a great deal in the offspring she bears. The young must first develop within her body and then she must nourish them by providing milk. Because of the female's high investment, the number of offspring she can produce in a breeding season or a lifetime is limited. A human female's gestation and lactation periods are such that she can have, at most, approximately one infant per year regardless of how many different males she mates with.

Things are different for the male. His involvement with offspring is, at minimum, simply the production of sperm cells and the act of copulation. These require little time and energy, so his maximum reproductive potential is limited not by parental investment but by the number of fertile females he mates with. A male who mates with 20 females can in theory produce 20 offspring a year. When the evolutionary advantage in mating with multiple partners is greater for males than for females, a pattern evolves in which males compete with one another to mate with as many females as they can.

Among mammals, males' competition for females often involves one-on-one battles, which the larger and stronger combatant most often wins. This leads to a selective advantage for increased size and strength in males, up to some maximum beyond which the size advantage in obtaining mates is outweighed by disadvantages, such as difficulty in finding sufficient food to support the large size. In general, the more polygynous a species, the greater is the average size difference between males and females. An extreme example is the elephant seal. Males of this species fight one another, sometimes to the death, for mating rights to groups averaging about 50 females, and the males outweigh females several-fold (Hoelzel et al., 1999). In the evolution of elephant seals, those males whose genes made them large, strong, and ferocious enough to defeat other males sent many copies of their genes on to the next generation, while their weaker or less aggressive opponents sent few or none.

For the same reason that the female mammal usually has less evolutionary incentive than the male to mate with many individuals, she has more incentive to be discriminating in her choice of mate. Because she invests so much, risking her life and decreasing her future reproductive potential whenever she becomes pregnant, her genetic interests lie in producing offspring that will have the highest possible



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■ **Who's bigger and stronger?** These male elephant seals are sizing each other up for possible battle over mating rights to the many females in the background. Because the larger combatant usually wins, male elephant seals have through natural selection become huge compared with females.

chance to survive and reproduce (Campbell & Cross, 2012). To the degree that the male affects the young, either through his genes or through other resources he provides, females would be expected to select males whose contribution will be most beneficial. In elephant seals, it is presumably to the female's evolutionary advantage to mate with the winner of battles. The male victor's genes increase the chance that the female's sons will win battles in the future and produce many young themselves.

Polyandry Is Related to High Male and Low Female Parental Investment

Polyandry is not the primary mating pattern for any species of mammal, but it is for some species of fishes and birds (Andersson, 2005). Polyandry is more likely to evolve in egg-laying species than in mammals, because a smaller proportion of an egg layer's reproductive cycle is tied to the female's body. Once the eggs are laid, they can be cared for by either parent, and, depending on other conditions, evolution can lead to greater male than female parental investment. Polyandry seems to come about in cases where the female can produce more eggs during a single breeding season than either she alone or she and one male can care for (Andersson, 2005). Her best strategy then becomes that of mating with multiple males and leaving each batch of fertilized eggs with the father, who becomes the main or sole caretaker.

Consistent with Trivers's theory, females of polyandrous species are the more active and aggressive courters, and they have evolved to be larger, stronger, and in some cases more brightly colored than the males (Berglund & Rosenqvist, 2001). An example is the spotted sandpiper, a common freshwater shorebird. A female spotted sandpiper can lay up to three clutches of eggs in rapid succession, each cared for by a different male that has mated with her (Oring, 1995). At the beginning of the breeding season, the females—which outweigh the males by about 20% and have somewhat more conspicuous spots—stake out territories where they actively court males and drive out other females.



Larry Selman/MostlyBirds.com/Getty Images



FOCUS 35

What conditions promote the evolution of polyandry? How do sex differences within polyandrous species support Trivers's theory?

■ **An aggressive female** The spotted sandpiper is a polyandrous species. The female mates with several males and defends her territory from invading females. This female is stretching her wings in a threat display.

FOCUS 36

What conditions promote the evolution of monogamy? Why are sex differences in size and strength generally lacking in monogamous species?



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■ **A not-so-faithful couple** The superb fairy wren is socially but not sexually monogamous. The male (at the left) and the female stay together at the nest and raise the young together, but DNA testing has shown that about 75% of the offspring, on average, are sired by neighboring males.

FOCUS 37

For what evolutionary reasons might monogamously mated females and males sometimes copulate with partners other than their mates?

FOCUS 38

What appear to be the evolutionary advantages of promiscuity for chimpanzees and bonobos? In what ways is promiscuity more fully developed for bonobos than for chimpanzees?

Monogamy Is Related to Equivalent Male and Female Parental Investment

According to Trivers's theory, when the two sexes make approximately equal investments in their young, their degree of competition for mates will also be approximately equal, and monogamy will prevail. Equal parental investment is most likely to come about when conditions make it impossible for a single adult to raise the young but quite possible for two to raise them. Under these circumstances, if either parent leaves, the young fail to survive, so natural selection favors genes that lead parents to stay together and care for the young together. Because neither sex has a much greater likelihood of fighting over mates, there is little or no natural selection for sex differences in size and strength, and, in general, males and females of monogamous species are nearly identical in these characteristics.

Consistent with the view that monogamy arises from the need for more than one adult to care for offspring, over 90% of bird species are predominantly monogamous (Cézilly & Zayan, 2000). Among most species of birds, unlike most mammals, a single parent would usually not be able to raise the young. Birds must incubate and protect their eggs until they hatch, then must guard the hatchlings and fetch food for them until they can fly. One parent alone cannot simultaneously guard the nest and leave it to get food, but two together can. Among mammals, monogamy has arisen in some species that are like birds in the sense that their young must be given food other than milk, of a type that the male can provide. The best-known examples are certain carnivores, including foxes and coyotes (Malcolm, 1985). Young carnivores must be fed meat until they have acquired the necessary strength, agility, and skills to hunt on their own, and two parents are much better than one at accomplishing this task. Monogamy also occurs in several species of rodents, where the male may play a crucial role in protecting the young from predators while the mother forages (Sommer, 2000), and some South American monkeys (i.e., owl, Goeldi's, and titi monkeys), where the father actually engages in more childcare than the mother (Schradin et al., 2003).

With modern DNA techniques to determine paternity, researchers have learned that *social monogamy* (the faithful pairing of female and male for raising young) does not necessarily imply *sexual monogamy* (fidelity in copulation between that female and male). Researchers commonly find that between 5 and 35% of offspring in socially monogamous birds are sired by a neighboring male rather than by the male at the nest (Birkhead & Moller, 1992); for one species, the superb fairy wren, that average is 75% (Mulder, 1994).

Why does such extra-mate copulation occur? From the female's evolutionary perspective, copulation with a male that is genetically superior to her own mate (as manifested in song and feathers) results in genetically superior young, and copulation with any additional male increases the chance that all her eggs will be fertilized by viable sperm (Zeh & Zeh, 2001). For the male, evolutionary advantage rests in driving neighboring males away from his own mate whenever possible and in copulating with neighboring females whenever possible. Genes that build brain mechanisms that promote such behaviors are passed along to more offspring than are genes that do not.

Promiscuity Is Related to Investment in the Group

Among the clearest examples of promiscuous species are chimpanzees and bonobos, which happen to be our two closest animal relatives (refer back to Figure 3.16). Bonobos are similar in appearance to chimpanzees but are rarer and have only recently been studied in the wild. The basic social structure of both species is the troop, which consists usually of two to three dozen adults of both sexes and their offspring. When the female is ovulating, she develops on her rump a prominent pink swelling, which she actively displays to advertise her condition. During the time of this swelling, which lasts about a week in chimps and three weeks in bonobos, she is likely to mate with most of the adult males of the troop, though she



■ **Bonobo sex** Bonobos seem to live by the motto, “Make love, not war.” Research suggests that they are the most sexually active and the most peaceful of all primates. Here a male has mounted a female in a face-to-face position—a position long thought to be unique to humans. But bonobo sex occurs in all possible partner combinations (homosexual as well as heterosexual) and essentially all imaginable positions.

may actively choose to mate with some more often than with others, especially at the point in her cycle when she is most fertile (Goodall, 1986; Kano, 1992).

Promiscuity has apparently evolved in these ape species because it permits a group of adult males and females to live together in relative harmony, without too much fighting over who mates with whom. A related advantage, from the female's perspective, is paternity confusion (Hrdy, 2009). Among many species of primates, males kill young that are not their own, and such behavior has been observed in chimpanzees when a female migrates into a troop bringing with her an infant that was sired elsewhere (Wrangham, 1993). Because almost any chimp or bonobo male in the colony could be the father of any infant born within the troop, each male's evolutionary interest lies not in attacking the young but in helping to protect and care for the group as a whole.

Promiscuity seems to be more fully developed in bonobos than in chimps. Male chimps sometimes use force to monopolize the sexual activity of a female throughout her ovulatory cycle or during the period of peak receptivity (Goodall, 1986; Wrangham, 1993), but this does not appear to occur among bonobos (Hohmann & Fruth, 2003; Wrangham, 1993). In fact, among bonobos sex appears to be more a reducer of aggression than a cause of it (Parish & de Waal, 2000; Wrangham, 1993). Unlike any other apes, female bonobos copulate at all times of their reproductive cycle, not just near the time of ovulation. In addition to their frequent heterosexual activity, bonobos of the same sex often rub their genitals together, and genital stimulation of all types occurs most often following conflict and in situations that could potentially elicit conflict, such as when a favorite food is discovered (Hohmann & Fruth, 2000). Field studies suggest that bonobos are the most peaceful of primates and that their frequent promiscuous sexual activity helps keep them that way (de Waal, 2005; Kano, 1992).

What About Human Mating Patterns?

A Largely Monogamous, Partly Polygynous Species

When we apply the same criteria that are used to classify the mating systems of other species, we find that humans fall on the boundary between monogamy and polygyny (Dewsbury, 1988). In no culture are human beings as sexually promiscuous as are our closest ape relatives, the chimpanzees and bonobos. In every culture, people form



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What evidence suggests that humans evolved as a partly monogamous, partly polygynous species? How is this consistent with Trivers's parental investment theory?

long-term mating bonds, which are usually legitimized through some sort of culturally recognized marriage contract. Anthropologists have found that the great majority of non-Western cultures, where Western influence has not made polygyny illegal, practice a mixture of monogamy and polygyny (Marlowe, 2000; Murdock, 1981). In such cultures, men who have sufficient wealth or status have two or more wives, while the great majority of men have one wife and a few have none. Thus, even in cultures that permit and idealize polygyny, most marriages are monogamous.

Human children, more so than the young of any other primates, require an extended period of care before they can play full adult roles in activities such as food gathering. Cross-cultural research shows that in every culture mothers provide most of the direct physical care of children, but fathers contribute in various ways, which is rare among mammals. Humans are among the 5% of mammals in which the male provides some support to his offspring (Clutton-Brock, 1991). In many cultures—especially in hunter-gatherer cultures—fathers share to some degree in the physical care of their offspring (Marlowe, 2000), and in nearly all cultures fathers provide indirect care in the form of food and other material provisions. In fact, in 77% of the cultures for which data are available, fathers contribute more of the provisions for young than do mothers (Marlowe, 2000). Taking both direct and indirect care into account, humans are a species in which fathers typically lag somewhat behind mothers, but not greatly behind them, in degree of parental investment. This, in line with Trivers's parental investment theory, is consistent with our being a primarily monogamous but moderately polygynous species.

The moderate size difference between men and women is also consistent with this conclusion (Dewsbury, 1988). The average size difference between males and females in humans is nowhere near that observed in highly polygynous species, such as elephant seals and gorillas, but is greater than that observed in monogamous species.

Another clue to *Homo sapiens*' prehistorical mating patterns comes from a comparative analysis of the different types of white blood cells—which play an important role in the immune system—between humans and other primates with different types of mating systems (Nunn et al., 2000). Sexually transmitted diseases can be a problem not just for humans but for other species as well, and the more sex partners one has, the stronger one's immune system needs to be to combat infection. Nunn and his colleagues found that sexually promiscuous species, such as chimpanzees and bonobos, had more types of white blood cells than monogamous species, such as owl monkeys. Humans' immune system was between those of the polygynous, harem-based gorilla and the monogamous gibbon (a lesser ape). This suggests that the marginally monogamous/marginally polygynous relationships that characterize modern and historic humans also characterized our species' prehistoric ancestors.

Roles of Emotions in Human Mating Systems

The biological equipment that predisposes humans for mating bonds includes brain mechanisms that promote the twin emotions of romantic love and sexual jealousy. These emotions are found in people of every culture that has been studied (Buss, 2011; Fisher, 2004). People everywhere develop strong emotional ties to those toward whom they are sexually drawn. The predominant feeling is a need to be regularly near the other person. People everywhere also feel intensely jealous when “their” mates appear to be sexually drawn to others. While love tends to create mating bonds, jealousy tends to preserve such bonds by motivating each member of a mated pair to act in ways designed to prevent the other from involvement with someone else.

Other animals that form long-term mating bonds show evidence of emotions that are functionally similar to human love and jealousy (e.g., Lazarus et al., 2004). In this



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From an evolutionary perspective, what are the functions of romantic love and sexual jealousy, and how is this supported by cross-species comparisons? How is sexual unfaithfulness explained?

sense, we are more like monogamous birds than we are like our closest ape relatives. The similarities between humans and birds in sexual love and jealousy are clearly analogies, not homologies. They evolved separately in humans and birds as means to create and preserve mating bonds that are durable enough to enable biparental care of offspring. Unlike humans and monogamous birds, chimpanzees and bonobos (especially the latter) can engage in open, promiscuous sex with little emotional consequence because they have not evolved strong emotions of sexual love and jealousy. The difference has to do with species differences in the need for care from both parents.

Although love and jealousy tend to promote bonding, there is another product of evolution—lust—that tends to motivate both men and women to engage surreptitiously in sex outside of such bonds. In this sense we are like those socially monogamous birds that are sexually unfaithful. A man who can inseminate women beyond his wife may send more copies of his genes into the next generation than a completely faithful man. A woman who has sex with men other than her husband may also benefit evolutionarily. Such escapades may (a) increase her chances of conception by serving as a hedge against the possibility that her husband's sperm are not viable or are genetically incompatible with her eggs; (b) increase the evolutionary fitness of her offspring if she mates with a man whose genes are evolutionarily superior to those of her husband; and/or (c) result in provisions from more than one man (Hrdy, 2009). And so the human soap opera continues, much like that of the superb fairy wren, though not to such an extreme. Studies involving DNA testing, in cultures ranging from hunter-gatherer groups to modern Western societies, suggest that somewhere between 2 and 10% of children in socially monogamous families are sired by someone other than the mother's husband (Marlowe, 2000).

What about polyandry—one woman and several men? Do humans ever engage in it? Not typically, but it is not unheard of. Polyandry occurs in some cultures when one man cannot secure enough resources to support a wife and her children. When it does happen, usually two brothers will share a wife. In this way, a man can be assured that any child the woman conceives shares at least some of his genes: 50% if he's the father and 25% if his brother is the father. When one of the brothers acquires enough resources to support a wife on his own, he often does so, leaving the polyandrous family (Schmitt, 2005).

A special form of polyandry occurs in some South American hunter-gatherer groups, who believe that a child possesses some of the characteristics of any man the mother has sex with approximately 10 months before birth, termed *partible paternity*. Although a woman may have a husband and be in a monogamous relationship, a pregnant woman may initiate affairs with other, often high-status men. As a result, these men may protect or even provide resources to “their” child, resulting in a higher survival rate for children compared to those without “multiple fathers” (Beckerman & Valentine, 2002).

Sex Differences in Aggression

From an evolutionary perspective, other members of one's species are competitors for food, mates, safe places to live, and other limited resources. Ultimately, such competition is the foundation of aggression.

Aggression, as the term is used here, is defined as behavior intended to harm another member of the same species. Brain mechanisms that motivate and organize such behavior have evolved because they help animals acquire and retain resources needed to survive and reproduce. As you saw in the previous section, much animal aggression centers on mating. Polygynous males and polyandrous females fight for mates; monogamous males fight to prevent other males from copulating with their mates; monogamous females fight to keep other females from leading their mates away; and promiscuous females fight to keep immigrating females from competing for resources (Kahlenberg et al., 2008; Tobias & Seddon, 2000). Aggression can also serve to protect a feeding ground for oneself and one's



offspring, to drive away individuals that may be a threat to one's young, and to elevate one's status within a social group. Much could be said from an evolutionary perspective about all aspects of aggression, but here we will focus just on sex differences in how aggression is manifested.

Why Male Primates Are Generally More Violent Than Female Primates

Among most species of mammals, and especially among primates, males are much more violently aggressive than are females. Female primates are not unaggressive, but their aggression is typically aimed directly toward obtaining resources and defending their young. When they have achieved their ends, they stop fighting. Male primates, in contrast, seem at times to go out of their way to pick fights, and they are far more likely to maim or kill their opponents than are females.

Most of the violence perpetrated by male primates has to do directly or indirectly with sex. Male monkeys of several species have been observed to kill infants fathered by others, apparently as a means to get the females to stop lactating so they will ovulate again and become sexually active. Males also fight with one another, sometimes brutally, to gain access to a particular female or to raise their rank in the dominance hierarchy of the troop. High rank generally increases both their attractiveness to females and their ability to intimidate sexual rivals (Cowlshaw & Dunbar, 1991). Males are also often violent toward females; they use violence to force copulation or to prevent the female from copulating with other males. All of these behaviors have been observed in chimpanzees and many other primate species (Goodall, 1986).

Evolution, remember, is not a moral force; it merely promotes those behaviors that tend to get one's genes passed on to the next generation. Female primates don't need to fight to get the opposite sex interested in them. Moreover, aggression may have a higher cost for females than for males: The female at battle risks not just her life but also that of any fetus she is gestating or young she is nursing—the repositories of her genes (Campbell, 1999). The male at battle risks just himself; in the calculus of evolution, his life isn't worth anything unless he can get a female to mate with him. Genes that promote mating, by whatever means, proliferate, and genes that fail to promote it vanish.

Male Violence in Humans

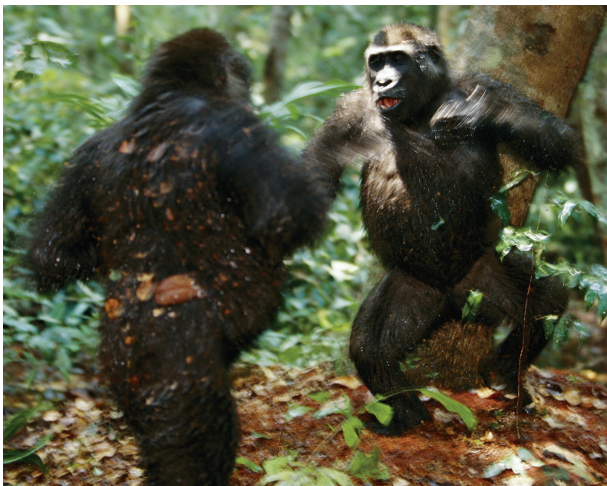
Humans are no exception to the usual primate rule. Cross-cultural studies show that men are more violent, more likely to maim or kill, than are women. In fact, in a survey of cross-cultural data on

this issue, Martin Daly and Margo Wilson (1988) were unable to find any society in which the number of women who killed other women was even one tenth as great as the number of men who killed other men. On average, in the data they examined, male–male killings outnumbered female–female killings by more than 30 to 1. One might construe a scenario through which such a difference in violence would be purely a product of learning in every culture, but the hypothesis that the difference resides at least partly in inherited sex differences seems more plausible.

According to Daly and Wilson's analyses, the apparent motives underlying male violence and homicide are very much in accord with predictions from evolutionary theory. Among the leading motives for murder among men in every culture is sexual jealousy. Some cultures have traditionally expected men to attack or even kill other men who have sex with their wives (Buss, 2000; Symons, 1979), and in others, such murders are common even though they are illegal (Daly & Wilson, 1988). Men also fight over status, which can affect their degree of success in mating (Kruger & Fitzgerald, 2012). One man insults another and then the two fight it out—with fists,

FOCUS 41

How is male violence toward infants, toward other males, and toward females explained from an evolutionary perspective?



MICHAEL NICHOLS/National Geographic Creative

■ **Tough young males** Male mammals of many species compete with one another for dominance. Much of their competition, however, involves threat and bluff rather than bloodshed, as illustrated by these two young mountain gorillas.

knives, or guns. And, like many male monkeys and apes, men often use violence to control females. Across cultures, between 19% and 75% of women experience violence at the hands of their intimate partners (Garcia-Moreno et al., 2006). Analyses of domestic violence cases indicate that they frequently have to do with the man's belief (often unfounded) that his partner has been or might become sexually unfaithful (Goetz, 2008; Goetz & Romero, 2012).

Patterns of Helping

Although humans and other animals may use aggression to get what they need and want, at the same time, others of one's kind are potential helpmates. Many life-promoting tasks can be better accomplished by two or more together than by one struggling alone. The human drama, like that of other social species, involves the balancing of competitiveness with the need for others' help.

From an evolutionary perspective, **helping** can be defined as any behavior that increases the survival chance or reproductive capacity of another individual. Given this definition, it is useful to distinguish between two categories of helping: cooperation and altruism.

Cooperation occurs when an individual helps another while helping itself. This sort of helping happens all the time in the animal world and is easy to understand from an evolutionary perspective. It occurs when a mated pair of foxes work together to raise their young, a pack of wolves work together to kill an antelope, or a group of chimpanzees work together to chase off a predator or a rival group of chimpanzees. Most of the advantages of social living lie in cooperation. By working with others for common ends, each individual has a better chance of survival and reproduction than it would have alone. Whatever costs accrue are more than repaid by the benefits. Human beings everywhere live in social groups and derive the benefits of cooperation. Those who live as our ancestors did cooperate in hunting and gathering food, caring for children, building dwellings, defending against predators and human invaders, and, most human of all, in exchanging, through language, information that bears on all aspects of the struggle for survival. Cooperation, and behaving fairly toward other people in general, develops quite early in life, suggesting that it is not simply a reflection of children bowing to the requests and admonishments of their parents, but an aspect of sociality that runs deep in human nature (Tomasello, 2009; Warneken & Melis, 2012).

Altruism, in contrast, occurs when an individual helps another while decreasing its own survival chance or reproductive capacity. This is less common than cooperation, but many animals do behave in ways that at least appear to be altruistic. For example, some animals, including female ground squirrels, emit a loud, distinctive call when they spot an approaching predator. The cry warns others of the predator's approach and, at the same time, tends to attract the predator's attention to the caller (Sherman, 1977). (See **Figure 3.21**.) The selfish response would be to remain quiet and hidden or to move away quietly, rather than risk being detected by warning others. How can such behavior be explained from an evolutionary perspective? As Trivers (1971) pointed out long ago, any evolutionary account of apparent altruism must operate by showing that from a broader perspective, focusing on the propagation of one's genes, the behavior is not truly altruistic. Evolutionists have developed two broad theories to account for ostensible altruism in animals: the kin selection theory and the reciprocity theory.

The Kin Selection Theory of Altruism

The **kin selection theory** holds that behavior that seems to be altruistic came about through natural selection because it preferentially helps close relatives, who are genetically most similar to the helper (Hamilton, 1964). What actually survives over evolutionary time, of course, is not the individual but the individual's genes. Any gene that promotes the production and preservation of copies of itself can be a fit



FIGURE 3.21 An alarm-calling ground squirrel When they spot a predator, female ground squirrels often emit an alarm call, especially if they are living in a group of close kin. Males are less likely to live near close kin and do not show this response.



FOCUS 42

How do the kin selection and reciprocity theories take the altruism out of "altruism"? What observations show that both theories apply to humans as well as to other animals?

gene, from the vantage point of natural selection, even if it reduces the survival chances of a particular carrier of the gene.

Imagine a ground squirrel with a rare gene that promotes the behavior of calling out when a predator is near. The mathematics of inheritance are such that, on average, one-half of the offspring or siblings of the individual with this gene would be expected to have the same gene, as would one-fourth of the nieces or nephews and one-eighth of the cousins. Thus, if the altruist incurred a small risk (Δ) to its own life while increasing an offspring's or a sibling's chances of survival by more than 2Δ , a niece's or nephew's by more than 4Δ , or a cousin's by more than 8Δ , the gene would increase in the population from one generation to the next.

Many research studies have shown that animals do help kin more than nonkin. For example, ground squirrels living with kin are more likely to emit alarm calls than are those living with nonkin (Sherman, 1977). Chimpanzees and other primates are more likely to help kin than nonkin in all sorts of ways, including sharing food, providing assistance in fights, and helping take care of young (Goodall, 1986; Nishida, 1990). Consistent with the mathematics of genetic relatedness, macaque monkeys have been observed to help their brothers and sisters more readily than their cousins and their cousins more readily than more distant relatives (Silk, 2002). In these examples, the helpers can apparently distinguish kin from nonkin, and this ability allows them to direct help selectively to kin (Pfennig & Sherman, 1995; Silk, 2002). In theory, however, altruistic behavior can evolve through kin selection even without such discrimination. An indiscriminate tendency to help any member of one's species can evolve if the animal's living arrangements are such that, by chance alone, a high percentage of help is directed toward kin.

Cross-cultural research shows that among humans the selective helping of kin more than nonkin is widespread (Essock-Vitale & McGuire, 1980; Stewart-Williams, 2007). If a mother dies or for other reasons is unable to care for a child, the child's grandmother, aunt, or other close relative is by far the most likely adopter (Kurland, 1979). Close kin are also most likely to share dwellings or land, hunt together, or form other collaborative arrangements. Genetic kin living in the same household are also less often violent toward one another than are nonkin living in the same household (Daly & Wilson, 1988), and studies in non-Western cultures have shown that villages in which most people are closely related have less internal friction than those in which people are less closely related (Chagnon, 1979). People report feeling emotionally closer to their kin than to their nonkin friends, even if they live farther away from kin and see them less often than nonkin (Neyer & Lang, 2003).

When leaders call for patriotic sacrifice or universal cooperation, they commonly employ kinship terms (Johnson, 1987). At times of war, political leaders ask citizens to fight for the "motherland" or "fatherland"; at other times, religious leaders and humanists strive to promote world peace by speaking of our "brothers and sisters" everywhere. The terms appeal to our tendencies to be kind to relatives. Our imagination and intelligence allow us to extend our concept of kinship to all humanity.

The Reciprocity Theory of Apparent Altruism

The *reciprocity theory* provides an account of how acts of apparent altruism can arise even among nonkin. According to this theory, behaviors that seem to be altruistic are actually forms of long-term cooperation (Trivers, 1971). Computer simulations of evolution have shown that a genetically induced tendency to help nonkin can evolve if it is tempered by (a) an ability to remember which individuals have reciprocated such help in the past and (b) a tendency not to help those who failed to reciprocate previous help. Under these conditions, helping another is selfish because it increases the chance of receiving help from that other in the future.

Behavior fitting this pattern is found in various niches of the animal world. As one example, vampire bats frequently share food with unrelated members of their species that have shared food with them in the past (Wilkinson, 1988). As another example, bonobo females that establish friendship coalitions are often unrelated to

one another, having immigrated from different natal troops (Kano, 1992; Parish & de Waal, 2000). The help each gives the others, in such acts as chasing off offending males, is reciprocated at another time.

The greatest reciprocal helpers of all, by far, are human beings. People in every culture feel a strong drive to return help that is given to them (Hill, 2002). Humans, more than any other species, can keep track of help given, remember it over a long period of time, and think of a wide variety of ways of reciprocating. Moreover, to ensure reciprocity, people everywhere have a highly developed sense of fairness and behave in ways that punish those who fail to fulfill their parts in reciprocal relationships (Baumard et al., 2013; Fehr & Fischbacher, 2003).

In one study, Canadian college students reported that they exchanged help more with close relatives (siblings) than more distant relatives (cousins), consistent with kin-selection theory. However, consistent with reciprocity theory, they reported that they received as much or more help from friends as kin (Stewart-Williams, 2007). People’s willingness to help kin versus friends varied with the cost of helping, however: For low-cost help, people helped friends more than kin; for medium-cost help they helped kin and friends equally; and for high-cost help they helped kin more than friends.

Certain human emotions seem to be well designed by natural selection to promote reciprocity. We feel gratitude toward those who help us, pride when we return such help, guilt when we fail to return help, and anger when someone fails repeatedly to return help we have given. Humans also help others, including others who may never be able to reciprocate, in order to develop a good reputation in the community at large, and those with a good reputation are valued and helped by the community (Fehr & Fischbacher, 2003).



Gunter Ziesler/Getty Images

■ **Helpful little demons** Vampire bats are gregarious mammals that demonstrate reciprocal altruism. After gorging itself on a blood meal, a bat will share some of what it has ingested with another bat, usually one that has fed it in the past.

SECTION REVIEW

An evolutionary perspective offers functionalist explanations of mating, aggression, and helping.

Relation of Mating Patterns to Parental Investment <ul style="list-style-type: none">■ Trivers theorized that sex differences in parental investment (time, energy, risk involved in bearing and raising young) explain mating patterns and sex differences in size, aggressiveness, competition for mates, and selectivity in choosing mates.■ Consistent with Trivers’s theory, polygyny is associated with high female and low male parental investment; polyandry is associated with the opposite; monogamy is associated with approximately equal investment by the two sexes; and promiscuity, common to chimps and bonobos, seems to be associated with high investment in the group.	Human Mating Patterns <ul style="list-style-type: none">■ Parental investment is somewhat lower for human fathers than for mothers, consistent with the human mix of monogamy and polygyny.■ Romantic love and jealousy help promote and preserve bonding of mates, permitting two-parent care of offspring.■ Both sexual faithfulness and unfaithfulness can be evolutionarily adaptive, depending on conditions.	Male Violence <ul style="list-style-type: none">■ Male primates, including men, are generally more violent than are females of their species.■ Most aggression and violence in male primates relate directly or indirectly to sex. Genes that promote violence are passed to offspring to the degree that they increase reproduction.	Helping <ul style="list-style-type: none">■ Helping (promoting another’s survival or reproduction) takes two forms: cooperation and altruism.■ Cooperation (helping others while also helping oneself, as in the case of wolves hunting together) is easy to understand evolutionarily.■ Apparent acts of altruism (helping others at a net cost to oneself) make evolutionary sense if explained by the kin selection or reciprocity theories.
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Thinking Critically About Genetics and Evolution

1. Many scientists believed that once we had a full description of the human genome we would be able to understand human functioning, including human thought and psychopathology. Few believe this now. Why the change? What are the advantages and limitations of genetic knowledge on understanding human thought and behavior?

2. Does an evolutionary perspective of human thought and behavior imply genetic determinism? Why or why not?

Reflections and Connections

1. **The indirect nature of genetic influences on behavior** Genes are simply DNA molecules that provide the code for building the body's proteins. But genes never produce behaviors directly—they work in conjunction with the environment, so their effects depend on environmental conditions. Our behavior results from an interplay between the environment in which we live and our bodies' biological mechanisms, which themselves were built through an interplay between genes and environment. We need to keep in mind the complex interaction of genes and environment when trying to make sense of people's behavior: A person's behavior is not determined solely by genes, and neither can a group of people be described as genetically predisposed to behaving in one way versus another.

2. **The unconscious nature of distal functions** Sigmund Freud (discussed in Chapters 14 and 16) is famous for his claim that we are often unconscious of the real reasons for our actions. On that point, at least, modern evolutionary psychologists and Freud agree. Our species-typical drives and behavioral tendencies evolved to promote functions related to survival and reproduction, but we rarely think of those functions, and we are often completely unaware of them.

Infants babble and attempt to stand and walk because it is “fun” to do so, without any thought about the value of such play in learning to talk and walk. We all smile, automatically or because it seems like the right thing to do, when we are happy or when we meet someone, without thinking about the functions that smiling might serve. When we fall in love, we are far more likely to attribute that feeling to the sweet, charming, and irresistible nature of the beloved person than to anything having to do with the value of bonding for producing and raising children. When we feel jealous because

of attention another is paying to our beloved, we think angry thoughts about betrayal and unfaithfulness, not about the role of jealousy in preserving monogamy. When we help a person in need, we do it out of felt sympathy and compassion; we do not coldly, consciously calculate the costs and long-term benefits to ourselves.

The reasons we give ourselves for what we do are an aspect of the *proximate causation* of our behavior. We are often no more aware of the *distal functions* of our actions than the cabbage butterfly is of why it is irresistibly drawn to plants of the cabbage family as the only proper place to lay its eggs.

3. **Evolution as an integrative theme in psychology** The evolutionary perspective provides the broadest view we can take in psychology. It is concerned with the origins and distal functions of all aspects of human nature (and the nature of other animals). It is a perspective that can be applied to the whole vast range of topics related to psychology (see the many chapters in *The Handbook of Evolutionary Psychology*, Buss, 2016). The complex biological mechanisms that underlie our psychological nature came about because they helped our ancestors to survive and reproduce. We can expect, therefore, that all of our basic motivational and emotional mechanisms are biased toward generating behaviors that promote survival and reproduction; and we can expect that our sensory, perceptual, memory, and reasoning mechanisms are biased toward picking up and using information essential to those purposes. We are not general learning or thinking machines that indiscriminately analyze all information available; we are biological survival machines designed to use information selectively to achieve our ends. As you go through the rest of this book, crossing the whole range of psychology, you will see this idea applied in every chapter.
- ## Key Terms
- | | | | |
|-------------------------|-------------------------|------------------------------|------------------------------|
| adaptation 78 | epigenetics 70 | mitosis 63 | promiscuity 87 |
| aggression 93 | evolution 60 | monogamy 87 | proximate explanations 76 |
| alleles 64 | fraternal twins 64 | mutations 73 | recessive 64 |
| altruism 95 | functionalism 76 | natural selection 73 | reciprocity theory 96 |
| analogy 84 | genes 60 | naturalistic fallacy 75 | selective breeding 68 |
| artificial selection 72 | genotype 62 | normal distribution 68 | species-typical behaviors 80 |
| chromosomes 62 | helping 95 | parental investment 87 | vestigial characteristics 77 |
| cooperation 95 | homology 84 | phenotype 62 | zygote 64 |
| distal explanations 76 | identical twins 64 | polyandry 87 | |
| DNA 60 | kin selection theory 95 | polygenic characteristics 68 | |
| dominant 64 | meiosis 63 | polygyny 87 | |
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Find Out More

Charles Darwin (1859; reprinted 1963). *The origin of species*. New York, NY: Washington Square Press.

Darwin was an engaging writer as well as a brilliant thinker. Why not read at least part of this book, which revolutionized the intellectual world? The most relevant chapter for psychologists is Chapter 8, *Instinct*, which includes Darwin's research on hive building in bees and many other insights about the behavior of wild and domesticated animals. This is a free download on both iTunes and Amazon.

David Sloan Wilson (2007). *Evolution for everyone: How Darwin's theory can change the way we think about our lives*. New York, NY: Delacorte Press.

Wilson is a brilliant biologist, a broad-ranging philosopher, a great storyteller, and a self-described optimist. His goal in this book is to prove how all of us can benefit by understanding evolutionary theory and applying it in our everyday thinking. Wilson shows how evolutionary theory sheds insight on topics ranging from species of beetles, to Abraham Lincoln, to organized religions.

Robert M. Sapolsky (2017). *Behave: The biology of humans at our best and worst*. New York, NY: Penguin Press.

Writing with clarity and humor, Robert Sapolsky—a behavioral neuroscientist, primatologist, and recipient of a MacArthur Foundation genius award—guides readers through the fascinating, complex, nuanced, and context-dependent relations between brains, hormones, and behaviors, focusing on some of the best (love, compassion, morality) and worst (aggression, xenophobia) aspects of human behavior.

Susan M. Schneider (2012). *The science of consequences: How they affect genes, change the brain, and impact our world*. Amherst, NY: Prometheus Books.

Schneider takes complex and challenging scientific concepts and presents them in an everyday manner. This often humorous book connects several levels of analysis from the long-standing science of biology and genetics to current investigations in learning psychology. Schneider explores how consequences change who we are as a species, how we got to be this way, and how individual experience changes what we do.

David S. Moore (2015). *The developing genome: An introduction to behavioral epigenetics*. New York, NY: Oxford University Press.

Epigenetics has emerged as a hot and important topic. This engaging and accessible book uses clear examples to show the relevance of epigenetics to human behavior. It can be easily understood by students and consumers.

Jane Goodall (2002, March). What separates us from chimpanzees? Monterey, CA: TED 2002. https://www.ted.com/talks/jane_goodall_on_what_separates_us_from_the_apes

The highly acclaimed primatologist Jane Goodall discusses the difference between the great apes and humans in this compelling talk. She makes the argument that language is the great separator between human phylogeny and apes, and encourages us all to use this gift to better the world.

The Evolution Institute <https://evolution-institute.org>

The Evolution Institute “connects the world of evolutionary science to the world of public policy formulation.” On its website you will find dozens of articles relating evolutionary research and theory to contemporary issues in biology, psychology, culture, and politics. There is virtually something for everyone.



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