Eleventh Edition

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5

Evolution and Gene Frequencies

Inherited variations help determine whether or not this African white-fronted bee-eater (*Merops bullockoides*) can catch enough food to enable it to reproduce. The evolution of this species will be reflected in how common, or how rare, specific alleles are in future generations.
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Chapter Outline

Natural selection can be envisioned as operating in two ways, and both are important perspectives on evolution. One way (e.g., the focus of chapter 4) looks at characteristics of individual animals. When a population of birds acquires an adaptation through natural selection that permits its members to feed more efficiently on butterflies, the trait is described in terms of physical characteristics (e.g., bill shape) or inherited behaviors. This description of natural selection recognizes that natural selection must act in the context of living organisms.

The organism, however, must be viewed as a vehicle that permits the phenotypic expression of genes. This chapter examines the second way that natural selection operates—on genes. Birds and butterflies are not permanent—they die. The genes they carry, however, are potentially immortal. The result of natural selection (and evolution in general) is reflected in how common, or how rare, specific alleles are in a group of animals that are interbreeding—and therefore sharing genes.

5.1 POPULATIONS AND GENE POOLS

LEARNING OUTCOMES

1. Relate the concept of a gene pool to a population of animals.
2. Explain why different individuals within a population are genetically different from each other.

Individuals do not evolve. Evolution requires that genetic changes are passed from one generation to another within larger groups called populations. **Populations** are groups of individuals of the same species that occupy a given area at the same time and share a common set of genes. With the possible exception of male and female differences, individuals of a population have the same number of genes and the same kinds of genes. A "kind" of gene would be a gene that codes for a given trait, such as hair length or the color of a mammal's coat. Differences within a population are based on variety within each trait, such as red or white hair in a mammal's coat. As described in chapter 3, this variety results from varying expressions of genes at each of the loci of an animal's chromosomes. Recall that these varying expressions of genes at each locus are called alleles. A population can be characterized by the frequency of alleles for a given trait, that is, the abundance of a particular allele in relation to the sum of all alleles at that locus.
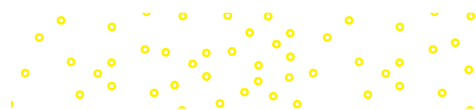
The sum of all the alleles for all traits in a sexually reproducing population is a pool of hereditary resources for the entire population and is called the **gene pool.**

Variety within individuals of a population results from having various combinations of alleles at each locus. Some of the sources of this variety have been discussed in chapter 3. These sources of variation include (1) the independent assortment of chromosomes that results in the random distribution of chromosomes into gametes, (2) the crossing-over that results in a shuffling of alleles between homologous chromosomes, and (3) the chance fertilization of an egg by a sperm cell. Variations also arise from (4) rearrangements in the number and structure of chromosomes and (5) mutations of existing alleles. Mutations are the only source of new alleles and will be discussed in greater detail later in this chapter. This chapter also describes how genetic variation may confer an advantage to individuals, leading to natural selection. It describes how other variations may become common in, or lost from, populations even though no particular advantage, or disadvantage, is derived from them.

The potential for genetic variation in individuals of a population is virtually unlimited. When generations of individuals of a population undergo sexual reproduction, there is a constant shuffling of alleles. The shuffling of alleles and the interaction of resulting phenotypes with the environment have one of two consequences for the population. Either the relative frequencies of alleles change across generations or they do not. In the former case, evolution has occurred. In chapter 4, a change in the relative frequency of genes in a population across generations was defined as microevolution. In the next sections of this chapter, circumstances that favor microevolution are discussed in more detail.

SECTION 5.1 THINKING BEYOND THE FACTS

Based on what you know about natural selection, why does evolution occur in groups of individuals of the same species over many generations (i.e., within populations)?

5.2 MUST EVOLUTION HAPPEN?

LEARNING OUTCOME

1. Justify the statement "most populations are evolving."

Evolution is central to biology, but is evolution always occurring in a particular population? Sometimes the rate of evolution is slow, and sometimes it is rapid. But are there times when evolution does not occur at all? The answer to this question lies in the theories of **population genetics,** the study of the genetic events in gene pools.

The Hardy–Weinberg Theorem

In 1908, English mathematician Godfrey H. Hardy and German physician Wilhelm Weinberg independently derived a mathematical model describing what happens to the relative frequency of alleles in a sexually reproducing population over time. Their combined ideas became known as the **Hardy–Weinberg theorem.** It states that the mixing of alleles at meiosis and their subsequent recombination do not alter the relative frequencies of the alleles in future generations, if certain assumptions are met. Stated another way, if certain assumptions are met, evolution will not occur because the relative allelic frequencies will not change from generation to generation, even though the specific mixes of alleles in individuals may vary.

The assumptions of the Hardy–Weinberg theorem are as follows:

1. The population size must be large. Large size ensures that gene frequency will not change by chance alone.
2. Individuals cannot migrate into, or out of, the population. Migration may introduce new alleles into the gene pool or add or delete copies of existing alleles.
3. Mutations must not occur. If they do, mutational equilibrium must exist. Mutational equilibrium exists when mutation from the wild-type allele to a mutant form is balanced by mutation from the mutant form back to the wild type. In either case, no new genes are introduced into the population from this source.
4. Sexual reproduction within the population must be random. Every individual must have an equal chance of mating with any other individual in the population. If this condition is not fulfilled, then some individuals are more likely to reproduce than others, and natural selection may occur.

These assumptions must be met if allelic frequencies are not changing—that is, if evolution is not occurring. Clearly, these assumptions are restrictive, and few, if any, real populations meet them. This means that most populations are evolving. The Hardy–Weinberg theorem, however, does provide a useful theoretical framework for examining changes in allelic frequencies in populations.

The next section explains how, when the assumptions are not met, microevolutionary change occurs.

Animation
Evolutionary Change

SECTION 5.2 THINKING BEYOND THE FACTS

Why is it accurate to say that evolution does not have to be occurring in all populations but most populations are evolving?

5.3 EVOLUTIONARY MECHANISMS

LEARNING OUTCOMES

1. Explain the four mechanisms of evolutionary change.
2. Compare the founder effect and the bottleneck effect, explaining why each is an example of neutral evolution and genetic drift.
3. Explain how selection pressure operates in each mode of natural selection.
4. Critique the statement "Natural selection always eliminates deleterious alleles from populations."

Evolution is neither a creative force working for progress nor a dark force sacrificing individuals for the sake of the group. It is neither moral nor immoral. It has neither a goal nor a mind to conceive a goal. Such goal-oriented thinking is said to be teleological. Evolution is simply a result of some individuals in a population surviving and being more effective at reproducing than others in the population, leading to changes in relative allelic frequencies. This section examines some of the situations when the Hardy–Weinberg assumptions are not met—situations in which gene frequencies change from one generation to the next and evolution occurs.

Neutral Theory and Genetic Drift

Evolution does not always occur because one allele provides a selective advantage over a second allele. Many times two alleles provide neither advantage nor disadvantage to animals in a population. These alleles are said to be selectively neutral. **Neutral theory** describes mechanisms of evolutionary change when alleles are selectively neutral.

Chance often plays an important role in the perpetuation of genes in a population, and the smaller the population, the more significant the chance may be. Fortuitous circumstances, such as a chance encounter between reproductive individuals, may promote reproduction. Some traits of a population survive not because they convey increased fitness, but because they happen to be in gametes involved in fertilization. Chance events influencing the frequencies of genes in populations result in **genetic drift.**

The process of genetic drift is analogous to flipping a coin. The likelihood of getting a head or a tail is equal. The 50:50 ratio of heads and tails is most likely in a large number of tosses. In only 10 tosses, for example, the ratio may be a disproportionate 7 heads and 3 tails. Similarly, the chance of one or the other of two equally adaptive alleles being incorporated into a gamete, and eventually into an individual in a second generation, is equal. Gamete sampling in a small population may show unusual proportions of alleles in any one generation of gametes because meiotic events, like tossing a coin, are random. Assuming that both alleles have equal fitness, these unusual proportions are reflected in the genotypes of the next generation. These chance events may result in a particular allele increasing or decreasing in frequency (figure 5.1). In small populations, inbreeding is also common. Genetic drift and inbreeding are likely to reduce genetic variation within a small population.

In many cases, one member of a pair of alleles is lost in a population. When this happens the surviving allele is said to be fixed in the population. Fixation of an allele can occur within just a few generations of random mating. The likelihood of genetic drift occurring in small populations suggests that a Hardy–Weinberg equilibrium will not occur and evolution is occurring. Two special cases promote genetic drift and are described next.

The Founder Effect

When a few individuals from a parental population colonize new habitats, they seldom carry alleles in the same frequency as the alleles in the gene pool from which they came. The new colony that emerges from the founding individuals is likely to have a distinctive
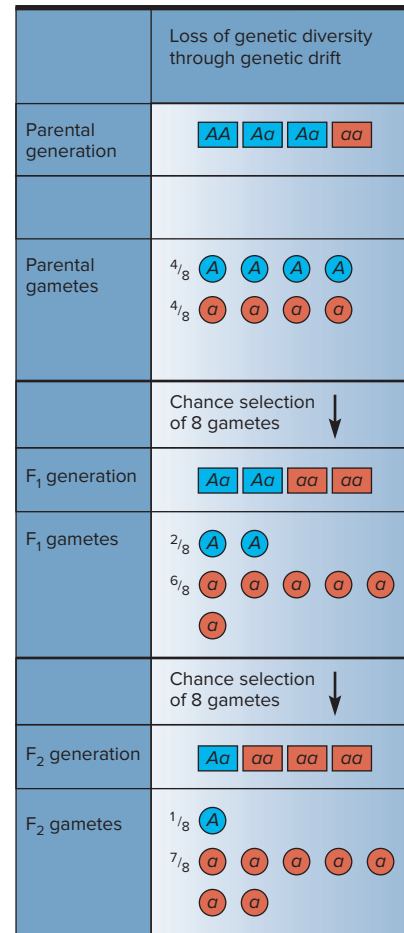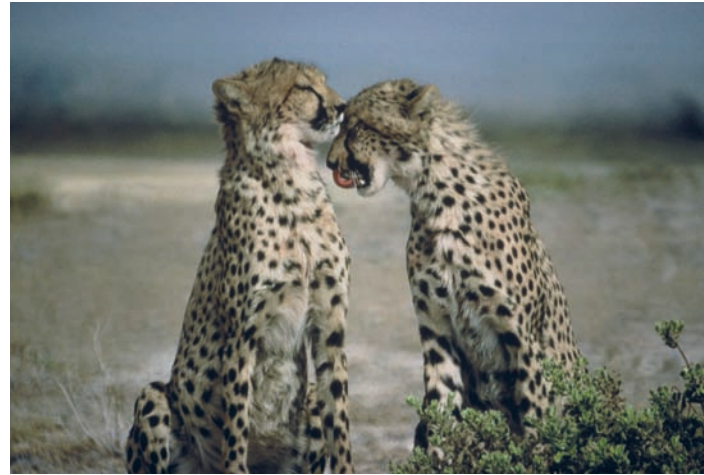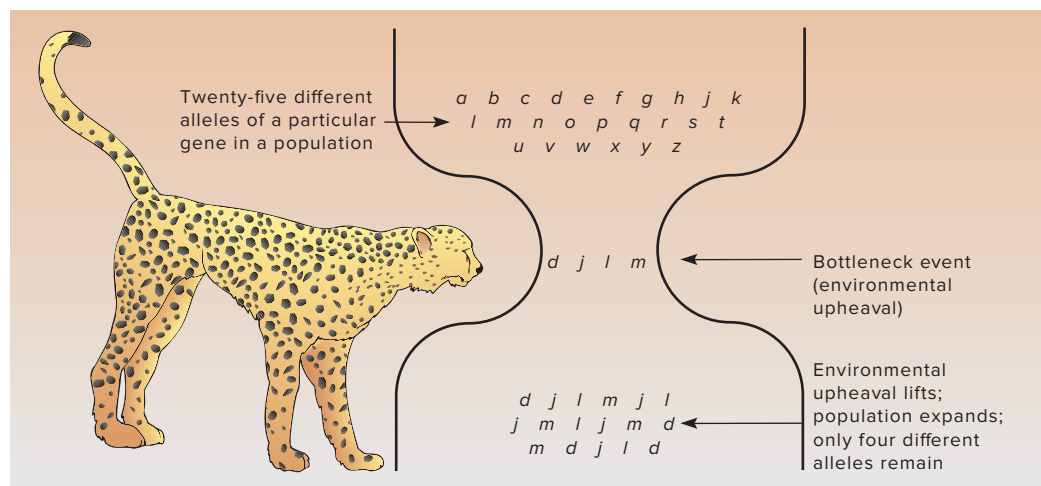

FIGURE 5.1

Genetic Drift. Genetic diversity may be lost as a result of genetic drift. Assume that alleles *a* and *A* are equally adaptive. Allele *a* might be incorporated into gametes more often than *A,* or it could be involved in more fertilizations. In either case, the frequency of *a* increases and the frequency of *A* decreases because of random events operating at the level of gametes.

genetic makeup with far less variation than the larger population. This form of genetic drift is the **founder effect.**

The importance of the founder effect in influencing natural populations is controversial. Founder events are rarely observed and difficult to study. In 2004, a hurricane swept through the Bahamas and submerged several islands that were the homes of the brown anole lizard, *Anolis sagrei*. Lizards on these islands were all killed. In 2005, researchers from the University of California, Davis, placed one male and one female lizard on each of these islands from a nearby island that was not submerged. Over the next four years, offspring lizards on the formerly submerged islands were studied and compared to populations from the source island and other islands that were not submerged. These comparisons demonstrated that allelic variation within larger populations on the unsubmerged islands allowed natural selection to influence traits like leg length. The same traits in descendants of founding lizards on the formerly submerged islands were less responsive to natural selection because of limited genetic variation in these populations.

(a)

Twenty-five different alleles of a particular gene in a population

a b c d e f g h j k
l m n o p q r s t
u v w x y z

d j l m

Bottleneck event (environmental upheaval)

Environmental upheaval lifts; population expands; only four different alleles remain

d j l m j l
j m l j m d
m d j l d

(b)

FIGURE 5.2

Bottleneck Effect. (*a*) Cheetahs (*Acinonyx jubatus*) of South and East Africa are endangered. (*b*) Severe reduction in the original population has caused a bottleneck effect. Even if the population size recovers, genetic diversity has been significantly reduced.
Source: Gary M. Stolz/U.S. Fish & Wildlife Service

The Bottleneck Effect

A second special case of genetic drift can occur when the number of individuals in a population is drastically reduced. For example, cheetah populations in South and East Africa are endangered. During the Pleistocene era, about one million years ago, there were four subspecies of cheetahs in North America, Europe, Asia, and Africa. About 12,000 years ago, they underwent a near extinction event brought about by climate change and human hunting that also affected many other large mammal species. Cheetahs are now found only in eastern and southern Africa, and their populations continue to decline (100,000 in 1900, 10,000 today) due to loss of habitat from farming and bush encroachment, population fragmentation, and declining prey density. Cheetah nucleotide diversity is very low (0.182%) compared to leopards (1.3%) and other large cat species. This genetic diversity is so low that even if population sizes are restored, cheetahs will have only a

remnant of the original gene pool. This form of genetic drift is called the **bottleneck effect** (figure 5.2). A similar example concerns the northern elephant seal (*Mirounga angustirostris*), which was hunted to near extinction in the late 1800s for its blubber, which was used to make prized oil (figure 5.3). The population was reduced to about 100 individuals. Because males compete for reproductive rights, very few males actually passed their genes on to the next generation. Legislation to protect the elephant seal was enacted in 1922, and now the population is greater than 100,000 individuals. In spite of this relatively large number, the genetic variability in the population is very low. One study showed no genetic variation at 24 protein-coding loci.

The effects of bottlenecks are not well understood. The traditional interpretation is that decreases in genetic diversity make populations less likely to withstand environmental stress and more susceptible to extinction. That is, a population with high genetic

FIGURE 5.3

Bottleneck Effect. The northern elephant seal (*Mirounga angustirostris*) lives along the western coast of North America from Alaska to Baja, California. It gets its name from the very large proboscis of the male, which is used in producing very loud vocalizations during breeding off the coast of southern California and Baja. Males average 1,800 kg and females average 650 kg. This photograph of a large male and a group of females was taken on San Benito Island, Baja, Mexico. Males compete for females during breeding, and a single male may win the right to mate with up to 50 females. The northern elephant seal was severely overhunted in the late 1800s. Even though its numbers are now increasing, its genetic diversity is very low.
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diversity is more likely to have some individuals with a combination of genes that allows them to withstand environmental changes (*see Wildlife Alert, chapter 3*).

Gene Flow

The Hardy–Weinberg theorem assumes that no individuals enter a population from the outside (immigrate) and that no individuals leave a population (emigrate). Immigration or emigration upsets the Hardy–Weinberg equilibrium, resulting in changes in relative allelic frequency (evolution). Changes in relative allelic frequency from the migration of individuals are called **gene flow.** Although some natural populations do not have significant gene flow, most populations do.

The effects of gene flow can differ, depending on the circumstances. The exchange of alleles between an island population and a neighboring continental population, for example, can change the genetic makeup of those populations. If gene flow continues and occurs in both directions, the two populations will become more similar, and this reduces the chances that speciation will occur. The absence of gene flow can lead to genetic isolation and, as discussed in section 5.4, the formation of a new species.

Natural barriers, such as mountain ranges and deserts, can limit gene flow. So can human influences such as the construction of barriers, like highways and The Great Wall of China. Highways can interrupt the connectivity of populations and have been linked to the loss of genetic diversity in desert bighorn sheep.* The melting of polar ice has changed historical patterns of gene flow within polar bear (*Ursus maritimus*) populations. In some populations, polar bears are migrating into more geographically restricted regions that maintain longer periods of continuous sea-ice cover (figure 5.4). In other subpopulations, gene flow is restricted by the absence of sea-ice connections between populations, which historically provided avenues for genetic exchange during the breeding season.

Mutation

Mutations are changes in the structure of genes and chromosomes (*see chapter 3*). The Hardy–Weinberg theorem assumes that no mutations occur or that mutational equilibrium exists. Mutations, however, are a fact of life. Most important, mutations are the origin of all new alleles and a source of variation that may be adaptive for an animal. Mutation counters the loss of genetic material from natural selection and genetic drift, and it increases the likelihood that variations will be present that allow some individuals to survive future environmental shocks. Mutations make extinction less likely.

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* Epps CW, Palsbøll JD, Wehausen GK, Roderick GK, Ramey II RR, McCullough DR. 2005. Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters. 8:1029–1038.
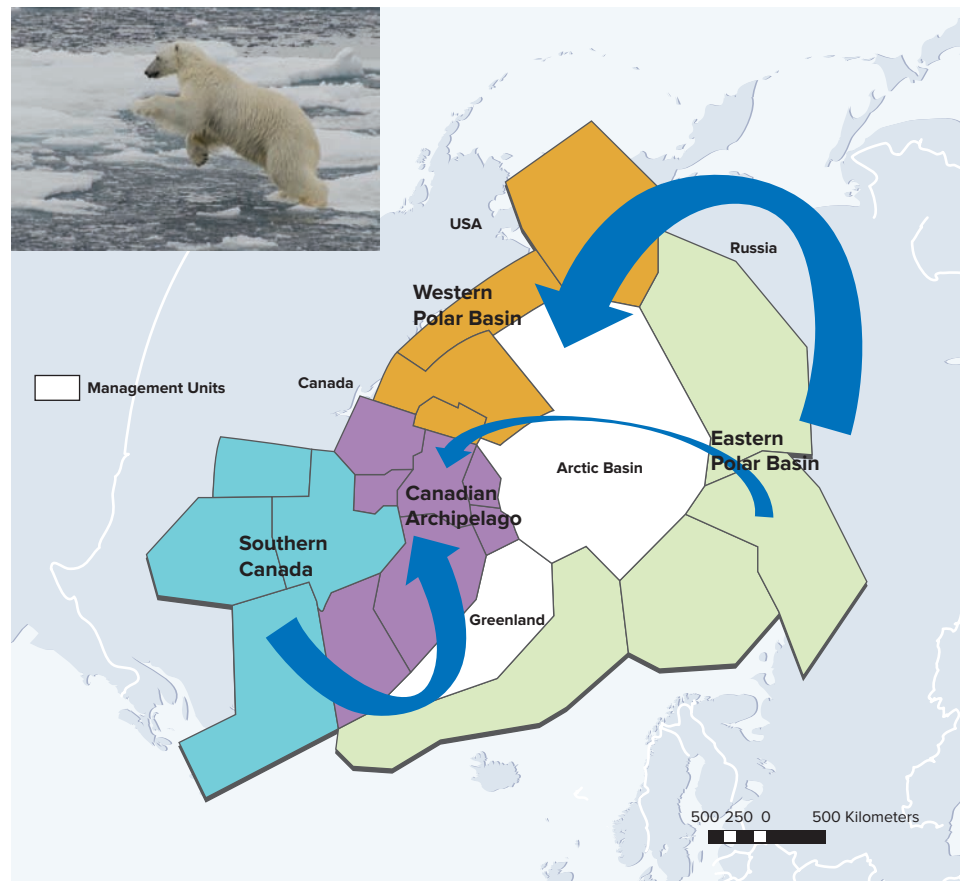
FIGURE 5.4

Gene Flow in Polar Bear (*Ursus maritimus*) Populations. Melting of sea ice has promoted the migration of polar bears from genetically distinct subpopulations into the Canadian Archipelago, which is somewhat insulated from sea-ice melting. This historically altered gene flow pattern has the potential to alter the genetic composition of the species. In small subpopulations within this larger range, the melting of sea ice breaks down ice corridors that historically promoted gene flow and higher genetic diversity.

Mutations are random events, and the likelihood of a mutation is not affected by the mutation's usefulness. Organisms cannot filter harmful genetic changes from advantageous changes before they occur.

The effects of mutations vary enormously. Neutral mutations are neither harmful nor helpful to the organism. Neutral mutations may occur in regions of DNA that do not code for proteins. Other neutral mutations may change a protein's structure, but some proteins tolerate minor changes in structure without affecting the function of the protein. Genetic drift may permit the new allele to become established in the population, or the new allele may be lost because of genetic drift. Mutations that do affect protein function are more likely to be detrimental than beneficial. This is true because a random change in an established protein upsets millions of years of natural selection that occurred during the protein's evolution. Mutations in DNA that is incorporated into a gamete have the potential to affect the function of every cell in an individual in the next generation. These mutations are likely to influence the evolution of a group of organisms.

Mutational equilibrium exists when a mutation from the wild-type allele to a mutant form is balanced by a mutation from the mutant back to the wild type. This has the same effect on allelic frequency as if no mutation had occurred. Mutational equilibrium rarely exists, however. **Mutation pressure** is a measure of the tendency for gene frequencies to change through mutation.

Natural Selection Reexamined

The theory of natural selection remains preeminent in modern biology. Natural selection occurs whenever some phenotypes are more successful at leaving offspring than other phenotypes. The tendency for natural selection to occur—and upset Hardy–Weinberg equilibrium—is **selection pressure.** Although natural selection is simple in principle, it is diverse in operation.

Modes of Selection

For certain traits, many populations have a range of phenotypes, characterized by a bell-shaped curve that shows that phenotypic extremes are less common than the intermediate phenotypes. Natural selection may affect a range of phenotypes in three ways.

Directional selection occurs when individuals at one phenotypic extreme are at a disadvantage compared to all other individuals in the population (figure 5.5a). In response to this selection, the deleterious gene(s) decreases in frequency, and all other genes increase in frequency. Directional selection may occur when a mutation gives rise to a new gene, or when the environment changes to select against an existing phenotype.

Industrial melanism, a classic example of directional selection, occurred in England during the Industrial Revolution. Museum records and experiments document how environmental changes affected selection against one phenotype of the peppered moth, *Biston betularia*.

In the early 1800s, a gray form made up about 99% of the peppered moth population. That form still predominates in nonindustrial northern England and Scotland. In industrial areas of England, a black form replaced the gray form over a period of about 50 years. In these areas, the gray form made up only about 5% of the population, and 95% of the population was black. The gray phenotype, previously advantageous, had become deleterious.

The nature of the selection pressure was understood when investigators discovered that birds prey more effectively on moths resting on a contrasting background. Prior to the Industrial Revolution, gray moths were favored because they blended with the bark of trees on which they rested. The black moth contrasted with the lighter, lichen-covered bark and was easily spotted by birds (figure 5.6a). Early in the Industrial Revolution, however, factories used soft coal, and spewed soot and other pollutants into the air. Soot covered
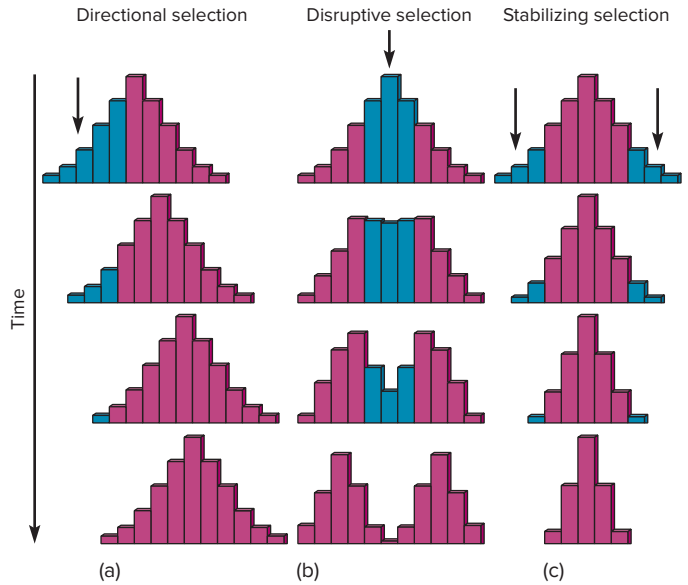

FIGURE 5.5

Modes of Selection. (*a*) Directional selection occurs when individuals at one phenotypic extreme are selected against. It shifts phenotypic distribution toward the advantageous phenotype. (*b*) Disruptive (diversifying) selection occurs when an intermediate phenotype is selected against. It produces distinct subpopulations. (*c*) Stabilizing selection occurs when individuals at both phenotypic extremes are selected against. It narrows at both ends of the range. Arrows indicate selection against one or more phenotypes. The X-axis of each graph indicates the range of phenotypes for the trait in question.

the tree trunks and killed the lichens where the moths rested. Bird predators now could easily pick out gray moths against the black background of the tree trunk, while the black form was effectively camouflaged (figure 5.6b).

FIGURE 5.6

Directional Selection of the Peppered Moth, *Biston betularia*. Each photo shows two forms of the moth: black and gray. (*a*) Prior to the Industrial Revolution, bird predators easily spotted the black form of moth, and the gray form was camouflaged. (*b*) In industrial regions after the Industrial Revolution, selection was reversed because pollution killed lichens that covered the bark of trees where moths rested. Note how clearly the gray form is seen, whereas the black form is less visible.

In the 1950s, the British Parliament enacted air pollution standards that have reduced soot in the atmosphere. As expected, the gray form of the moth has experienced a small but significant increase in frequency.

Another form of natural selection involves circumstances selecting against individuals of an intermediate phenotype (figure 5.5*b*). **Disruptive** or **diversifying selection** produces distinct subpopulations (*see figure 1.2 and the accompanying discussion*). An interesting example of disruptive selection also illustrates another form of selection, sexual selection. **Sexual selection** occurs when individuals have varying success obtaining mates. It often results in the evolution of structures used in combat between males for mates, such as antlers and horns, or ornamentation that attracts individuals of the opposite sex, such as the brightly colored tail feathers of a peacock. Sexual selection is considered by some to be a form of natural selection, but others consider it separately from natural selection.

The plainfin midshipman (*Porichthys notatus*) inhabit depths of up to 400 m along the Pacific coast of North America. They are named for rows of bioluminescent photophores that reminded some of the rows of buttons on a naval uniform. Males move to shallower water for reproduction. The male establishes a nest in rock crevices and cares for young after attracting a female and spawning. Males of the species have one of two body forms (morphs) designated as type I and type II males. Type I males have an exaggerated morphology that probably arose as a result of sexual selection. Their very large heads and wide mouths (figure 5.7) are used in defending territories and nests under rocks. Their exaggerated sonic musculature is used to court females with loud humming vocalizations that can be heard by boaters and beachcombers. Aggressive vocalizations are used to ward off other males. The larger the males, the more effective they are in establishing large nests and providing long-term care for young. Type II males have a smaller, drab morphology and look similar to females. These males (*see figure 5.7*) are sometimes called "sneakers" because they dart into type I males' nests and fertilize eggs without having to invest their time and energy into nest construction, defense, and mate attraction. The type II morphology is apparently not recognized readily by type I males as a threat to their reproductive success. Type II males are tolerated near the nests of type I males, which improves the chances that type II males succeed with their "sneaker" strategy. Disruptive selection favors the retention of the reduced type II morphology because of the energy savings in not having to establish and defend a nest and in not supporting a larger body size. Disruptive selection also favors the retention of the exaggerated type I morphology because that is the body form that can establish territories and nests, defend them from other type I males, and attract females.

When both phenotypic extremes are deleterious, a third form of natural selection—**stabilizing selection**—narrows the phenotypic range (figure 5.5*c*). During long periods of environmental constancy, new variations that arise, or new combinations of genes that occur, are unlikely to result in more fit phenotypes than the genes that have allowed a population to survive for thousands of years, especially when the new variations are at the extremes of the phenotypic range.

A good example of stabilizing selection is the horseshoe crab (*Limulus*), which lives along the Atlantic coast of the United States

FIGURE 5.7

Disruptive Selection. Males of the plainfin midshipman (*Porichthys notatus*) have two body forms. Type I males (center) have exaggerated heads and mouths, which are used in defending territories and nests from other type I males. Type II males (far left) lack the exaggerated heads and mouths and resemble females (far right). These "sneaker" males are tolerated near the nests of type I males and attempt to fertilize eggs deposited by females in type I male nests by darting into the nest during spawning. Disruptive selection has resulted in the maintenance of both of these body forms in plainfin midshipman populations.
©Margaret Marchaterre, Cornell University

(*see figure 14.8*). Comparison of the fossil record with living forms indicates that this body form has changed little over 200 million years. Apparently, the combination of characteristics present in this group of animals is adaptive for the horseshoe crab's environment.

Neutralist/Selectionist Controversy

Most biologists recognize that both natural selection and neutral evolution occur, but they may not be equally important in all circumstances. For example, during long periods when environments are relatively constant, and stabilizing selection is acting on phenotypes, genetic drift may operate at the molecular level. Certain genes could be randomly established in a population. Occasionally, however, the environment shifts, and directional or disruptive selection begins to operate, resulting in gene frequency changes (often fairly rapid).

The relative importance of neutral evolution and natural selection in natural populations is debated and is an example of the kinds of debates that occur among evolutionists. These debates concern the mechanics of evolution and are the foundations of science. They lead to experiments that will ultimately present a clearer understanding of evolution.

Balanced Polymorphism and Heterozygote Superiority

Polymorphism occurs in a population when two or more distinct forms exist without a range of phenotypes between them. **Balanced polymorphism** (Gr. *poly*, many + *morphe*, form) occurs

when different phenotypes are maintained at relatively stable frequencies in the population and may resemble a population in which disruptive selection operates.

Sickle-cell anemia results from a change in the structure of the hemoglobin molecule. Some of the red blood cells of persons with the disease are misshapen, reducing their ability to carry oxygen. In the heterozygous state, the quantities of normal and sickled cells are roughly equal. Sickle-cell heterozygotes occur in some African populations with a frequency as high as 0.4. The maintenance of the sickle-cell heterozygotes and both homozygous genotypes at relatively unchanging frequencies makes this trait an example of a balanced polymorphism.

Why hasn't natural selection eliminated such a seemingly deleterious allele? The sickle-cell allele is most common in regions of Africa that are heavily infected with the malarial parasite *Plasmodium falciparum.* This parasite is transmitted by mosquitoes and has a life cycle that involves the invasion of red blood cells and liver cells (*see figure 6, appendix C*). Symptoms of the disease include recurring bouts of chills and fever, and it remains one of the greatest killers of humanity. Sickle-cell heterozygotes are less susceptible to malarial infections; if infected, they experience less severe symptoms than do homozygotes without sickled cells. Individuals homozygous for the normal allele are at a disadvantage because they experience more severe malarial infections, and individuals homozygous for the sickle-cell allele are at a disadvantage because they suffer from the severe anemia that the sickle cells cause. The heterozygotes, who usually experience no symptoms of anemia, are more likely to survive than either homozygote. This system is also an example of heterozygote superiority—when the heterozygote is more fit than either homozygote. Heterozygote superiority can lead to balanced polymorphism because perpetuation of the alleles in the heterozygous condition maintains both alleles at a higher frequency than would be expected if natural selection acted only on the homozygous phenotypes.

The processes that change relative allelic frequencies in populations can, over geological time periods (measured in thousands of years), result in the formation of new species. Species can become extinct very quickly when climatic or geological events cause abrupt environmental changes. The formation of new species and the extinction of species were defined in chapter 4 as macroevolution. Even though the formation of new species is difficult to observe directly because of the long time frames involved, the evidence presented in chapter 4 has convinced the vast majority of scientists that macroevolution occurs. The rest of this chapter continues the theme of macroevolutionary change.

Section 5.3 Thinking Beyond the Facts

Conservation biologists attempt to preserve genetic diversity within populations. Which of the four evolutionary mechanisms described in this section has/have the potential to increase genetic diversity of populations? What does this say about the challenge faced by conservation biologists?

5.4 SPECIES AND SPECIATION

LEARNING OUTCOMES

1. Assess the usefulness of definitions of a species.
2. Compare the isolating mechanisms involved in each of the three forms of speciation.

Taxonomists classify organisms according to their similarities and differences (*see chapters 1 and 7*). The fundamental unit of classification is the species. Unfortunately, formulating a universally applicable definition of species is difficult. According to the **biological species concept,** a **species** is a group of populations in which genes are actually, or potentially, exchanged through interbreeding.

Although concise, this definition has problems associated with it. Taxonomists often work with morphological characteristics, and the reproductive criterion must be assumed based on morphological and ecological information. Also, some organisms do not reproduce sexually. Obviously, other criteria need to be applied in these cases. Another problem concerns fossil material. Paleontologists describe species of extinct organisms, but how can they test the reproductive criterion? Finally, populations of similar organisms may be so isolated from each other that gene exchange is geographically impossible. To test a reproductive criterion, biologists can transplant individuals to see if mating can occur, but mating of transplanted individuals does not necessarily prove what would happen if animals were together in a natural setting. In chapter 7, an increasingly popular phylogenetic species concept will be discussed. This concept depicts a species as a group of populations that have evolved independently of other groups of populations. Species groups are studied using phylogenetic analysis principles, which are discussed in chapter 7.

Rather than trying to establish a definition of a species that solves all these problems, it is probably better to simply understand the problems associated with the biological definition. In describing species, taxonomists use morphological, physiological, embryological, behavioral, molecular, and ecological criteria, realizing that all of these have a genetic basis.

Speciation is the formation of new species. A requirement of speciation is that subpopulations are prevented from interbreeding. For some reason, gene flow between populations or subpopulations does not occur. This is called **reproductive isolation.** When populations are reproductively isolated, natural selection and genetic drift can result in evolution taking a different course in each subpopulation. Reproductive isolation can occur in different ways.

Some forms of isolation may prevent mating from occurring. For example, barriers such as rivers or mountain ranges may separate subpopulations. Other forms of isolation may be behavioral. If the courtship behavior patterns of two animals are not mutually appropriate, or mating periods differ, mating does not occur. Other forms of isolation prevent successful fertilization and development even though mating may have occurred. Conditions within a female's reproductive tract may prevent fertilization by sperm of another

species. The failure of hybrids to produce offspring of their own is a form of isolation that occurs even though mating and fertilization do occur. This hybrid nonviability is caused by structural differences between chromosomes—preventing the formation of viable gametes because chromosomes cannot synapse properly during meiosis.

Allopatric Speciation

Allopatric (Gr. *allos,* other + *patria,* fatherland) **speciation** occurs when subpopulations become geographically isolated from one another. For example, a mountain range or river may permanently separate members of a population. Adaptations to different environments or genetic drift in these separate populations may result in members not being able to mate successfully with each other, even if experimentally reunited. Many biologists believe that allopatric speciation is the most common kind of speciation.

The finches that Darwin saw on the Galápagos Islands are a classic example of allopatric speciation, as well as adaptive radiation (*see Evolutionary Insights, page 82, and chapter 4*). Adaptive radiation occurs when a number of new forms diverge from an ancestral form, usually in response to the opening of major new habitats.

Fourteen species of finches evolved from the original finches that colonized the Galápagos Islands. Ancestral finches, having emigrated from the mainland, probably were distributed among a few of the islands of the Galápagos. Populations became isolated on various islands over time, and though the original population probably displayed some genetic variation, even greater variation arose. The original finches were seed eaters, and after their arrival, they probably filled their preferred habitats rapidly. Variations within the original finch population may have allowed some birds to exploit new islands and habitats where no finches had been. Mutations changed the genetic composition of the isolated finch populations, introducing further variations. Natural selection favored the retention of the variations that promoted successful reproduction.

The combined forces of isolation, mutation, and natural selection allowed the finches to diverge into a number of species with specialized feeding habits (*see figure 4.4*). Of the 14 species of finches, 6 have beaks specialized for crushing seeds of different sizes. Others feed on flowers of the prickly pear cactus or in the forests on insects and fruit.

Parapatric Speciation

Another form of speciation, called **parapatric** (Gr. *para,* beside) **speciation,** occurs in small, local populations, called **demes.** For example, all of the frogs in a particular pond or all of the sea urchins in a particular tidepool make up a deme. Individuals of a deme are more likely to breed with one another than with other individuals in the larger population, and because they experience the same environment, they are subject to similar selection pressures. Demes are not completely isolated from each other because individuals, developmental stages, or gametes can move among demes of a population. On the other hand, the relative isolation of a deme may mean

that its members experience different selection pressures than other members of the population. If so, speciation can occur. Although most evolutionists theoretically agree that parapatric speciation is possible, no certain cases are known. Parapatric speciation is therefore considered of less importance in the evolution of animal groups than allopatric speciation.

Sympatric Speciation

A third kind of speciation, called **sympatric** (Gr. *sym,* together) **speciation,** occurs within a single population (*see Evolutionary Insights, page 82*). Even though organisms are sympatric, they still may be reproductively isolated from one another. In order to demonstrate sympatric speciation, researchers must demonstrate that two species share a common ancestor and then that the two species arose without any form of geographic isolation. The latter is especially difficult to demonstrate. The driving forces for speciation are difficult to reconstruct because current ecological and selective factors may not reflect those present in the evolutionary past.

In spite of these difficulties, evidence is mounting that sympatric speciation plays a larger role in speciation than previously thought. Studies of indigobirds from Africa suggest sympatric speciation. Indigobirds lay their eggs in the nests of other bird species. They are called brood parasites. When eggs hatch, indigobird chicks learn the song of the host species that rears them. Mating is then more likely to occur between indigobirds reared by the same host species. Molecular evidence suggests genetic differences between species that are compatible with recent origins and sympatric speciation.

Sympatric speciation has also been important within the cat family (Felidae). Molecular and ecological evidence suggests that over 50% of speciation events in cat evolution have been sympatric in nature. Closely related cat species partition resources based on 24-h activity patterns, preferred habitats, and preferred foods. Such partitioning apparently led to reproductive isolation in spite of shared geographical locations.

SECTION 5.4 THINKING BEYOND THE FACTS

How does reproductive isolation occur in each of the three forms of speciation described in this section?

5.5 RATES OF EVOLUTION

LEARNING OUTCOME

1. Compare phyletic gradualism and punctuated equilibrium models of evolution.

Charles Darwin perceived evolutionary change as occurring gradually over millions of years. This concept, called **phyletic gradualism,** has been the traditional interpretation of the tempo, or rate, of evolution.

EVOLUTIONARY INSIGHTS

Speciation of Darwin's Finches

When Charles Darwin visited the Galápagos Islands in 1835, he observed the dark-bodied finches whose adaptive radiation has become a classic example of speciation (box figure 5.1). Studies of these finches have provided insight into some of the ways in which speciation can occur. Peter R. and B. Rosemary Grant have been studying these finches for more than 40 years. They have directly observed microevolutionary change reflected in bill morphology in response to changes in rainfall and food availability. Other molecular studies have also contributed to our knowledge of the adaptive radiation of this group of birds.

Molecular studies of mitochondrial DNA have identified the most likely South American relatives of Darwin's finches, members of the grassquit genus *Tiaris*. Comparisons of the mitochondrial DNA of this group with Darwin's finches suggest that the latter colonized some of the Galápagos Islands not more than 3 million years ago (mya). A very rapid adaptive radiation occurred, with the number of finch species doubling approximately every 750,000 years. No other group of birds studied has undergone a more rapid evolutionary diversification (*see figure 4.4*). Darwin's finches have served as a model to answer questions of how and why species diverge.

The traditional explanation of speciation within Darwin's finches is based on the allopatric model discussed in this chapter. This explanation is based upon differences in food resources, and the observations of the Grants have provided support for this model. Geographic isolation of populations of finches occurred as finches competed for limited food resources. Finch survival depended on food availability, bill shape and size, and the presence or absence of competing species. Species diverged as bill morphology changed and as populations became ecologically isolated (*see figure 4.4*). Interbreeding became less likely. Molecular studies have complemented these observations. Genes have been identified that regulate bill size and shape and are being tracked through finch species.

The Grants have discovered, however, that the allopatric model is not the entire explanation for finch adaptive radiation. Three million years ago, the Galápagos Islands were much simpler than they are today. In fact, there were fewer islands when they were first colonized by finches. Apparently, the number of finch species increased as the number of islands increased as a result of volcanic activity. The increasing number of islands and oscillations in temperature and precipitation naturally affected vegetation. Habitats available for finches became more diverse and complex. The original warm, wet islands favored long, narrow bills that were used in gathering nectar and insects. The islands' moisture now fluctuates and the climate is more seasonal. The increasing diversity in habitats and food supply over 3 million years apparently promoted very rapid speciation among the finch populations.

The Grants have also discovered that sympatric forces probably have also promoted speciation. Different species of finches that live on the same island rarely hybridize because visual and acoustic cues are used in mate choice. In these finches, only the males sing, and both male and female offspring respond to and learn the song of their fathers. The young associate the song and the bill shape of their fathers. Females tend to mate with males that have the bill shape and song of their fathers. The fact that learned behaviors are influencing speciation introduces new sets of variables that may influence speciation. Errors in learning, variations in the vocal apparatus of individuals, and characteristics of sound transmission through the environment could all result in changes in song characteristics and could influence mate choice.

Observations of Darwin's finches have helped revolutionize biology. They played an important role in the development of Darwin's theory of evolution by natural selection, and they continue to provide important evidence of how evolution occurs at ecological and molecular levels.
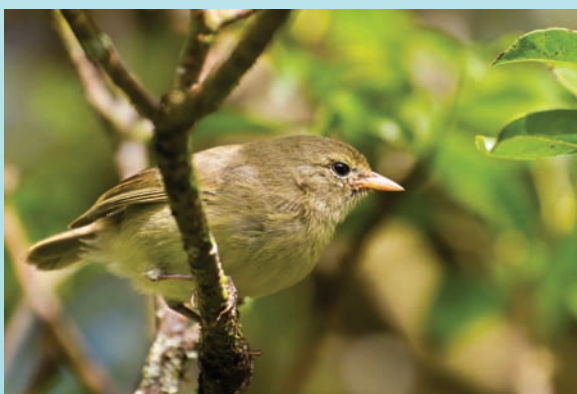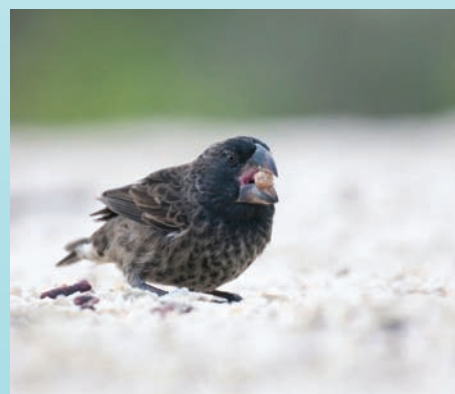
(a)   (b)

BOX FIGURE 5.1   **Speciation of Darwin's Finches.**   Speciation and adaptive radiation of Darwin's finches has been used as a classic example of allopatric speciation. Isolation of finches on different islands, and differences in food resources on those islands, selected for morphological differences in finch bills. For example, (*a*) the warbler finch (*Certhidea olivacea*) has a bill that is adapted for probing for insects and (*b*) the large ground finch (*Geospiza magnirostris*) has a bill that is adapted for crushing seeds. Studies show that increasing numbers of islands over the last 3 million years and changes in temperature and precipitation resulted in very rapid speciation. In addition, sympatric influences regarding the role of the males' song and bill shape probably also promoted speciation.

Some evolutionary changes, however, happen very rapidly. Studies of the fossil record show that many species do not change significantly over millions of years. These periods of stasis (Gr. *stasis,* standing still), or equilibrium, are interrupted when a group encounters an ecological crisis, such as a change in climate or a major geological event. Over the next 10,000 to 100,000 years, a variation that previously was selectively neutral or disadvantageous might now be advantageous. Alternatively, geological events might result in new habitats becoming available. (Events that occur in 10,000 to 100,000 years are almost instantaneous in an evolutionary time frame.) This geologically brief period of change "punctuates" the previous million or so years of equilibrium and eventually settles into the next period of stasis (figure 5.8). Long periods of stasis interrupted by brief periods of change characterize the **punctuated equilibrium model** of evolution.

Biologists have observed such rapid evolutionary changes in small populations. In a series of studies over a 20-year period, Peter R. Grant has shown that natural selection results in rapid morphological changes in the bills of Galápagos finches. A long, dry period from the middle of 1976 to early January 1978 resulted in birds with larger, deeper bills. Early in this dry period, birds quickly consumed smaller, easily cracked seeds. As they were forced to turn to larger seeds, birds with weaker bills were selected against, resulting in a measurable change in the makeup of the finch population of the island Daphne Major.

The evolution of multiple species of cichlid fish in Lake Victoria (*see chapter 1*) in the last 14,000 years is another example of rapid evolutionary change leading to speciation. One cichlid species (*Haplochromis pyrrhocephalus*) was nearly extirpated from Lake Victoria following the introduction of the Nile perch. Subsequent fishing pressure on the Nile perch allowed this cichlid population to recover somewhat; however, decreased water quality and oxygen levels placed additional selection pressures on its survival. Over a brief span of 20 years, researchers have documented a 64% increase in gill surface area and corresponding changes in head morphology that are allowing this cichlid population to recover once again.

Periods of stasis in the punctuated equilibrium model may be the result of stabilizing selection during times when environmental conditions are not changing. The ability of some organisms to escape changing environments through migration when environments are changing may also promote stasis.

One advantage of the punctuated equilibrium model is its explanation for the fossil record not always showing transitional stages between related organisms. The absence of transitional forms can often be attributed to fossilization being an unlikely event; thus, many transitional forms disappeared without leaving a fossil record. Because punctuated equilibrium involves rapid changes in small, isolated populations, preservation of intermediate forms in the fossil record is even less likely. The rapid pace (geologically speaking) of evolution resulted in apparent "jumps" from one form to another.

Phyletic gradualism and punctuated equilibrium are both valid models that explain evolutionary rates. Gradualism best describes the evolutionary history of some groups (e.g., mammals). Punctuated equilibrium best describes the evolutionary history of others
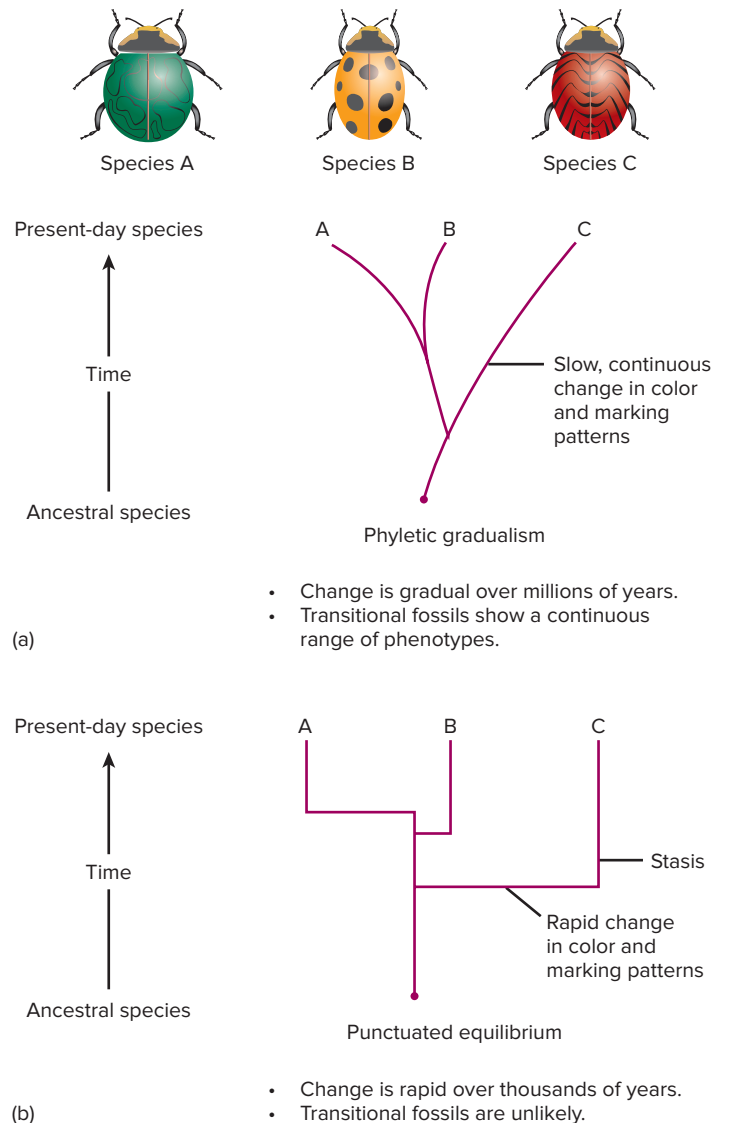

(a)

- Change is gradual over millions of years.
- Transitional fossils show a continuous range of phenotypes.

(b)

- Change is rapid over thousands of years.
- Transitional fossils are unlikely.

FIGURE 5.8

Rates of Evolution. A comparison of phyletic gradualism and punctuated equilibrium in three hypothetical beetle species. (*a*) In the phyletic gradualism model of evolution, changes are gradual over long time periods. Note that this tree implies a gradual change in color and marking patterns in the three beetle species. (*b*) In the punctuated equilibrium model of evolution, rapid periods of change interrupt long periods of stasis. This tree implies that the color and marking patterns in the beetles changed rapidly and did not change significantly during long periods of stabilizing selection (stasis).

(e.g., some marine invertebrates). For still other groups, evolution has been accented by periods when gradualism prevailed and other periods of rapid change and stasis.

SECTION 5.5 THINKING BEYOND THE FACTS

How would you explain the presence of gaps in the fossil record of a group of organisms to someone challenging evolution? List at least three reasons why gaps appear.

5.6 MOLECULAR EVOLUTION

LEARNING OUTCOMES

1. Hypothesize the differences between a comparison of the nonconserved DNA sequences of a horse and a zebra, and the nonconserved DNA sequences of a frog and a fish.
2. Explain the role of gene duplication in the evolution of new genes.

Many evolutionists study changes in animal structure and function that are observable on a large scale—for example, changes in the shape of a bird's bill or in the length of an animal's neck. All evolutionary change, however, results from changes in the base sequences in DNA and amino acids in proteins. Molecular evolutionists investigate evolutionary relationships among organisms by studying DNA and proteins. For example, cytochrome *c* is a protein present in the cellular respiration pathways in all eukaryotic organisms (table 5.1). Cellular respiration is the set of metabolic pathways that convert energy in organic molecules, such as the simple sugar glucose, into energy tied up in the bonds of adenosine triphosphate (ATP). ATP is the form of chemical energy immediately useful in cells. Organisms that other research has shown to be closely related have similar cytochrome *c* molecules. That cytochrome *c* has changed so little during hundreds of millions of years does not suggest that mutations of the cytochrome *c* gene do not occur. Rather, it suggests that mutations of the cytochrome *c* gene are nearly always detrimental and are selected against. Because it has changed so little, cytochrome *c* is said to have been conserved evolutionarily and is very useful for establishing relationships among distantly related organisms.

Not all proteins are conserved as rigorously as cytochrome *c*. Some regions of DNA that do not code for proteins can change without detrimental effects and accumulate base changes over relatively short periods of time. Comparing these regions of DNA can provide information on the relationships among closely related organisms.

Gene Duplication

Recall that most mutations are selected against. Sometimes, however, an extra copy of a gene is present. One copy may be modified, but as long as the second copy furnishes the essential protein, the organism is likely to survive. Gene duplication, the accidental duplication of a gene on a chromosome, is one way that extra genetic material can arise.

Vertebrate hemoglobin and myoglobin are believed to have arisen from a common ancestral molecule (*see figure 4.14*). Hemoglobin carries oxygen in red blood cells, and myoglobin is an oxygen storage molecule in muscle. The ancestral molecule probably carried out both functions. However, about 800 mya, gene duplication followed by mutation of one gene resulted in the formation of two polypeptides: myoglobin and hemoglobin. Further gene duplications over the last 500 million years probably explain why most vertebrates, other than primitive fishes, have hemoglobin molecules consisting of four polypeptides.

SECTION 5.6 THINKING BEYOND THE FACTS

There are six subspecies of wild turkeys (**Meleagris gallopavo**) *in North America. If one wanted to investigate evolutionary relationships among these subspecies, would it be better to use the cytochrome* **c** *gene or a non-protein-coding region of DNA? Explain.*

5.7 MOSAIC EVOLUTION

LEARNING OUTCOME

1. Explain the concept of mosaic evolution.

As discussed earlier, rates of evolution can vary both in populations and in molecules and structures. A species is a mosaic of different molecules and structures that have evolved at different rates. Some molecules or structures are conserved in evolution; others change more rapidly. The basic design of a bird provides a simple example. All birds are easily recognizable as birds because of highly conserved structures, such as feathers, bills, and a certain body form. Particular parts of birds, however, are less conservative and have a higher rate of change. Wings have been modified for hovering, soaring, and swimming. Similarly, legs have been modified for wading, swimming, and perching. These are examples of **mosaic evolution.**

SECTION 5.7 THINKING BEYOND THE FACTS

What is another example of mosaic evolution?

TABLE 5.1
**AMINO ACID DIFFERENCES IN CYTOCHROME *C*
FROM DIFFERENT ORGANISMS**

ORGANISMS	NUMBER OF VARIANT AMINO ACID RESIDUES
Cow and sheep	0
Cow and whale	2
Horse and cow	3
Rabbit and pig	4
Horse and rabbit	5
Whale and kangaroo	6
Rabbit and pigeon	7
Shark and tuna	19
Tuna and fruit fly	21
Tuna and moth	28
Yeast and mold	38
Wheat and yeast	40
Moth and yeast	44

SUMMARY

5.1 Populations and Gene Pools

- Organic evolution is a change in the frequency of alleles in a population. Virtually unlimited genetic variation, in the form of new alleles and new combinations of alleles, increases the chances that a population will survive future environmental changes.

5.2 Must Evolution Happen?

- Population genetics is the study of events occurring in gene pools. The Hardy–Weinberg theorem states that if certain assumptions are met, gene frequencies of a population remain constant from generation to generation.

5.3 Evolutionary Mechanisms

- The assumptions of the Hardy–Weinberg theorem, when not met, define circumstances under which evolution will occur.
- Neutral theory describes mechanisms of evolutionary change when alleles are selectively neutral. Genetic drift occurs when chance events cause allelic frequencies to change. Two forms of genetic drift are the founder effect and the bottleneck effect.
- Gene flow occurs when allelic frequencies change as a result of migration into or out of a population.
- Mutations are changes in the structure of genes and chromosomes. They are the source of new alleles and genetic variation. Mutational equilibrium rarely exists, and thus, mutations usually result in changing allelic frequencies.
- The tendency for allelic frequencies to change through natural selection is called selection pressure. Selection may be directional, disruptive, or stabilizing.
- Balanced polymorphism occurs when two or more phenotypes are maintained in a population. Heterozygote superiority can lead to balanced polymorphism.

5.4 Species and Speciation

- According to a biological definition, a species is a group of populations within which there is potential for the exchange of genes. Significant problems are associated with the application of this definition.
- Speciation requires reproductive isolation.
- Allopatric speciation occurs when subpopulations become geographically isolated. It is probably the most common form of speciation.
- Parapatric speciation occurs in small local populations, called demes.
- Sympatric speciation occurs within a single population. Isolation occurs as a result of changing activity patterns, courtship behaviors, and partitioned habitats.

5.5 Rates of Evolution

- Phyletic gradualism is a model of evolution that depicts change as occurring gradually, over millions of years. Punctuated equilibrium is a model of evolution that depicts long periods of stasis interrupted by brief periods of relatively rapid change.

5.6 Molecular Evolution

- The study of rates of molecular evolution helps establish evolutionary interrelationships among organisms. A mutation may modify a duplicated gene, which then may serve a function other than its original role.

5.7 Mosaic Evolution

- A species is a mosaic of different molecules and structures that have evolved at differing rates.

CONCEPT REVIEW QUESTIONS

1. Groups of individuals of the same species occupying a given area at the same time and sharing a common set of genes are called
   a. clades.
   b. demes.
   c. populations.
   d. species units.

2. The Hardy–Weinberg theorem predicts that allele frequencies will remain constant in populations (evolution will not occur) when all of the following are true, except one. Select the exception.
   a. The population must be large so that genetic drift is not occurring.
   b. Migration into a population ensures new alleles are randomly distributed within a population.
   c. All individuals within the population have an equal opportunity for reproduction.
   d. No mutations are occurring or mutational equilibrium exists.

3. If genetic drift occurs in a population, then
   a. the population is probably large.
   b. the population will likely suffer a loss of alleles and become more genetically uniform.
   c. directional selection is occurring.
   d. gene flow will prevent loss of alleles.

4. A community of ground nesting birds and lizards experiences an environmental change that expands the area of arid habitat favored by the lizards and that is less usable by the birds for nesting. Which of the following scenarios would be most likely for this community?
   a. Directional selection could result in an increased prevalence of alleles that promote drought tolerance in the birds.
   b. Disruptive selection could result in the formation of two species of birds.
   c. Stabilizing selection could promote the formation of two species of lizards.
   d. Directional selection could promote the formation of two species of lizards.

5. Rapid periods of genetic change followed by extended periods of stabilizing selection and evolutionary stasis describe
   a. phyletic gradualism.
   b. punctuated equilibrium.
   c. parapatric speciation.
   d. sympatric speciation.

ANALYSIS AND APPLICATION QUESTIONS

1. Can natural selection act on variations that are not inherited? (Consider, for example, physical changes that arise from contracting a disease.) If so, what is the effect of that selection on subsequent generations?

2. In what way does overuse of antibiotics and pesticides increase the likelihood that these chemicals will eventually become ineffective? This is an example of which one of the three modes of natural selection?

3. What are the implications of the "bottleneck effect" for wildlife managers who try to help endangered species, such as the whooping crane, recover from near extinction?

4. What does it mean to think of evolutionary change as being goal-oriented? Explain why this way of thinking is wrong.

5. Imagine that two species of butterflies resemble one another closely. One of the species (the model) is distasteful to bird predators, and the other species (the mimic) is not. How could directional selection have resulted in the mimic species evolving a resemblance to the model species?