

22

Descent with Modification: A Darwinian View of Life

KEY CONCEPTS

- 22.1 The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species
- 22.2 Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life
- 22.3 Evolution is supported by an overwhelming amount of scientific evidence

▲ **Figure 22.1** How is this caterpillar protecting itself from predators?

Endless Forms Most Beautiful

A hungry bird would have to look very closely to spot this caterpillar of the moth *Synchlora aerata*, which blends in well with the flowers on which it feeds. The disguise is enhanced by the caterpillar's flair for "decorating"—it glues pieces of flower petals to its body, transforming itself into its own background (**Figure 22.1**).

This distinctive caterpillar is a member of a diverse group, the more than 120,000 species of lepidopteran insects (moths and butterflies). All lepidopterans go through a juvenile stage characterized by a well-developed head and many chewing mouthparts: the ravenous, efficient feeding machines we call caterpillars. As adults, all lepidopterans share other features, such as three pairs of legs and two pairs of wings covered with small scales. But the many lepidopterans also differ from one another. How did there come to be so many different moths and butterflies, and what causes their similarities and differences? The self-decorating caterpillar and its many close relatives illustrate three key observations about life:

- the striking ways in which organisms are suited for life in their environments*
- the many shared characteristics (unity) of life
- the rich diversity of life

*Here and throughout this text, the term *environment* refers to other organisms as well as to the physical aspects of an organism's surroundings.

More than a century and a half ago, Charles Darwin was inspired to develop a scientific explanation for these three broad observations. When he published his hypothesis in his book *The Origin of Species*, Darwin ushered in a scientific revolution—the era of evolutionary biology.

For now, we will define **evolution** as *descent with modification*, a phrase Darwin used in proposing that Earth's many species are descendants of ancestral species that were different from the present-day species. Evolution can also be defined more narrowly as a change in the genetic composition of a population from generation to generation (see Chapter 23).

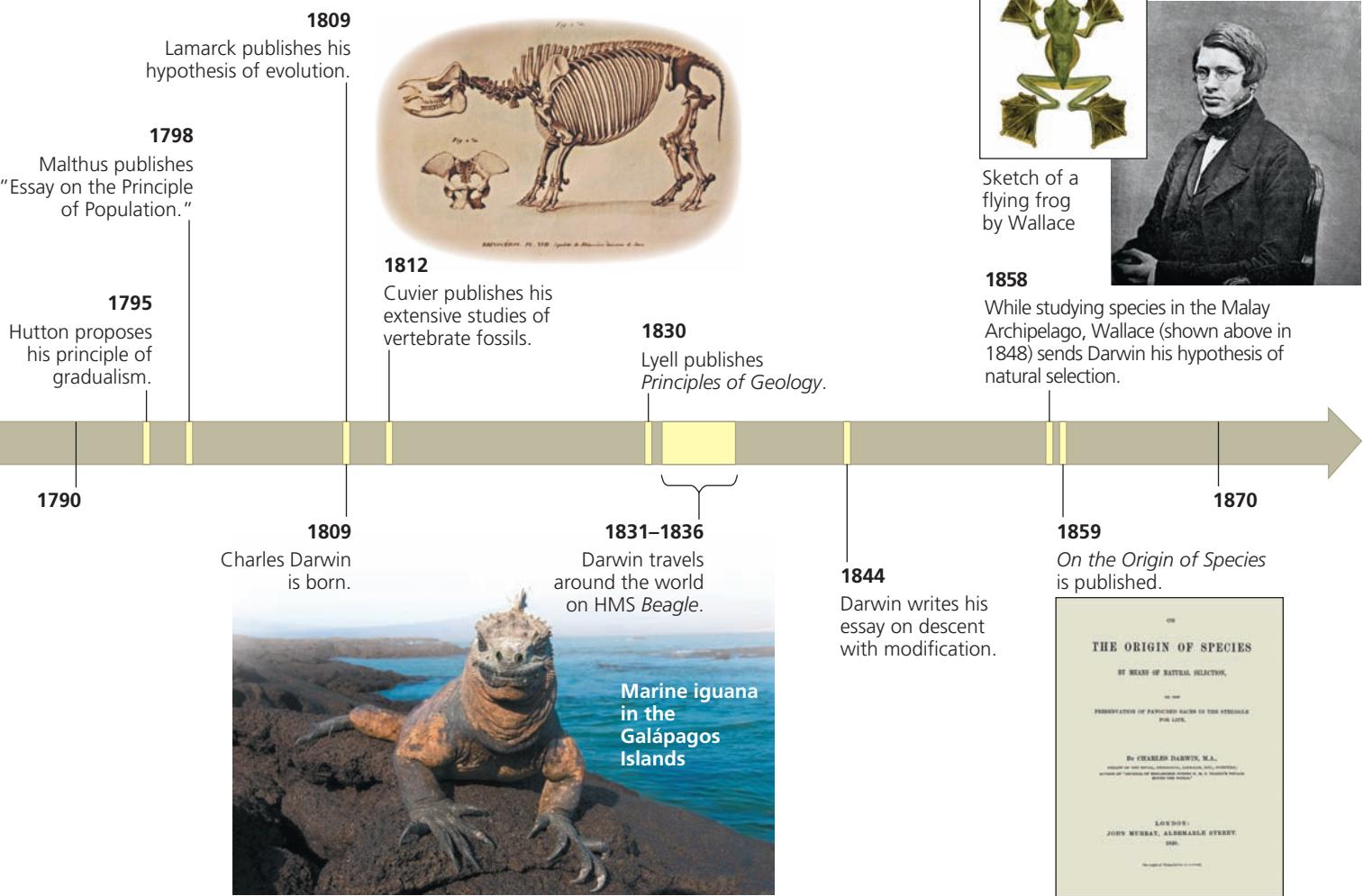
We can also view evolution in two related but different ways: as a pattern and as a process. The *pattern* of evolutionary change is revealed by data from many scientific disciplines, including biology, geology, physics, and chemistry. These data are facts—they are observations about the natural world. The *process* of evolution consists of the mechanisms that produce the observed pattern of change. These mechanisms represent natural causes of the natural phenomena we observe. Indeed, the power of evolution as a unifying theory is its ability to explain and connect a vast array of observations about the living world.

As with all general theories in science, we continue to test our understanding of evolution by examining whether it can account for new observations and experimental results. In this and the following chapters, we'll examine how ongoing discoveries shape what we know about the pattern and process of evolution. To set the stage, we'll first retrace Darwin's quest to explain the adaptations, unity, and diversity of what he called life's “endless forms most beautiful.”

CONCEPT 22.1

The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species

What impelled Darwin to challenge the prevailing views about Earth and its life? Darwin developed his revolutionary proposal over time, influenced by the work of others and by his travels (Figure 22.2). As we'll see, his ideas also had deep historical roots.



▲ Figure 22.2 The intellectual context of Darwin's ideas.

Scala Naturae and Classification of Species

Long before Darwin was born, several Greek philosophers suggested that life might have changed gradually over time. But one philosopher who greatly influenced early Western science, Aristotle (384–322 BCE), viewed species as fixed (unchanging). Through his observations of nature, Aristotle recognized certain “affinities” among organisms. He concluded that life-forms could be arranged on a ladder, or scale, of increasing complexity, later called the *scala naturae* (“scale of nature”). Each form of life, perfect and permanent, had its allotted rung on this ladder.

These ideas were generally consistent with the Old Testament account of creation, which holds that species were individually designed by God and therefore perfect. In the 1700s, many scientists interpreted the often remarkable match of organisms to their environment as evidence that the Creator had designed each species for a particular purpose.

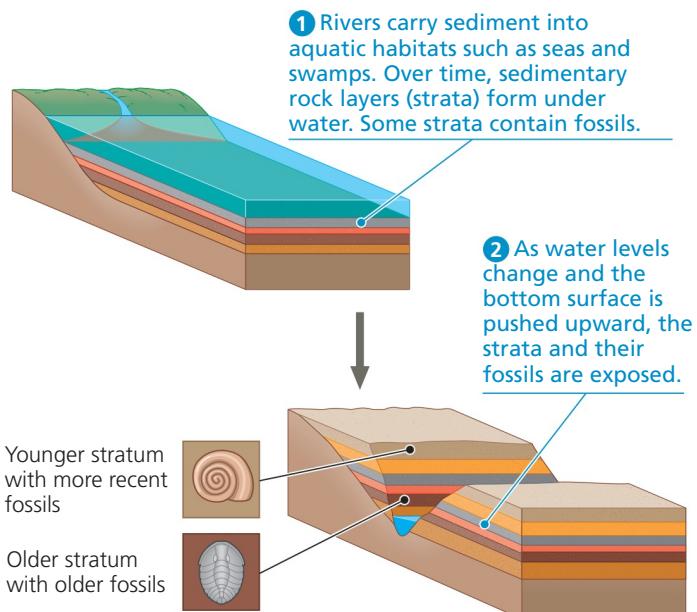
One such scientist was Carolus Linnaeus (1707–1778), a Swedish physician and botanist who sought to classify life’s diversity, in his words, “for the greater glory of God.” Linnaeus developed the two-part, or *binomial*, format for naming species (such as *Homo sapiens* for humans) that is still used today. In contrast to the linear hierarchy of the *scala naturae*, Linnaeus adopted a nested classification system, grouping similar species into increasingly general categories. For example, similar species are grouped in the same genus, similar genera (plural of genus) are grouped in the same family, and so on (see Figure 1.12).

Linnaeus did not ascribe the resemblances among species to evolutionary kinship, but rather to the pattern of their creation. A century later, however, Darwin argued that classification should be based on evolutionary relationships. He also noted that scientists using the Linnaean system often grouped organisms in ways that reflected those relationships.

Ideas About Change over Time

Among other sources of information, Darwin drew from the work of scientists studying **fossils**, the remains or traces of organisms from the past. Many fossils are found in sedimentary rocks formed from the sand and mud that settle to the bottom of seas, lakes, and swamps (Figure 22.3). New layers of sediment cover older ones and compress them into superimposed layers of rock called **strata** (singular, *stratum*). The fossils in a particular stratum provide a glimpse of some of the organisms that populated Earth at the time that layer formed. Later, erosion may carve through upper (younger) strata, revealing deeper (older) strata that had been buried.

Paleontology, the study of fossils, was developed in large part by French scientist Georges Cuvier (1769–1832). In



▲ Figure 22.3 Formation of sedimentary strata with fossils.

examining strata near Paris, Cuvier noted that the older the stratum, the more dissimilar its fossils were to current life-forms. He also observed that from one layer to the next, some new species appeared while others disappeared. He inferred that extinctions must have been a common occurrence, but he staunchly opposed the idea of evolution. Cuvier speculated that each boundary between strata represented a sudden catastrophic event, such as a flood, that had destroyed many of the species living in that area. Such regions, he reasoned, were later repopulated by different species immigrating from other areas.

In contrast, other scientists suggested that profound change could take place through the cumulative effect of slow but continuous processes. In 1795, Scottish geologist James Hutton (1726–1797) proposed that Earth’s geologic features could be explained by gradual mechanisms, such as valleys being formed by rivers. The leading geologist of Darwin’s time, Charles Lyell (1797–1875), incorporated Hutton’s thinking into his proposal that the same geologic processes are operating today as in the past, and at the same rate.

Hutton and Lyell’s ideas strongly influenced Darwin’s thinking. Darwin agreed that if geologic change results from slow, continuous actions rather than from sudden events, then Earth must be much older than the widely accepted age of a few thousand years. It would, for example, take a very long time for a river to carve a canyon by erosion. He later reasoned that perhaps similarly slow and subtle processes could produce substantial biological change. Darwin was not the first to apply the idea of gradual change to biological evolution, however.

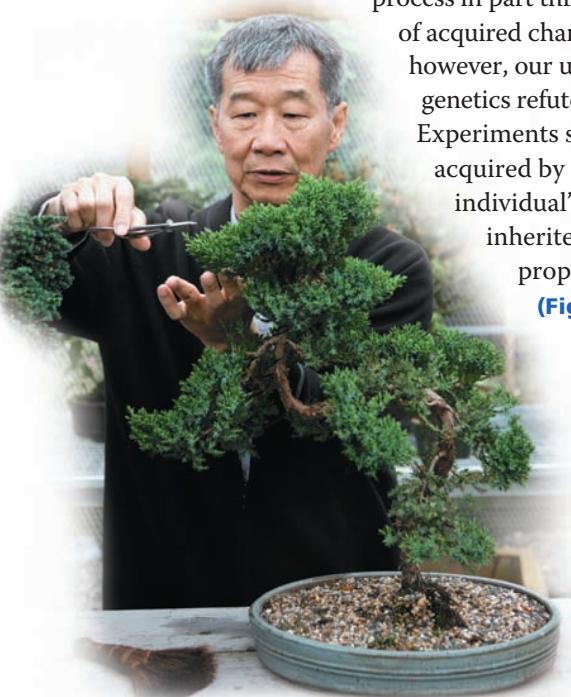
Lamarck's Hypothesis of Evolution

Although some 18th-century naturalists suggested that life evolves as environments change, only one proposed a mechanism for *how* life changes over time: French biologist Jean-Baptiste de Lamarck (1744–1829). Alas, Lamarck is primarily remembered today *not* for his visionary recognition that evolutionary change explains patterns in fossils and the match of organisms to their environments, but for the incorrect mechanism he proposed.

Lamarck published his hypothesis in 1809, the year Darwin was born. By comparing living species with fossil forms, Lamarck had found what appeared to be several lines of descent, each a chronological series of older to younger fossils leading to a living species. He explained his findings using two principles that were widely accepted at the time. The first was *use and disuse*, the idea that parts of the body that are used extensively become larger and stronger, while those that are not used deteriorate. Among many examples, he cited a giraffe stretching its neck to reach leaves on high branches. The second principle, *inheritance of acquired characteristics*, stated that an organism could pass these modifications to its offspring. Lamarck reasoned that the long, muscular neck of the living giraffe had evolved over many generations as giraffes stretched their necks ever higher.

Lamarck also thought that evolution happens because organisms have an innate drive to become more complex. Darwin rejected this idea, but he, too, thought that variation was introduced into the evolutionary process in part through inheritance of acquired characteristics. Today, however, our understanding of genetics refutes this mechanism:

Experiments show that traits acquired by use during an individual's life are not inherited in the way proposed by Lamarck
(Figure 22.4).



▲ **Figure 22.4 Acquired traits cannot be inherited.** This bonsai tree was “trained” to grow as a dwarf by pruning and shaping. However, seeds from this tree would produce offspring of normal size.

Lamarck was vilified in his own time, especially by Cuvier, who denied that species ever evolve. In retrospect, however, Lamarck did recognize that the match of organisms to their environments can be explained by gradual evolutionary change, and he did propose a testable explanation for how this change occurs.

CONCEPT CHECK 22.1

1. How did Hutton’s and Lyell’s ideas influence Darwin’s thinking about evolution?
2. **MAKE CONNECTIONS** Scientific hypotheses must be testable (see Concept 1.3). Applying this criterion, are Cuvier’s explanation of the fossil record and Lamarck’s hypothesis of evolution scientific? Explain your answer in each case.

For suggested answers, see Appendix A.

CONCEPT 22.2

Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life

As the 19th century dawned, it was generally thought that species had remained unchanged since their creation. A few clouds of doubt about the permanence of species were beginning to gather, but no one could have forecast the thundering storm just beyond the horizon. How did Charles Darwin become the lightning rod for a revolutionary view of life?

Darwin’s Research

Charles Darwin (1809–1882) was born in Shrewsbury, in western England. Even as a boy, he had a consuming interest in nature. When he was not reading nature books, he was fishing, hunting, riding, and collecting insects. However, Darwin’s father, a physician, could see no future for his son as a naturalist and sent him to medical school in Edinburgh. But Charles found medicine boring and surgery before the days of anesthesia horrifying. He quit medical school and enrolled at Cambridge University, intending to become a clergyman. (At that time, many scholars of science belonged to the clergy.)

At Cambridge, Darwin became the protégé of John Henslow, a botany professor. Soon after Darwin graduated, Henslow recommended him to Captain Robert FitzRoy, who was preparing the survey ship HMS *Beagle* for a long voyage around the world. Darwin would pay his own way and serve as a conversation partner to the young captain. FitzRoy, who

was himself an accomplished scientist, accepted Darwin because he was a skilled naturalist and because they were of similar age and social class.

The Voyage of the Beagle

Darwin embarked from England on the *Beagle* in December 1831. The primary mission of the voyage was to chart poorly known stretches of the South American coastline. Darwin, however, spent most of his time on shore, observing and collecting thousands of plants and animals. He described features of organisms that made them well suited to such diverse environments as the humid jungles of Brazil, the expansive grasslands of Argentina, and the towering peaks of the Andes. He also noted that the plants and animals in temperate regions of South America more closely resembled species living in the South American tropics than species living in temperate regions of Europe. Furthermore, the fossils he found, though clearly different from living species, distinctly resembled the living organisms of South America.

Darwin also spent much time thinking about geology. Despite repeated bouts of seasickness, he read Lyell's *Principles of Geology* during the voyage. He experienced geologic change firsthand when a violent earthquake shook the coast of Chile, and he observed afterward that rocks along the coast had been thrust upward by several feet. Finding fossils of ocean organisms high in the Andes, Darwin inferred that the rocks containing the fossils must have been raised there by many similar earthquakes. These observations reinforced what he had learned from Lyell: Physical evidence did not

support the traditional view that Earth was only a few thousand years old.

Darwin's interest in the species (or fossils) found in an area was further stimulated by the *Beagle*'s stop at the Galápagos, a group of volcanic islands located near the equator about 900 km west of South America (**Figure 22.5**). Darwin was fascinated by the unusual organisms there. The birds he collected included several kinds of mockingbirds. These mockingbirds, though similar to each other, seemed to be different species. Some were unique to individual islands, while others lived on two or more adjacent islands. Furthermore, although the animals on the Galápagos resembled species living on the South American mainland, most of the Galápagos species were not known from anywhere else in the world. Darwin hypothesized that the Galápagos had been colonized by organisms that had strayed from South America and then diversified, giving rise to new species on the various islands.

Darwin's Focus on Adaptation

During the voyage of the *Beagle*, Darwin observed many examples of **adaptations**, inherited characteristics of organisms that enhance their survival and reproduction in specific environments. Later, as he reassessed his observations, he began to perceive adaptation to the environment and the origin of new species as closely related processes. Could a new species arise from an ancestral form by the gradual accumulation of adaptations to a different environment? From studies made years after Darwin's voyage, biologists have concluded that this is indeed what happened to a diverse



▲ Figure 22.5 The voyage of HMS Beagle (December 1831–October 1836).

group of finches found on the Galápagos Islands (see Figure 1.20). The finches' various beaks and behaviors are adapted to the specific foods available on their home islands (**Figure 22.6**). Darwin realized that explaining such adaptations was essential to understanding evolution. His explanation of how adaptations arise centered on **natural selection**, a process in which individuals that have certain inherited traits tend to survive and reproduce at higher rates than other individuals *because of* those traits.

By the early 1840s, Darwin had worked out the major features of his hypothesis. He set these ideas on paper in 1844, when he wrote a long essay on descent with modification and its underlying mechanism, natural selection. Yet he was still reluctant to publish his ideas, in part because he anticipated the uproar they would cause. During this time, Darwin continued to compile evidence in support of his hypothesis. By the mid-1850s, he had described his ideas to Lyell and a few others. Lyell, who was not yet convinced of evolution, nevertheless urged Darwin to publish on the subject before someone else came to the same conclusions and published first.

In June 1858, Lyell's prediction came true. Darwin received a manuscript from Alfred Russel Wallace (1823–1913), a British naturalist working in the South Pacific islands of the Malay Archipelago (see Figure 22.2). Wallace had developed a hypothesis of natural selection nearly identical to Darwin's. He asked Darwin to evaluate his paper and forward it to Lyell if it merited publication. Darwin complied, writing to Lyell: "Your words have come true with a vengeance.... I never saw a more striking coincidence ... so all my originality, whatever it may amount to, will be smashed." On July 1, 1858, Lyell and a colleague presented Wallace's paper, along with extracts from Darwin's unpublished 1844 essay, to the

Linnean Society of London. Darwin quickly finished his book, titled *On the Origin of Species by Means of Natural Selection* (commonly referred to as *The Origin of Species*), and published it the next year. Although Wallace had submitted his ideas for publication first, he admired Darwin and thought that Darwin had developed the idea of natural selection so extensively that he should be known as its main architect.

Within a decade, Darwin's book and its proponents had convinced most scientists of the time that life's diversity is the product of evolution. Darwin succeeded where previous evolutionists had failed, mainly by presenting a plausible scientific mechanism with immaculate logic and an avalanche of evidence.

The Origin of Species

In his book, Darwin amassed evidence that three broad observations about nature—the unity of life, the diversity of life, and the match between organisms and their environments—resulted from descent with modification by natural selection.

Descent with Modification

In the first edition of *The Origin of Species*, Darwin never used the word *evolution* (although the final word of the book is "evolved"). Rather, he discussed *descent with modification*, a phrase that summarized his view of life. Organisms share many characteristics, leading Darwin to perceive unity in life. He attributed the unity of life to the descent of all organisms from an ancestor that lived in the remote past. He also thought that as the descendants of that ancestral organism lived in various habitats, they gradually accumulated diverse modifications, or adaptations, that fit them to



(a) Cactus-eater. The long, sharp beak of the cactus ground finch (*Geospiza scandens*) helps it tear and eat cactus flowers and pulp.



(b) Insect-eater. The green warbler finch (*Certhidea olivacea*) uses its narrow, pointed beak to grasp insects.

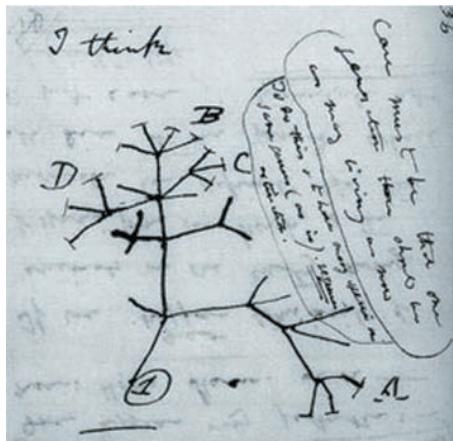


(c) Seed-eater. The large ground finch (*Geospiza magnirostris*) has a large beak adapted for cracking seeds found on the ground.

▲ Figure 22.6 Three examples of beak variation in Galápagos finches. The Galápagos Islands are home to more than a dozen species of closely related finches, some found only on a single island. A striking difference among them is their beaks, which are adapted for specific diets.

MAKE CONNECTIONS Review Figure 1.20. To which of the other two species shown above is the cactus-eater more closely related (that is, with which does the cactus-eater share a more recent common ancestor)?

► Figure 22.7
 “I think . . .” In this 1837 sketch, Darwin envisioned the branching pattern of evolution. Branches that end in twigs labeled A–D represent particular groups of living organisms; all other branches represent extinct groups.



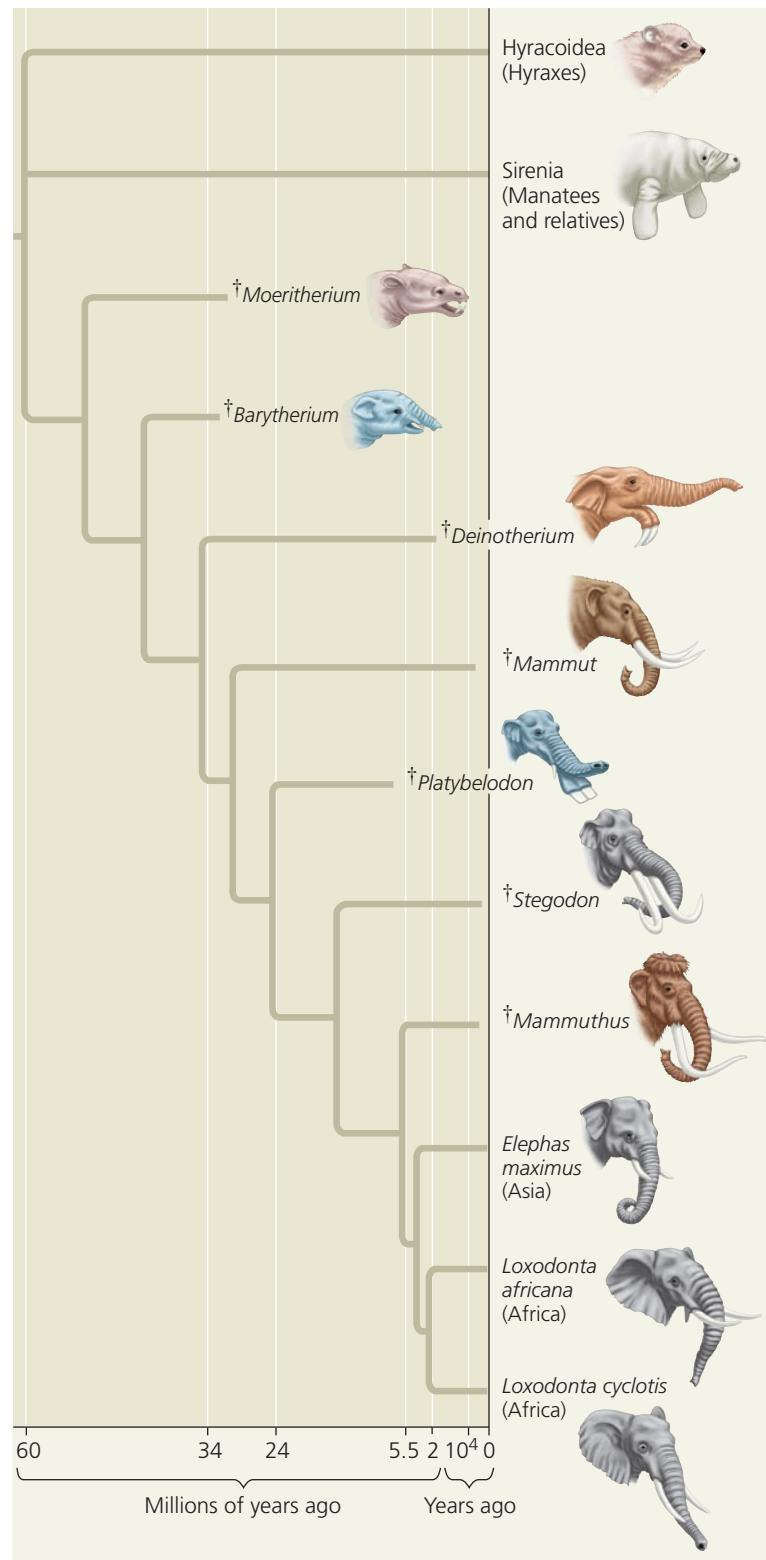
specific ways of life. Darwin reasoned that over a long period of time, descent with modification eventually led to the rich diversity of life we see today.

Darwin viewed the history of life as a tree, with multiple branchings from a common trunk out to the tips of the youngest twigs (Figure 22.7). In his diagram, the tips of the twigs that are labeled A–D represent several groups of organisms living in the present day, while the unlabeled branches represent groups that are extinct. Each fork of the tree represents the most recent common ancestor of all the lines of evolution that subsequently branch from that point. Darwin reasoned that such a branching process, along with past extinction events, could explain the large morphological gaps that sometimes exist between related groups of organisms.

As an example, let’s consider the three living species of elephants: the Asian elephant (*Elephas maximus*) and two species of African elephants (*Loxodonta africana* and *L. cyclotis*). These closely related species are very similar because they shared the same line of descent until a relatively recent split from their common ancestor, as shown in the tree diagram in Figure 22.8. Note that seven lineages related to elephants have become extinct over the past 32 million years. As a result, there are no living species that fill the morphological gap between the elephants and their nearest relatives today, the hyraxes and manatees. Such extinctions are not uncommon. In fact, many evolutionary branches, even some major ones, are dead ends: Scientists estimate that over 99% of all species that have ever lived are now extinct. As in Figure 22.8, fossils of extinct species can document the divergence of present-day groups by “filling in” gaps between them.

Artificial Selection, Natural Selection, and Adaptation

Darwin proposed the mechanism of natural selection to explain the observable patterns of evolution. He crafted his argument carefully, hoping to persuade even the most skeptical readers. First he discussed familiar examples of selective breeding of domesticated plants and animals. Humans

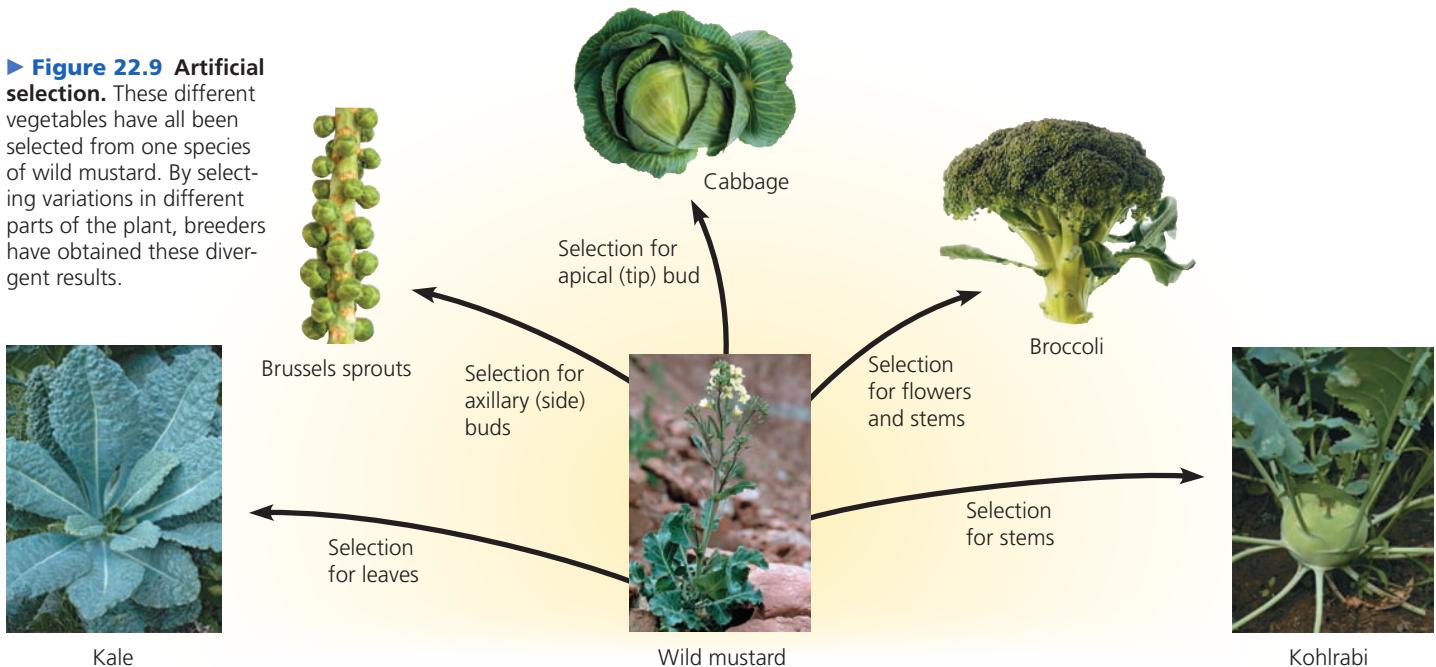


▲ Figure 22.8 Descent with modification. This evolutionary tree of elephants and their relatives is based mainly on fossils—their anatomy, order of appearance in strata, and geographic distribution. Note that most branches of descent ended in extinction (denoted by the dagger symbol †). (Time line not to scale.)

? Based on the tree shown here, approximately when did the most recent ancestor shared by Mammuthus (woolly mammoths), Asian elephants, and African elephants live?

► **Figure 22.9 Artificial selection.**

These different vegetables have all been selected from one species of wild mustard. By selecting variations in different parts of the plant, breeders have obtained these divergent results.



have modified other species over many generations by selecting and breeding individuals that possess desired traits, a process called **artificial selection** (Figure 22.9). As a result of artificial selection, crops, livestock animals, and pets often bear little resemblance to their wild ancestors.

Darwin then argued that a similar process occurs in nature. He based his argument on two observations, from which he drew two inferences:

Observation #1: Members of a population often vary in their inherited traits (Figure 22.10).

Observation #2: All species can produce more offspring than their environment can support (Figure 22.11), and many of these offspring fail to survive and reproduce.

Inference #1: Individuals whose inherited traits give them a higher probability of surviving and reproducing in a given environment tend to leave more offspring than other individuals.

Inference #2: This unequal ability of individuals to survive and reproduce will lead to the accumulation of favorable traits in the population over generations.

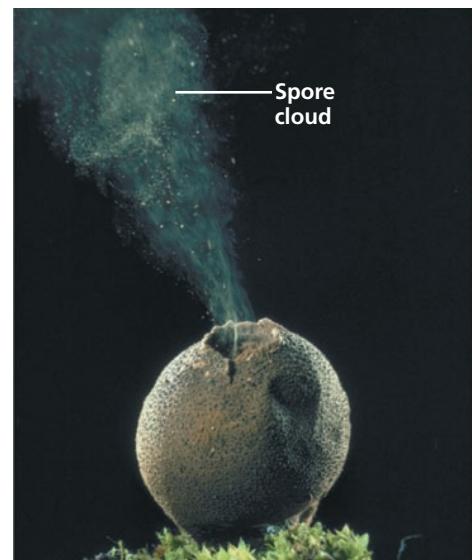
As these two inferences suggest, Darwin saw an important connection between natural selection and the capacity of organisms to “overreproduce.” He began to make this connection after reading an essay by economist Thomas Malthus, who contended that much of human suffering—disease, famine, and war—resulted from the human population’s potential to increase faster than food supplies and other resources. Similarly, Darwin realized that the capacity to overreproduce was characteristic of all species. Of the many eggs laid, young born, and seeds spread, only a tiny fraction complete their development and leave offspring of



▲ **Figure 22.10 Variation in a population.** Individuals in this population of Asian ladybird beetles vary in color and spot pattern. Natural selection may act on these variations only if (1) they are heritable and (2) they affect the beetles’ ability to survive and reproduce.

► **Figure 22.11 Overproduction of offspring.**

A single puffball fungus can produce billions of offspring. If all of these offspring and their descendants survived to maturity, they would carpet the surrounding land surface.



their own. The rest are eaten, starved, diseased, unmated, or unable to tolerate physical conditions of the environment such as salinity or temperature.

An organism's heritable traits can influence not only its own performance, but also how well its offspring cope with environmental challenges. For example, an organism might have a trait that gives its offspring an advantage in escaping predators, obtaining food, or tolerating physical conditions. When such advantages increase the number of offspring that survive and reproduce, the traits that are favored will likely appear at a greater frequency in the next generation. Thus, over time, natural selection resulting from factors such as predators, lack of food, or adverse physical conditions can lead to an increase in the proportion of favorable traits in a population.

How rapidly do such changes occur? Darwin reasoned that if artificial selection can bring about dramatic change in a relatively short period of time, then natural selection should be capable of substantial modification of species over many hundreds of generations. Even if the advantages of some heritable traits over others are slight, the advantageous variations will gradually accumulate in the population, and less favorable variations will diminish. Over time, this process will increase the frequency of individuals with favorable adaptations and hence refine the match between organisms and their environment.

Natural Selection: A Summary

Let's now recap the main ideas of natural selection:

- Natural selection is a process in which individuals that have certain heritable traits survive and reproduce at a higher rate than other individuals because of those traits.
- Over time, natural selection can increase the match between organisms and their environment (**Figure 22.12**).
- If an environment changes, or if individuals move to a new environment, natural selection may result in adaptation to these new conditions, sometimes giving rise to new species.

One subtle but important point is that although natural selection occurs through interactions between individual organisms and their environment, *individuals do not evolve*. Rather, it is the population that evolves over time.

A second key point is that natural selection can amplify or diminish only those heritable traits that differ among the individuals in a population. Thus, even if a trait is heritable, if all the individuals in a population are genetically identical for that trait, evolution by natural selection cannot occur.

Third, remember that environmental factors vary from place to place and over time. A trait that is favorable in one place or time may be useless—or even detrimental—in other places or times. Natural selection is always operating, but

► A flower mantid in Malaysia



◀ A flower-eyed mantid in South Africa



► A leaf mantid in Borneo

▲ **Figure 22.12 Camouflage as an example of evolutionary adaptation.** Related species of the insects called mantids have diverse shapes and colors that evolved in different environments.

? Explain how these mantids demonstrate the three key observations about life introduced at the beginning of the chapter: the match between organisms and their environments, unity, and diversity.

which traits are favored depends on the context in which a species lives and mates.

Next, we'll survey the wide range of observations that support a Darwinian view of evolution by natural selection.

CONCEPT CHECK 22.2

1. How does the concept of descent with modification explain both the unity and diversity of life?
2. **WHAT IF?** If you discovered a fossil of an extinct mammal that lived high in the Andes, would you predict that it would more closely resemble present-day mammals from South American jungles or present-day mammals that live high in African mountains? Explain.
3. **MAKE CONNECTIONS** Review the relationship between genotype and phenotype (see Figures 14.4 and 14.6). Suppose that in a particular pea population, flowers with the white phenotype are favored by natural selection. Predict what would happen over time to the frequency of the *p* allele in the population, and explain your reasoning.

For suggested answers, see Appendix A.

CONCEPT 22.3

Evolution is supported by an overwhelming amount of scientific evidence

In *The Origin of Species*, Darwin marshaled a broad range of evidence to support the concept of descent with modification. Still—as he readily acknowledged—there were instances in which key evidence was lacking. For example, Darwin referred to the origin of flowering plants as an “abominable mystery,” and he lamented the lack of fossils showing how earlier groups of organisms gave rise to new groups.

In the last 150 years, new discoveries have filled many of the gaps that Darwin identified. The origin of flowering plants, for example, is much better understood (see Chapter 30), and many fossils have been discovered that signify the origin of new groups of organisms (see Chapter 25). In this section, we’ll consider four types of data that document the pattern of evolution and illuminate how it occurs: direct observations, homology, the fossil record, and biogeography.

Direct Observations of Evolutionary Change

Biologists have documented evolutionary change in thousands of scientific studies. We’ll examine many such studies throughout this unit, but let’s look at two examples here.

Natural Selection in Response to Introduced Species

Animals that eat plants, called herbivores, often have adaptations that help them feed efficiently on their primary food sources. What happens when herbivores switch to a new food source with different characteristics?

An opportunity to study this question in nature is provided by soapberry bugs, which use their “beak,” a hollow, needlelike mouthpart, to feed on seeds located within the fruits of various plants. In southern Florida, the soapberry bug (*Jadera haematoloma*) feeds on the seeds of a native plant, the balloon vine (*Cardiospermum corindum*). In central Florida, however, balloon vines have become rare. Instead, soapberry bugs in that region now feed on the seeds of the goldenrain tree (*Koelreuteria elegans*), a species recently introduced from Asia.

Soapberry bugs feed most effectively when their beak length closely matches the depth at which seeds are found within the fruit. Goldenrain tree fruit consists of three flat lobes, and its seeds are much closer to the fruit surface than are the seeds of the plump, round fruit of the native balloon vine. These differences led researchers to predict that in populations that feed on goldenrain tree, natural selection would result in beaks that are *shorter* than those in populations that feed on balloon vine (Figure 22.13). Indeed, beak

▼ Figure 22.13

Inquiry

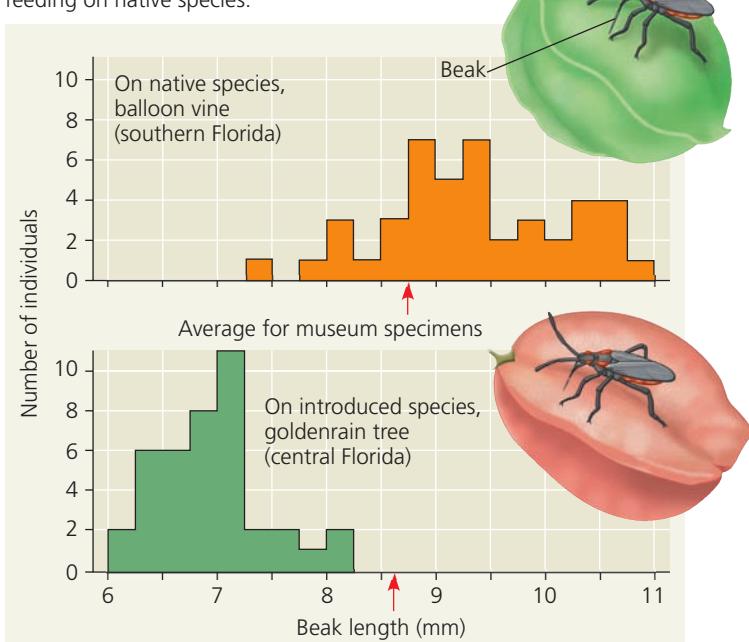
Can a change in a population’s food source result in evolution by natural selection?

Field Study Soapberry bugs feed most effectively when the length of their “beak” closely matches the depth of the seeds within the fruit. Scott Carroll and his colleagues measured beak lengths in soapberry bug populations feeding on the native balloon vine. They also measured beak lengths in populations feeding on the introduced goldenrain tree. The researchers then compared the measurements with those of museum specimens collected in the two areas before the goldenrain tree was introduced.



Soapberry bug with beak inserted in balloon vine fruit

Results Beak lengths were shorter in populations feeding on the introduced species than in populations feeding on the native species, in which the seeds are buried more deeply. The average beak length in museum specimens from each population (indicated by red arrows) was similar to beak lengths in populations feeding on native species.



Conclusion Museum specimens and contemporary data suggest that a change in the size of the soapberry bug’s food source can result in evolution by natural selection for matching beak size.

Source: S. P. Carroll and C. Boyd, Host race radiation in the soapberry bug: natural history with the history, *Evolution* 46:1052–1069 (1992).

WHAT IF? Data from additional studies showed that when soapberry bug eggs from a population fed on balloon vine fruits were reared on goldenrain tree fruits (or vice versa), the beak lengths of the adult insects matched those in the population from which the eggs were obtained. Interpret these results.

lengths are shorter in the populations that feed on goldenrain tree.

Researchers have also studied beak length evolution in soapberry bug populations that feed on plants introduced to Louisiana, Oklahoma, and Australia. In each of these locations, the fruit of the introduced plants is larger than the fruit of the native plant. Thus, in populations feeding on introduced species in these regions, researchers predicted that natural selection would result in the evolution of *longer* beak length. Again, data collected in field studies upheld this prediction.

The observed changes in beak lengths had important consequences: In Australia, for example, the increase in beak length nearly doubled the success with which soapberry bugs could eat the seeds of the introduced species. Furthermore, since historical data show that the goldenrain tree reached central Florida just 35 years before the scientific studies were initiated, the results demonstrate that natural selection can cause rapid evolution in a wild population.

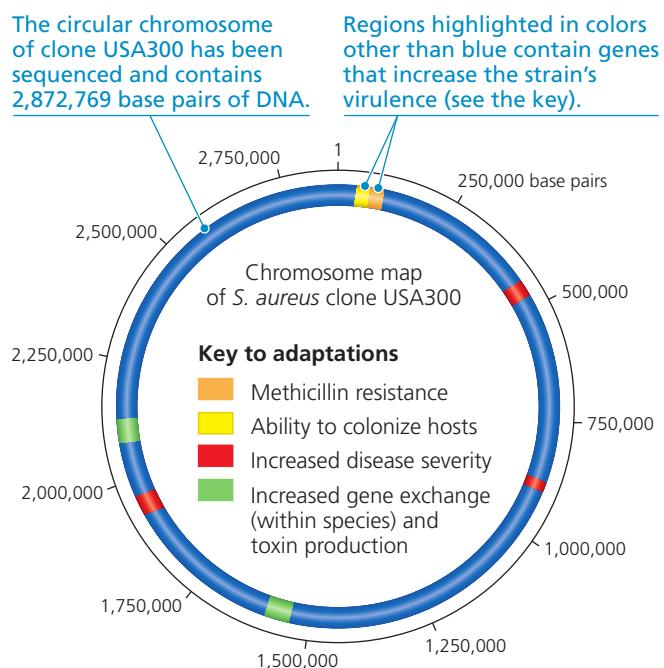
The Evolution of Drug-Resistant Bacteria

An example of ongoing natural selection that dramatically affects humans is the evolution of drug-resistant pathogens (disease-causing organisms and viruses). This is a particular problem with bacteria and viruses because resistant strains of these pathogens can proliferate very quickly.

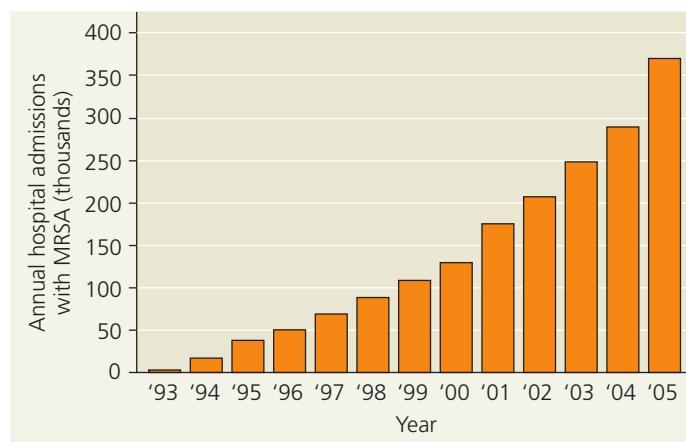
Consider the evolution of drug resistance in the bacterium *Staphylococcus aureus*. About one in three people harbor this species on their skin or in their nasal passages with no negative effects. However, certain genetic varieties (strains) of this species, known as methicillin-resistant *S. aureus* (MRSA), are formidable pathogens. The past decade has seen an alarming increase in virulent forms of MRSA such as clone USA300, a strain that can cause “flesh-eating disease” and potentially fatal infections (**Figure 22.14**). How did clone USA300 and other strains of MRSA become so dangerous?

The story begins in 1943, when penicillin became the first widely used antibiotic. Since then, penicillin and other antibiotics have saved millions of lives. However, by 1945, more than 20% of the *S. aureus* strains seen in hospitals were already resistant to penicillin. These bacteria had an enzyme, penicillinase, that could destroy penicillin. Researchers responded by developing antibiotics that were not destroyed by penicillinase, but some *S. aureus* populations developed resistance to each new drug within a few years.

Then, in 1959, doctors began using the powerful antibiotic methicillin. But within two years, methicillin-resistant strains of *S. aureus* appeared. How did these resistant strains emerge? Methicillin works by deactivating a protein that bacteria use to synthesize their cell walls. However, different *S. aureus* populations exhibited variations in how strongly their members were affected by the drug. In particular, some individuals were able to synthesize their cell walls using a different protein that was not affected by methicillin. These individuals survived the methicillin treatments and



- (a) Most MRSA infections are caused by recently appearing strains such as clone USA300. Resistant to multiple antibiotics and highly contagious, this strain and its close relatives can cause lethal infections of the skin, lungs, and blood. As shown here, researchers have identified key areas of the USA300 genome that code for adaptations that cause its virulent properties.



- (b) MRSA infections severe enough to result in hospital admission have proliferated greatly in the past few decades.

▲ Figure 22.14 The rise of methicillin-resistant *Staphylococcus aureus* (MRSA).

WHAT IF? Some drugs being developed specifically target and kill *S. aureus*; others slow the growth of MRSA but do not kill it. Based on how natural selection works and on the fact that bacterial species can exchange genes, explain why each of these strategies might be effective.

reproduced at higher rates than did other individuals. Over time, these resistant individuals became increasingly common, leading to the spread of MRSA.

Initially, MRSA could be controlled by antibiotics that work differently from the way methicillin works. But this has become less effective because some MRSA strains

are resistant to multiple antibiotics—probably because bacteria can exchange genes with members of their own and other species. Thus, the multidrug-resistant strains of today may have emerged over time as MRSA strains that were resistant to different antibiotics exchanged genes.

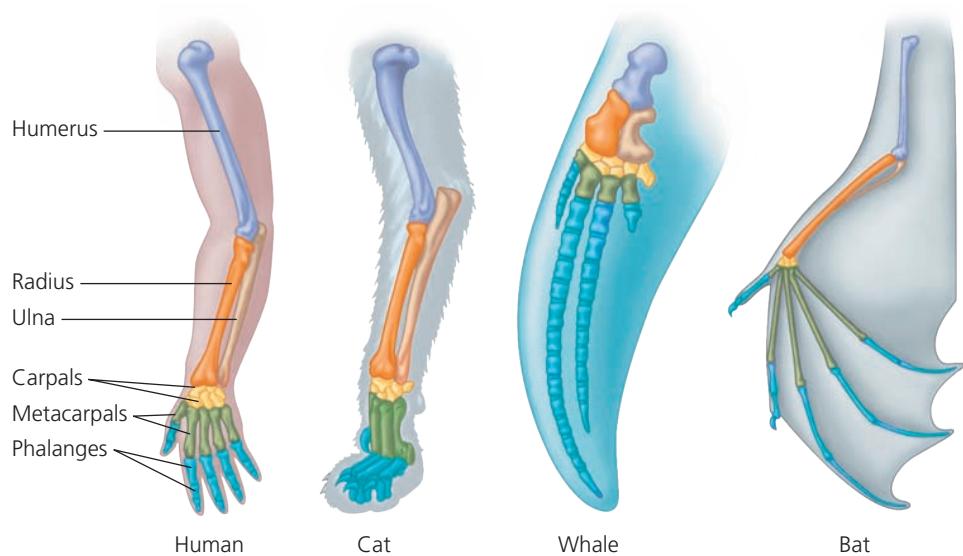
The *S. aureus* and soapberry bug examples highlight two key points about natural selection. First, natural selection is a process of editing, not a creative mechanism. A drug does not *create* resistant pathogens; it *selects for* resistant individuals that are already present in the population. Second, natural selection depends on time and place. It favors those characteristics in a genetically variable population that provide advantage in the current, local environment. What is beneficial in one situation may be useless or even harmful in another. Beak lengths that match the size of the typical fruit eaten by members of a particular soapberry bug population are favored by selection. However, a beak length suitable for fruit of one size can be disadvantageous when the bug is feeding on fruit of another size.

Homology

A second type of evidence for evolution comes from analyzing similarities among different organisms. As we've discussed, evolution is a process of descent with modification: Characteristics present in an ancestral organism are altered (by natural selection) in its descendants over time as they face different environmental conditions. As a result, related species can have characteristics that have an underlying similarity yet function differently. Similarity resulting from common ancestry is known as **homology**. As we'll describe in this section, an understanding of homology can be used to make testable predictions and explain observations that are otherwise puzzling.

Anatomical and Molecular Homologies

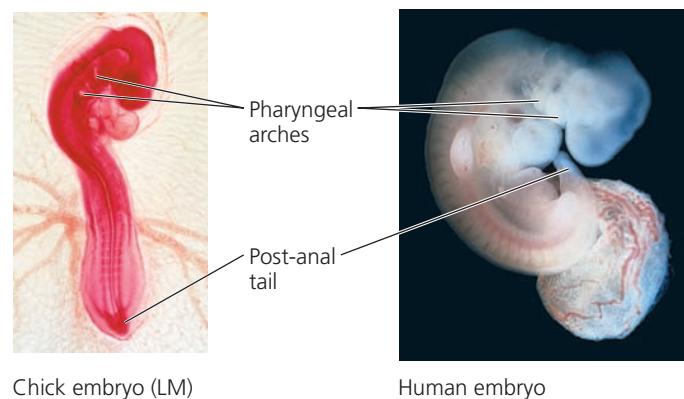
The view of evolution as a remodeling process leads to the prediction that closely related species should share similar features—and they do. Of course, closely related species share the features used to determine their relationship, but they also share many other features. Some of these shared features make little sense except in the context of evolution. For example, the forelimbs of all mammals, including humans, cats, whales, and bats, show the same arrangement of bones from the shoulder to the tips of the digits, even though the appendages have very different functions: lifting,



▲ Figure 22.15 Mammalian forelimbs: homologous structures. Even though they have become adapted for different functions, the forelimbs of all mammals are constructed from the same basic skeletal elements: one large bone (purple), attached to two smaller bones (orange and tan), attached to several small bones (gold), attached to several metacarpals (green), attached to approximately five digits, each of which is composed of phalanges (blue).

walking, swimming, and flying (Figure 22.15). Such striking anatomical resemblances would be highly unlikely if these structures had arisen anew in each species. Rather, the underlying skeletons of the arms, forelegs, flippers, and wings of different mammals are **homologous structures** that represent variations on a structural theme that was present in their common ancestor.

Comparing early stages of development in different animal species reveals additional anatomical homologies not visible in adult organisms. For example, at some point in their development, all vertebrate embryos have a tail located posterior to (behind) the anus, as well as structures called pharyngeal (throat) arches (Figure 22.16). These homologous throat arches ultimately develop into structures with



▲ Figure 22.16 Anatomical similarities in vertebrate embryos. At some stage in their embryonic development, all vertebrates have a tail located posterior to the anus (referred to as a post-anal tail), as well as pharyngeal (throat) arches. Descent from a common ancestor can explain such similarities.

very different functions, such as gills in fishes and parts of the ears and throat in humans and other mammals.

Some of the most intriguing homologies concern “left-over” structures of marginal, if any, importance to the organism. These **vestigial structures** are remnants of features that served a function in the organism’s ancestors. For instance, the skeletons of some snakes retain vestiges of the pelvis and leg bones of walking ancestors. Another example is provided by eye remnants that are buried under scales in blind species of cave fishes. We would not expect to see these vestigial structures if snakes and blind cave fishes had origins separate from other vertebrate animals.

Biologists also observe similarities among organisms at the molecular level. All forms of life use essentially the same genetic code, suggesting that all species descended from common ancestors that used this code. But molecular homologies go beyond a shared code. For example, organisms as dissimilar as humans and bacteria share genes inherited from a very distant common ancestor. Some of these homologous genes have acquired new functions, while others, such as those coding for the ribosomal subunits used in protein synthesis (see Figure 17.17), have retained their original functions. It is also common for organisms to have genes that have lost their function, even though the homologous genes in related species may be fully functional. Like vestigial structures, it appears that such inactive “pseudogenes” may be present simply because a common ancestor had them.

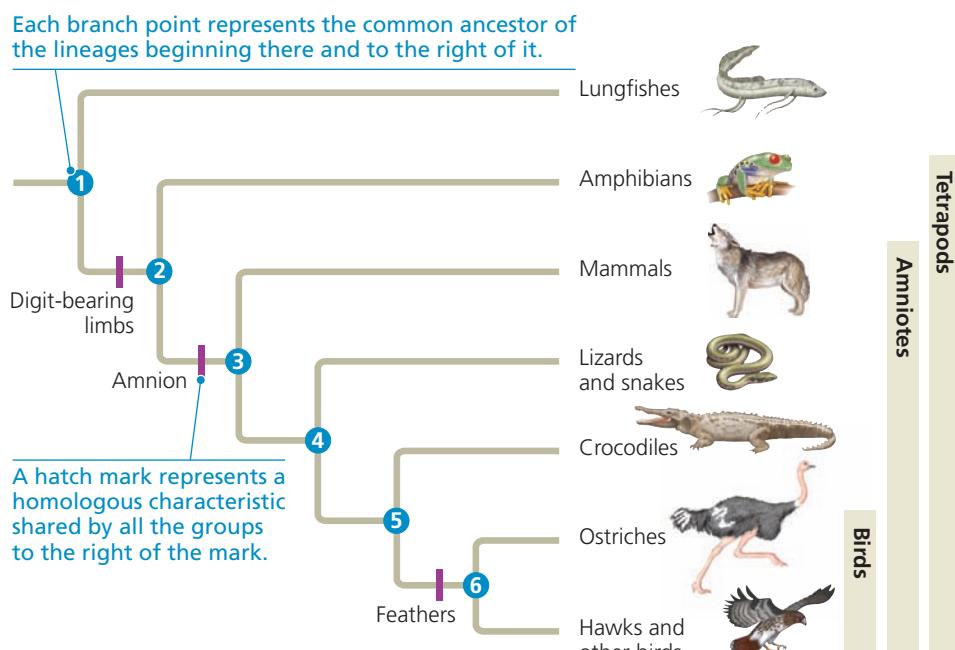
Homologies and “Tree Thinking”

Some homologous characteristics, such as the genetic code, are shared by all species because they date to the deep ancestral past. In contrast, homologous characteristics that evolved more recently are shared only within smaller groups of organisms. Consider the **tetrapods** (from the Greek *tetra*, four, and *pod*, foot), the vertebrate group that consists of amphibians, mammals, and reptiles (including birds—see Figure 22.17). All tetrapods have limbs with digits (see Figure 22.15), whereas other vertebrates do not. Thus, homologous characteristics form a nested pattern: All life shares the deepest layer, and each successive smaller group adds its own homologies to those it shares with larger groups. This nested pattern is exactly what we would expect to result from descent with modification from a common ancestor.

Biologists often represent the pattern of descent from common ancestors with an **evolutionary tree**, a diagram that reflects evolutionary relationships among groups of organisms. We will explore in detail how evolutionary trees are constructed in Chapter 26, but for now, let’s consider how we can interpret and use such trees.

Figure 22.17 is an evolutionary tree of tetrapods and their closest living relatives, the lungfishes. In this diagram, each branch point represents the common ancestor of all species that descended from it. For example, lungfishes and all tetrapods descended from ancestor ①, whereas mammals, lizards and snakes, crocodiles, and birds all descended from ancestor ③. As expected, the three homologies shown on the tree—limbs with digits, the amnion (a protective embryonic membrane), and feathers—form a nested pattern. Limbs with digits were present in common ancestor ② and hence are found in all of the descendants of that ancestor (the tetrapods). The amnion was present only in ancestor ③ and hence is shared only by some tetrapods (mammals and reptiles). Feathers were present only in common ancestor ⑥ and hence are found only in birds.

To explore “tree thinking” further, note that in Figure 22.17, mammals are positioned closer to amphibians than to birds. As a result, you might conclude that mammals are more closely related to amphibians than they are to birds. However, mammals are actually more closely related to birds than to amphibians because mammals and birds share a more recent



▲ Figure 22.17 Tree thinking: information provided in an evolutionary tree. This evolutionary tree for tetrapods and their closest living relatives, the lungfishes, is based on anatomical and DNA sequence data. The purple bars indicate the origin of three important homologies, each of which evolved only once. Birds are nested within and evolved from reptiles; hence, the group of organisms called “reptiles” technically includes birds.

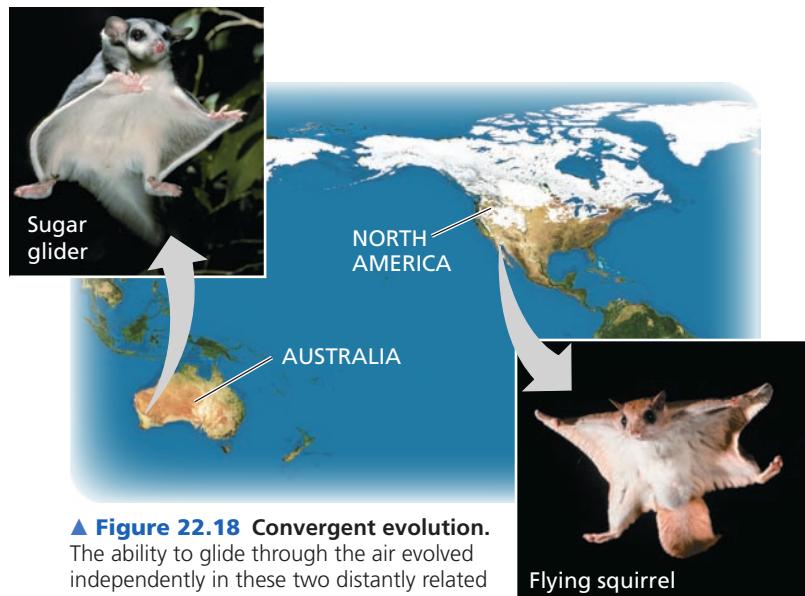
? Are crocodiles more closely related to lizards or birds? Explain your answer.

common ancestor (ancestor ③) than do mammals and amphibians (ancestor ②). Ancestor ② is also the most recent common ancestor of birds and amphibians, making mammals and birds equally related to amphibians. Finally, note that the tree in Figure 22.17 shows the relative timing of events but not their actual dates. Thus, we can conclude that ancestor ② lived before ancestor ③, but we do not know when that was.

Evolutionary trees are hypotheses that summarize our current understanding of patterns of descent. Our confidence in these relationships, as with any hypothesis, depends on the strength of the supporting data. In the case of Figure 22.17, the tree is supported by many different data sets, including both anatomical and DNA sequence data. As a result, biologists are confident that it accurately reflects evolutionary history. Scientists can use such well-supported evolutionary trees to make specific and sometimes surprising predictions about organisms (see Chapter 26).

A Different Cause of Resemblance: Convergent Evolution

Although organisms that are closely related share characteristics because of common descent, distantly related organisms can resemble one another for a different reason: **convergent evolution**, the independent evolution of similar features in different lineages. Consider marsupial mammals, many of which live in Australia. Marsupials are distinct from another group of mammals—the eutherians—few of which live in Australia. (Eutherians complete their embryonic development in the uterus, whereas marsupials are born as embryos and complete their development in an external pouch.) Some Australian marsupials have eutherian look-alikes with superficially similar adaptations. For instance, a forest-dwelling Australian marsupial called the sugar glider is superficially very similar to flying squirrels, gliding eutherians that live in North American forests (**Figure 22.18**). But the sugar glider has many other characteristics that make it a marsupial, much more closely related to kangaroos and other Australian marsupials than to flying squirrels or other eutherians. Once again, our understanding of evolution can explain these observations. Although they evolved independently from different ancestors, these two mammals have adapted to similar environments in similar ways. In such examples in which species share features because of convergent evolution, the resemblance is said to be **analogous**, not homologous. Analogous features share similar function, but not common ancestry, while homologous features share common ancestry, but not necessarily similar function.

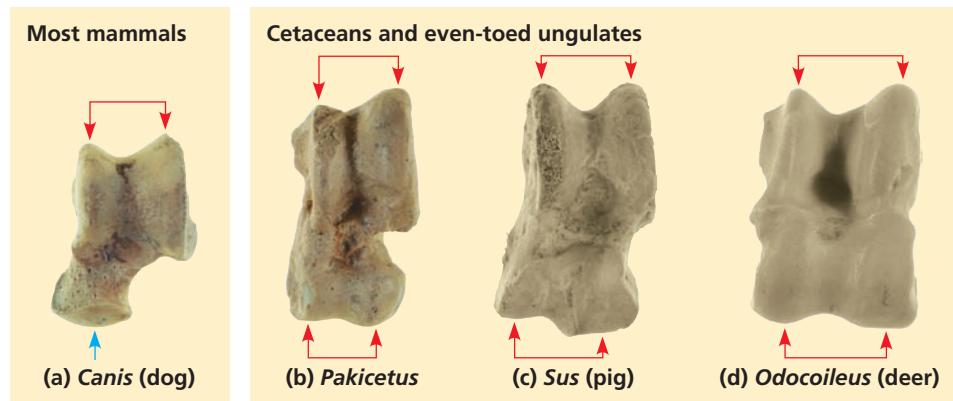


▲ Figure 22.18 Convergent evolution. The ability to glide through the air evolved independently in these two distantly related mammals.

The Fossil Record

A third type of evidence for evolution comes from fossils. The fossil record documents the pattern of evolution, showing that past organisms differed from present-day organisms and that many species have become extinct. Fossils also show the evolutionary changes that have occurred in various groups of organisms. To give one of hundreds of possible examples, researchers found that the pelvic bone in fossil stickleback fish became greatly reduced in size over time in a number of different lakes. The consistent nature of this change suggests that the reduction in the size of the pelvic bone may have been driven by natural selection.

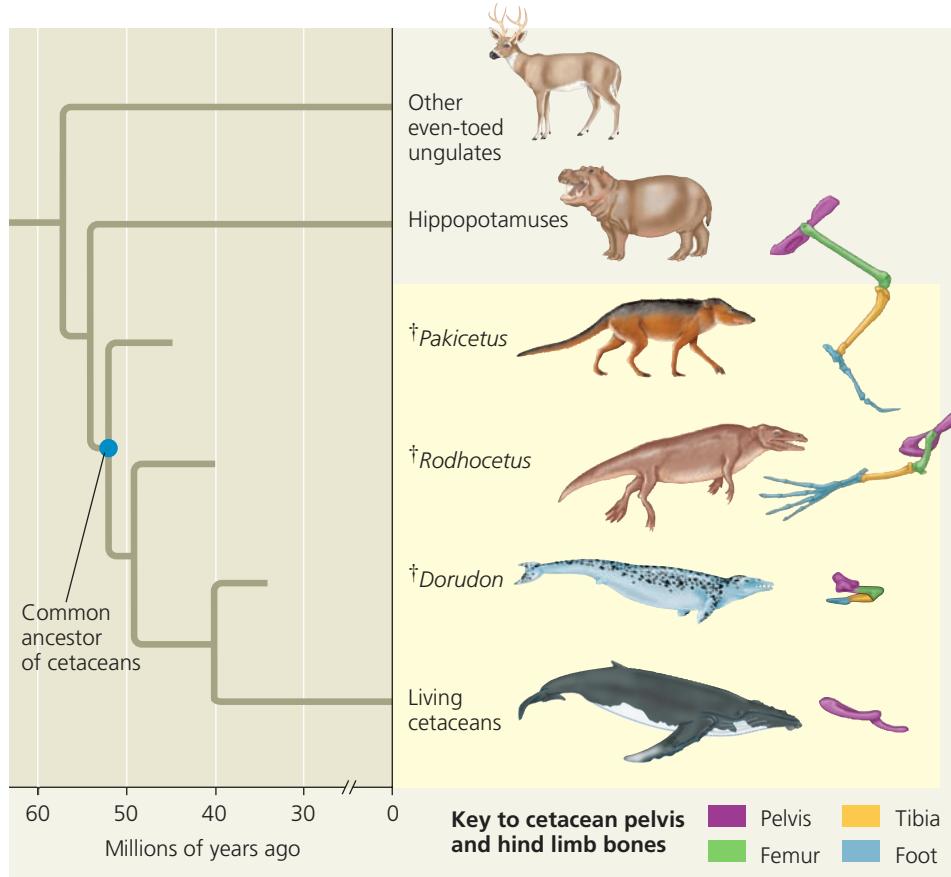
Fossils can also shed light on the origins of new groups of organisms. An example is the fossil record of cetaceans, the mammalian order that includes whales, dolphins, and porpoises. Some of these fossils (**Figure 22.19**) provided an



▲ Figure 22.19 Ankle bones: one piece of the puzzle. Comparing fossils and present-day examples of the astragalus (a type of ankle bone) indicates that cetaceans are closely related to even-toed ungulates. **(a)** In most mammals, the astragalus is shaped like that of a dog, with a double hump on one end (red arrows) but not at the opposite end (blue arrow). **(b)** Fossils show that the early cetacean *Pakicetus* had an astragalus with double humps at both ends, a shape otherwise found only in pigs (**c**), deer (**d**), and all other even-toed ungulates.

unexpected line of support for a hypothesis based on DNA sequence data: that cetaceans are closely related to even-toed ungulates, a group that includes deer, pigs, camels, and cows.

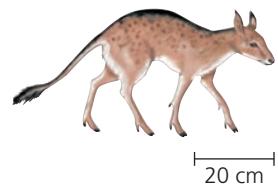
What else can fossils tell us about cetacean origins? The earliest cetaceans lived 50–60 million years ago. The fossil record indicates that prior to that time, most mammals were terrestrial. Although scientists had long realized that whales and other cetaceans originated from land mammals, few fossils had been found that revealed how cetacean limb structure had changed over time, leading eventually to the loss of hind limbs and the development of flippers and tail flukes. In the past few decades, however, a series of remarkable fossils have been discovered in Pakistan, Egypt, and North America. These fossils document steps in the transition from life on land to life in the sea, filling in some of the gaps between ancestral and living cetaceans (**Figure 22.20**).



▲ Figure 22.20 The transition to life in the sea. Cetacean lineages are highlighted in yellow in the above evolutionary tree diagram. Multiple lines of evidence support the hypothesis that cetaceans evolved from terrestrial mammals. Fossils document the reduction over time in the pelvis and hind limb bones of extinct cetacean ancestors, including *Pakicetus*, *Rodhocetus*, and *Dorudon*. DNA sequence data support the hypothesis that cetaceans are most closely related to hippopotamuses.

? Which happened first during the evolution of cetaceans: changes in hind limb structure or the origin of tail flukes? Explain.

Collectively, the recent fossil discoveries document the origin of a major new group of mammals, the cetaceans. These discoveries also show that cetaceans and their close living relatives (hippopotamuses, pigs, and other even-toed ungulates) are much more different from each other than were *Pakicetus* and early even-toed ungulates, such as *Diacodexis*. Similar patterns are seen in fossils documenting the origins of other major new groups of organisms, including mammals (see Chapter 25), flowering plants (see Chapter 30), and tetrapods (see Chapter 34). In each of these cases, the fossil record shows that over time, descent with modification produced increasingly large differences among related groups of organisms, ultimately resulting in the diversity of life we see today.



▲ *Diacodexis*, an early even-toed ungulate

Biogeography

A fourth type of evidence for evolution comes from **biogeography**, the scientific study of the geographic distributions of species. The geographic distributions of organisms are influenced by many factors, including *continental drift*, the slow movement of Earth's continents over time. About 250 million years ago, these movements united all of Earth's landmasses into a single large continent called **Pangaea** (see Figure 25.16). Roughly 200 million years ago, Pangaea began to break apart; by 20 million years ago, the continents we know today were within a few hundred kilometers of their present locations.

We can use our understanding of evolution and continental drift to predict where fossils of different groups of organisms might be found. For example, scientists have constructed evolutionary trees for horses based on anatomical data. These trees and the ages of fossils of horse ancestors suggest that the genus that includes present-day horses (*Equus*) originated 5 million years ago in North America. At that time, North and South America were close to their present locations, but they were not yet connected, making it difficult for horses to travel between them. Thus, we would predict that the oldest *Equus* fossils

should be found only on the continent on which the group originated—North America. This prediction and others like it for different groups of organisms have been upheld, providing more evidence for evolution.

We can also use our understanding of evolution to explain biogeographic data. For example, islands generally have many plant and animal species that are **endemic** (found nowhere else in the world). Yet, as Darwin described in *The Origin of Species*, most island species are closely related to species from the nearest mainland or a neighboring island. He explained this observation by suggesting that islands are colonized by species from the nearest mainland. These colonists eventually give rise to new species as they adapt to their new environments. Such a process also explains why two islands with similar environments in distant parts of the world tend to be populated not by species that are closely related to each other, but rather by species related to those of the nearest mainland, where the environment is often quite different.

SCIENTIFIC SKILLS EXERCISE

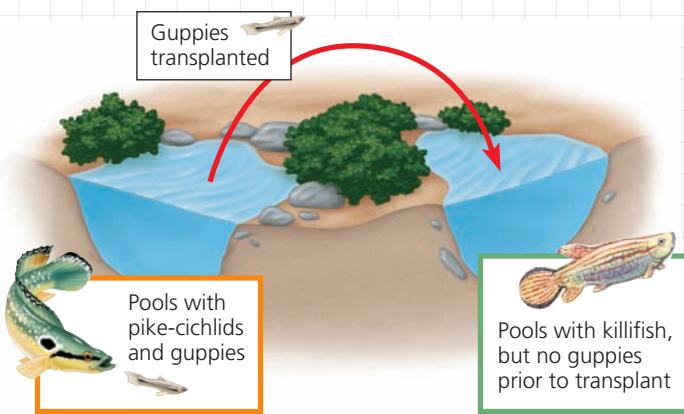
Making and Testing Predictions

Can Predation Result in Natural Selection for Color Patterns in Guppies?

What we know about evolution changes constantly as new observations lead to new hypotheses—and hence to new ways to test our understanding of evolutionary theory. Consider the wild guppies (*Poecilia reticulata*) that live in pools connected by streams on the Caribbean island of Trinidad. Male guppies have highly varied color patterns, which are controlled by genes that are only expressed in adult males. Female guppies choose males with bright color patterns as mates more often than they choose males with drab coloring. But the bright colors that attract females also make the males more conspicuous to predators. Researchers observed that in pools with few predator species, the benefits of bright colors appear to “win out,” and males are more brightly colored than in pools where predation is more intense.

One guppy predator, the killifish, preys on juvenile guppies that have not yet displayed their adult coloration. Researchers predicted that if guppies with drab colors were transferred to a pool with only killifish, eventually the descendants of these guppies would be more brightly colored (because of the female preference for brightly colored males).

How the Experiment Was Done Researchers transplanted 200 guppies from pools containing pike-cichlid fish, intense guppy predators, to



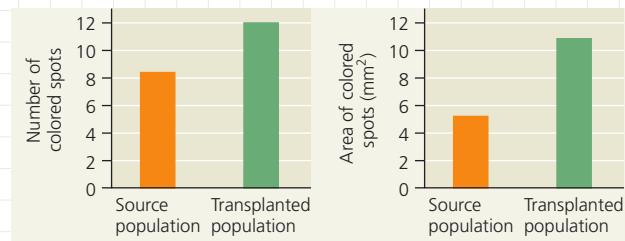
What Is Theoretical About Darwin's View of Life?

Some people dismiss Darwin's ideas as “just a theory.” However, as we have seen, the *pattern* of evolution—the observation that life has evolved over time—has been documented directly and is supported by a great deal of evidence. In addition, Darwin's explanation of the *process* of evolution—that natural selection is the primary cause of the observed pattern of evolutionary change—makes sense of massive amounts of data. The effects of natural selection also can be observed and tested in nature. Once such experiment is described in the **Scientific Skills Exercise**.

What, then, is theoretical about evolution? Keep in mind that the scientific meaning of the term *theory* is very different from its meaning in everyday use. The colloquial use of the word *theory* comes close to what scientists mean by a hypothesis. In science, a theory is more comprehensive

pools containing killifish, less active predators that prey mainly on juvenile guppies. They tracked the number of bright-colored spots and the total area of those spots on male guppies in each generation.

Data from the Experiment After 22 months (15 generations), researchers compared the color pattern data for the source and transplanted populations.



Interpret the Data

- Identify the following elements of hypothesis-based science in this example: (a) question, (b) hypothesis, (c) prediction, (d) control group, and (e) experimental group. (For additional information about hypothesis-based science, see Chapter 1 and the Scientific Skills Review in Appendix F and the Study Area of MasteringBiology.)
- Explain how the types of data the researchers chose to collect enabled them to test their prediction.
- (a) What conclusion would you draw from the data presented above? (b) What additional questions might you ask to determine the strength of this conclusion?
- Predict what would happen if, after 22 months, guppies from the transplanted population were returned to the source pool. Describe an experiment to test your prediction.

MB A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

Data from J. A. Endler, Natural selection on color patterns in *Poecilia reticulata*, *Evolution* 34:76–91 (1980).

than a hypothesis. A theory, such as the theory of evolution by natural selection, accounts for many observations and explains and integrates a great variety of phenomena. Such a unifying theory does not become widely accepted unless its predictions stand up to thorough and continual testing by experiment and additional observation (see Chapter 1). As the rest of this unit demonstrates, this has certainly been the case with the theory of evolution by natural selection.

The skepticism of scientists as they continue to test theories prevents these ideas from becoming dogma. For example, although Darwin thought that evolution was a very slow process, we now know that new species sometimes form in relatively short periods of time: a few thousand years or less (see Chapter 24). Furthermore, evolutionary biologists now recognize that natural selection is not the only mechanism responsible for evolution. Indeed, the study of evolution today is livelier than ever as scientists make new discoveries using a wide range of experimental approaches and genetic analyses; you can read about one such biologist, Dr. Hopi Hoekstra, and her work in the interview before this chapter.

Although Darwin's theory attributes life's diversity to natural processes, the diverse products of evolution are nevertheless elegant and inspiring. As Darwin wrote in the final sentence of *The Origin of Species*, "There is grandeur in this view of life . . . [in which] endless forms most beautiful and most wonderful have been, and are being, evolved."

CONCEPT CHECK 22.3

- Explain how the following statement is inaccurate: "Antibiotics have created drug resistance in MRSA."
- How does evolution account for (a) the similar mammalian forelimbs with different functions shown in Figure 22.15 and (b) the similar forms of the two distantly related mammals shown in Figure 22.18?
- WHAT IF?** Dinosaurs originated 250–200 million years ago. Would you expect the geographic distribution of early dinosaur fossils to be broad (on many continents) or narrow (on one or a few continents only)? Explain.

For suggested answers, see Appendix A.

22 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 22.1

The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species (pp. 463–465)

- Darwin proposed that life's diversity arose from ancestral species through natural selection, a departure from prevailing views.
- Cuvier studied fossils but denied that evolution occurs; he proposed that sudden catastrophic events in the past caused species to disappear from an area.
- Hutton and Lyell thought that geologic change could result from gradual mechanisms that operated in the past in the same manner as they do today.
- Lamarck hypothesized that species evolve, but the underlying mechanisms he proposed are not supported by evidence.

? Why was the age of Earth important for Darwin's ideas about evolution?

CONCEPT 22.2

Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life (pp. 465–470)

- Darwin's experiences during the voyage of the *Beagle* gave rise to his idea that new species originate from ancestral forms through the accumulation of **adaptations**. He refined his theory for many years and finally published it in 1859 after learning that Wallace had come to the same idea.

- In *The Origin of Species*, Darwin proposed that over long periods of time, descent with modification produced the rich diversity of life through the mechanism of **natural selection**.

Observations

Individuals in a population vary in their heritable characteristics.

Organisms produce more offspring than the environment can support.

Inferences

Individuals that are well suited to their environment tend to leave more offspring than other individuals.

and

Over time, favorable traits accumulate in the population.

- ?** Describe how overreproduction and heritable variation relate to evolution by natural selection.

CONCEPT 22.3

Evolution is supported by an overwhelming amount of scientific evidence (pp. 471–478)

- Researchers have directly observed natural selection leading to adaptive evolution in many studies, including research on soapberry bug populations and on MRSA.
- Organisms share characteristics because of common descent (**homology**) or because natural selection affects independently

evolving species in similar environments in similar ways (**convergent evolution**).

- Fossils show that past organisms differed from living organisms, that many species have become extinct, and that species have evolved over long periods of time; fossils also document the origin of major new groups of organisms.
- Evolutionary theory can explain biogeographic patterns.

? Summarize the different lines of evidence supporting the hypothesis that cetaceans descended from land mammals and are closely related to even-toed ungulates.

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Which of the following is *not* an observation or inference on which natural selection is based?
 - a. There is heritable variation among individuals.
 - b. Poorly adapted individuals never produce offspring.
 - c. Species produce more offspring than the environment can support.
 - d. Only a fraction of an individual's offspring may survive.
2. Which of the following observations helped Darwin shape his concept of descent with modification?
 - a. Species diversity declines farther from the equator.
 - b. Fewer species live on islands than on the nearest continents.
 - c. Birds live on islands located farther from the mainland than the birds' maximum nonstop flight distance.
 - d. South American temperate plants are more similar to the tropical plants of South America than to the temperate plants of Europe.

LEVEL 2: APPLICATION/ANALYSIS

3. Within six months of effectively using methicillin to treat *S. aureus* infections in a community, all new *S. aureus* infections were caused by MRSA. How can this best be explained?
 - a. A patient must have become infected with MRSA from another community.
 - b. In response to the drug, *S. aureus* began making drug-resistant versions of the protein targeted by the drug.
 - c. Some drug-resistant bacteria were present at the start of treatment, and natural selection increased their frequency.
 - d. *S. aureus* evolved to resist vaccines.
4. The upper forelimbs of humans and bats have fairly similar skeletal structures, whereas the corresponding bones in whales have very different shapes and proportions. However, genetic data suggest that all three kinds of organisms diverged from a common ancestor at about the same time. Which of the following is the most likely explanation for these data?
 - a. Forelimb evolution was adaptive in people and bats, but not in whales.
 - b. Natural selection in an aquatic environment resulted in significant changes to whale forelimb anatomy.
 - c. Genes mutate faster in whales than in humans or bats.
 - d. Whales are not properly classified as mammals.
5. DNA sequences in many human genes are very similar to the sequences of corresponding genes in chimpanzees. The most likely explanation for this result is that
 - a. humans and chimpanzees share a relatively recent common ancestor.
 - b. humans evolved from chimpanzees.
 - c. chimpanzees evolved from humans.
 - d. convergent evolution led to the DNA similarities.

LEVEL 3: SYNTHESIS/EVALUATION

6. EVOLUTION CONNECTION

Explain why anatomical and molecular features often fit a similar nested pattern. In addition, describe a process that can cause this not to be the case.

7. SCIENTIFIC INQUIRY

DRAW IT Mosquitoes resistant to the pesticide DDT first appeared in India in 1959, but now are found throughout the world. (a) Graph the data in the table below. (b) Examining the graph, hypothesize why the percentage of mosquitoes resistant to DDT rose rapidly. (c) Suggest an explanation for the global spread of DDT resistance.

Month	0	8	12
Mosquitoes Resistant* to DDT	4%	45%	77%

Source: C. F. Curtis et al., Selection for and against insecticide resistance and possible methods of inhibiting the evolution of resistance in mosquitoes, *Ecological Entomology* 3:273–287 (1978).

*Mosquitoes were considered resistant if they were not killed within 1 hour of receiving a dose of 4% DDT.

8. WRITE ABOUT A THEME: INTERACTIONS

Write a short essay (about 100–150 words) evaluating whether changes to an organism's physical environment are likely to result in evolutionary change. Use an example to support your reasoning.

9. SYNTHESIZE YOUR KNOWLEDGE



This honeypot ant (genus *Myrmecocystus*) can store liquid food inside its expandable abdomen. Consider other ants you are familiar with, and explain how a honeypot ant exemplifies three key features of life: adaptation, unity, and diversity.

For selected answers, see Appendix A.

MasteringBiology®

Students Go to **MasteringBiology** for assignments, the eText, and the Study Area with practice tests, animations, and activities.

Instructors Go to **MasteringBiology** for automatically graded tutorials and questions that you can assign to your students, plus Instructor Resources.

23

The Evolution of Populations



KEY CONCEPTS

- 23.1 Genetic variation makes evolution possible
- 23.2 The Hardy-Weinberg equation can be used to test whether a population is evolving
- 23.3 Natural selection, genetic drift, and gene flow can alter allele frequencies in a population
- 23.4 Natural selection is the only mechanism that consistently causes adaptive evolution

▲ **Figure 23.1** Is this finch evolving?

The Smallest Unit of Evolution

One common misconception about evolution is that individual organisms evolve. It is true that natural selection acts on individuals: Each organism's traits affect its survival and reproductive success compared with those of other individuals. But the evolutionary impact of natural selection is only apparent in the changes in a *population* of organisms over time.

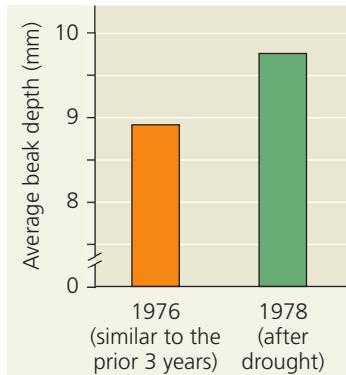
Consider the medium ground finch (*Geospiza fortis*), a seed-eating bird that inhabits the Galápagos Islands (Figure 23.1). In 1977, the *G. fortis* population on the island of Daphne Major was decimated by a long period of drought: Of some 1,200 birds, only 180 survived. Researchers Peter and Rosemary Grant observed that during the drought, small, soft seeds were in short supply. The finches mostly fed on large, hard seeds that were more plentiful. Birds with larger, deeper beaks were better able to crack and eat these larger seeds, and they survived at a higher rate than finches with smaller beaks. Since beak depth is an inherited trait in these birds, the average beak depth in the next generation of *G. fortis* was greater than it had been in the pre-drought population (Figure 23.2). The finch population had evolved by natural selection. However, the *individual* finches did not evolve. Each bird had a beak of a particular size, which did not grow larger during the drought. Rather, the proportion of large beaks in the population increased from generation to generation: The population evolved, not its individual members.



► **Figure 23.2 Evidence of selection by food source.**

The data represent adult beak depth measurements of medium ground finches hatched in the generations before and after the 1977 drought. In one generation, natural selection resulted in a larger average beak size in the population.

 A related Experimental Inquiry Tutorial can be assigned in MasteringBiology.



Focusing on evolutionary change in populations, we can define evolution on its smallest scale, called **microevolution**, as a change in allele frequencies in a population over generations. As you will see in this chapter, natural selection is not the only cause of microevolution. In fact, there are three main mechanisms that can cause allele frequency change: natural selection, genetic drift (chance events that alter allele frequencies), and gene flow (the transfer of alleles between populations). Each of these mechanisms has distinctive effects on the genetic composition of populations. However, only natural selection consistently improves the match between organisms and their environment (adaptation). Before we examine natural selection and adaptation more closely, let's revisit a prerequisite for these processes in a population: genetic variation.

CONCEPT 23.1

Genetic variation makes evolution possible

In *The Origin of Species*, Darwin provided abundant evidence that life on Earth has evolved over time, and he proposed natural selection as the primary mechanism for that change. He observed that individuals differ in their inherited traits and that selection acts on such differences, leading to evolutionary change. Although Darwin realized that variation in heritable traits is a prerequisite for evolution, he did not know precisely how organisms pass heritable traits to their offspring.

Just a few years after Darwin published *The Origin of Species*, Gregor Mendel wrote a groundbreaking paper on inheritance in pea plants (see Chapter 14). In that paper, Mendel proposed a model of inheritance in which organisms transmit discrete heritable units (now called genes) to their offspring. Although Darwin did not know about genes, Mendel's paper set the stage for understanding the genetic differences on which evolution is based. Here we'll examine such genetic differences and how they are produced.



▲ **Figure 23.3 Phenotypic variation in horses.** In horses, coat color varies along a continuum and is influenced by multiple genes.

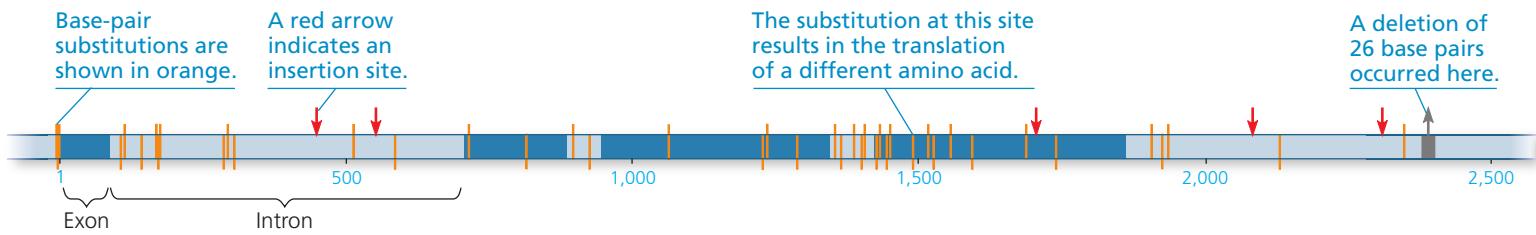
Genetic Variation

Individuals within a species vary in their specific characteristics. Among humans, you can easily observe phenotypic variation in facial features, height, and voice. Indeed, individual variation occurs in all species. And though you cannot identify a person's blood group (A, B, AB, or O) from his or her appearance, this and many other molecular traits also vary extensively among individuals.

Such phenotypic variations often reflect **genetic variation**, differences among individuals in the composition of their genes or other DNA sequences. Some heritable phenotypic differences occur on an "either-or" basis, such as the flower colors of Mendel's pea plants: Each plant had flowers that were either purple or white (see Figure 14.3). Characters that vary in this way are typically determined by a single gene locus, with different alleles producing distinct phenotypes. In contrast, other phenotypic differences vary in gradations along a continuum. Such variation usually results from the influence of two or more genes on a single phenotypic character. In fact, many phenotypic characters are influenced by multiple genes, including coat color in horses (**Figure 23.3**), seed number in maize (corn), and height in humans.

How much do genes and other DNA sequences vary from one individual to another? Genetic variation at the whole-gene level (*gene variability*) can be quantified as the average percentage of loci that are heterozygous. (Recall that a heterozygous individual has two different alleles for a given locus, whereas a homozygous individual has two identical alleles for that locus.) As an example, on average the fruit fly *Drosophila melanogaster* is heterozygous for about 1,920 of its 13,700 loci (14%) and homozygous for all the rest.

Considerable genetic variation can also be measured at the molecular level of DNA (*nucleotide variability*). But little of this variation results in phenotypic variation. The reason is that many of the differences occur within *introns*, noncoding segments of DNA lying between *exons*, the regions retained



▲ Figure 23.4 Extensive genetic variation at the molecular level. This diagram summarizes data from a study comparing the DNA sequence of the alcohol dehydrogenase (*Adh*) gene in several fruit flies (*Drosophila melanogaster*). The *Adh* gene has four exons (dark blue) separated by introns (light blue);

the exons include the coding regions that are ultimately translated into the amino acids of the *Adh* enzyme (see Figure 5.1). Only one substitution has a phenotypic effect, producing a different form of the *Adh* enzyme.

MAKE CONNECTIONS Review Figures 17.5 and 17.10. Explain how a base-pair substitution that alters a coding region of the *Adh* locus could have no effect on amino acid sequence. Then explain how an insertion in an exon could have no effect on the protein produced.

in mRNA after RNA processing (see Figure 17.11). And of the variations that occur within exons, most do not cause a change in the amino acid sequence of the protein encoded by the gene. For example, in the sequence comparison shown in **Figure 23.4**, there are 43 nucleotide sites with variable base pairs (where substitutions have occurred), as well as several sites where insertions or deletions have occurred. Although 18 variable sites occur within the four exons of the *Adh* gene, only one of these variations (at site 1,490) results in an amino acid change. Note, however, that this single variable site is enough to cause genetic variation at the level of the gene—and hence two different forms of the *Adh* enzyme are produced.

It is important to bear in mind that some phenotypic variation does not result from genetic differences among individuals (**Figure 23.5** shows a striking example in a caterpillar of the southwestern United States). Phenotype is the product of an inherited genotype and many environmental influences (see Concept 14.3). In a human example, body-builders alter their phenotypes dramatically but do not pass their huge muscles on to the next generation. In general, only the genetically determined part of phenotypic variation can have evolutionary consequences. As such, genetic variation provides the raw material for evolutionary change: Without genetic variation, evolution cannot occur.

Sources of Genetic Variation

The genetic variation on which evolution depends originates when mutation, gene duplication, or other processes produce new alleles and new genes. Genetic variants can be produced rapidly in organisms with short generation times. Sexual reproduction can also result in genetic variation as existing genes are arranged in new ways.

Formation of New Alleles

New alleles can arise by *mutation*, a change in the nucleotide sequence of an organism's DNA. A mutation is like a shot in the dark—we cannot predict accurately which segments of DNA will be altered or how. In multicellular organisms, only mutations in cell lines that produce gametes can be passed to offspring. In plants and fungi, this is not as limiting as it may sound, since many different cell lines can produce gametes. But in most animals, the majority of mutations occur in somatic cells and are not passed to offspring.

A change of as little as one base in a gene—a “point mutation”—can have a significant impact on phenotype, as in sickle-cell disease (see Figure 17.25). Organisms reflect many generations of past selection, and hence their phenotypes tend to be well matched to their environments. As a

result, most new mutations that alter a phenotype are at least slightly harmful. In some cases, natural selection quickly removes such harmful alleles. In diploid organisms, however, harmful alleles that are recessive can be hidden from selection. Indeed, a harmful recessive allele can persist for generations by propagation in heterozygous individuals (where its harmful effects are masked by the more favorable dominant allele). Such “heterozygote protection” maintains a huge pool of alleles that might not be favored under present conditions, but that could be beneficial if the environment changes.



▲ Figure 23.5 Nonheritable variation. These caterpillars of the moth *Nemoria arizonaria* owe their different appearances to chemicals in their diets, not to differences in their genotypes. (a) Caterpillars raised on a diet of oak flowers resemble the flowers, whereas (b) their siblings raised on oak leaves resemble oak twigs.

While many mutations are harmful, many others are not. Recall that much of the DNA in eukaryotic genomes does not encode proteins (see Figure 21.6). Point mutations in these noncoding regions generally result in **neutral variation**, differences in DNA sequence that do not confer a selective advantage or disadvantage. The redundancy in the genetic code is another source of neutral variation: even a point mutation in a gene that encodes a protein will have no effect on the protein's function if the amino acid composition is not changed. And even where there is a change in the amino acid, it may not affect the protein's shape and function. Finally, as you will see later in this chapter, a mutant allele may on rare occasions actually make its bearer better suited to the environment, enhancing reproductive success.

Altering Gene Number or Position

Chromosomal changes that delete, disrupt, or rearrange many loci are usually harmful. However, when such large-scale changes leave genes intact, they may not affect the organisms' phenotype. In rare cases, chromosomal rearrangements may even be beneficial. For example, the translocation of part of one chromosome to a different chromosome could link genes in a way that produces a positive effect.

A key potential source of variation is the duplication of genes due to errors in meiosis (such as unequal crossing over), slippage during DNA replication, or the activities of transposable elements (see Concept 21.5). Duplications of large chromosome segments, like other chromosomal aberrations, are often harmful, but the duplication of smaller pieces of DNA may not be. Gene duplications that do not have severe effects can persist over generations, allowing mutations to accumulate. The result is an expanded genome with new genes that may take on new functions.

Such increases in gene number appear to have played a major role in evolution. For example, the remote ancestors of mammals had a single gene for detecting odors that has since been duplicated many times. As a result, humans today have about 350 functional olfactory receptor genes, and mice have 1,000. This dramatic proliferation of olfactory genes probably helped early mammals, enabling them to detect faint odors and to distinguish among many different smells.

Rapid Reproduction

Mutation rates tend to be low in plants and animals, averaging about one mutation in every 100,000 genes per generation, and they are often even lower in prokaryotes. But prokaryotes have many more generations per unit of time, so mutations can quickly generate genetic variation in their populations. The same is true of viruses. For instance, HIV has a generation span of about two days. It also has an RNA genome, which has a much higher mutation rate than a typical DNA genome because of the lack of RNA repair mechanisms in host cells (see Chapter 19). For this reason,

single-drug treatments are unlikely to be effective against HIV; mutant forms of the virus that are resistant to a particular drug would tend to proliferate in relatively short order. The most effective AIDS treatments to date have been drug "cocktails" that combine several medications. It is less likely that a set of mutations that together confer resistance to *all* the drugs will occur in a short time period.

Sexual Reproduction

In organisms that reproduce sexually, most of the genetic variation in a population results from the unique combination of alleles that each individual receives from its parents. Of course, at the nucleotide level, all the differences among these alleles have originated from past mutations. Sexual reproduction then shuffles existing alleles and deals them at random to produce individual genotypes.

Three mechanisms contribute to this shuffling: crossing over, independent assortment of chromosomes, and fertilization (see Chapter 13). During meiosis, homologous chromosomes, one inherited from each parent, trade some of their alleles by crossing over. These homologous chromosomes and the alleles they carry are then distributed at random into gametes. Then, because myriad possible mating combinations exist in a population, fertilization brings together gametes that are likely to have different genetic backgrounds. The combined effects of these three mechanisms ensure that sexual reproduction rearranges existing alleles into fresh combinations each generation, providing much of the genetic variation that makes evolution possible.

CONCEPT CHECK 23.1

1. Explain why genetic variation within a population is a prerequisite for evolution.
2. Of all the mutations that occur in a population, why do only a small fraction become widespread?
3. **MAKE CONNECTIONS** If a population stopped reproducing sexually (but still reproduced asexually), how would its genetic variation be affected over time? Explain. (See Concept 13.4.)

For suggested answers, see Appendix A.

CONCEPT 23.2

The Hardy-Weinberg equation can be used to test whether a population is evolving

Although the individuals in a population must differ genetically for evolution to occur, the presence of genetic variation does not guarantee that a population will evolve. For that to happen, one of the factors that cause evolution must be at work. In this section, we'll explore one way to test whether

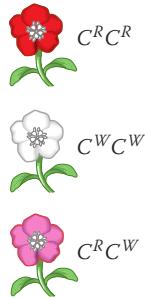
evolution is occurring in a population. First, let's clarify what we mean by a population.

Gene Pools and Allele Frequencies

A **population** is a group of individuals of the same species that live in the same area and interbreed, producing fertile offspring. Different populations of a species may be isolated geographically from one another, exchanging genetic material only rarely. Such isolation is common for species that live on widely separated islands or in different lakes. But not all populations are isolated (**Figure 23.6**). Still, members of a population typically breed with one another and thus on average are more closely related to each other than to members of other populations.

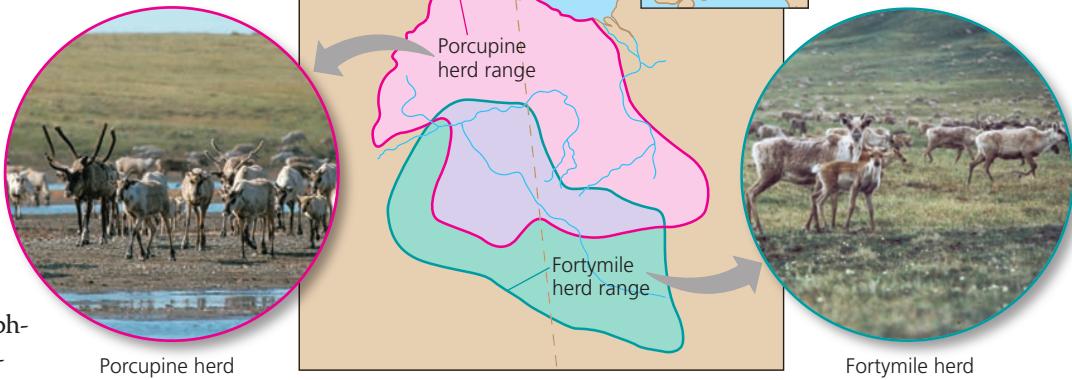
We can characterize a population's genetic makeup by describing its **gene pool**, which consists of all copies of every type of allele at every locus in all members of the population. If only one allele exists for a particular locus in a population, that allele is said to be *fixed* in the gene pool, and all individuals are homozygous for that allele. But if there are two or more alleles for a particular locus in a population, individuals may be either homozygous or heterozygous.

For example, imagine a population of 500 wildflower plants with two alleles, C^R and C^W , for a locus that codes for flower pigment. These alleles show incomplete dominance; thus, each genotype has a distinct phenotype. Plants homozygous for the C^R allele ($C^R C^R$) produce red pigment and have red flowers; plants homozygous for the C^W allele ($C^W C^W$) produce no red pigment and have white flowers; and heterozygotes ($C^R C^W$) produce some red pigment and have pink flowers.



Each allele has a frequency (proportion) in the population. For example, suppose our population has 320 plants with red flowers, 160 with pink flowers, and 20 with white flowers. Because these are diploid organisms, these 500 individuals have a total of 1,000 copies of the gene for flower color. The C^R allele accounts for 800 of these copies ($320 \times 2 = 640$ for $C^R C^R$ plants, plus $160 \times 1 = 160$ for $C^R C^W$ plants). Thus, the frequency of the C^R allele is $800/1,000 = 0.8$ (80%).

When studying a locus with two alleles, the convention is to use p to represent the frequency of one allele and q to represent the frequency of the other allele. Thus, p , the frequency of the C^R allele in the gene pool of this population, is $p = 0.8$ (80%). And because there are only two alleles for this gene, the frequency of the C^W allele, represented by q , must be $q = 1 - p = 0.2$ (20%). For loci that have more than two alleles, the sum of all allele frequencies must still equal 1 (100%).



▲ Figure 23.6 One species, two populations. These two caribou populations in the Yukon are not totally isolated; they sometimes share the same area. Still, members of either population are most likely to breed within their own population.

Next we'll see how allele and genotype frequencies can be used to test whether evolution is occurring in a population.

The Hardy-Weinberg Equation

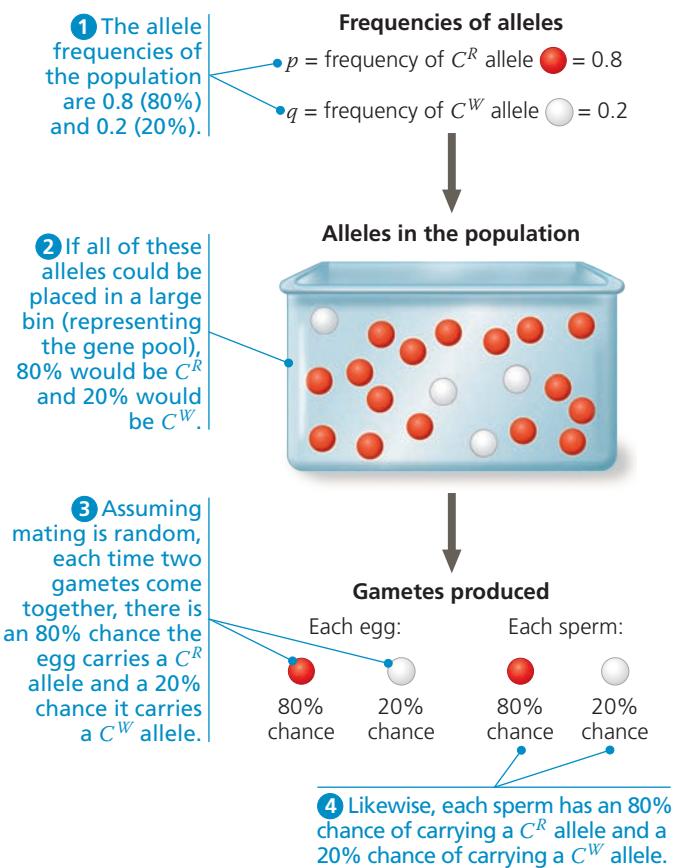
One way to assess whether natural selection or other factors are causing evolution at a particular locus is to determine what the genetic makeup of a population would be if it were *not* evolving at that locus. We can then compare that scenario with the data we actually observed for the population. If there are no differences, we can conclude that the population is not evolving. If there are differences, this suggests that the population may be evolving—and then we can try to figure out why.

Hardy-Weinberg Equilibrium

In a population that is not evolving, allele and genotype frequencies will remain constant from generation to generation, provided that only Mendelian segregation and recombination of alleles are at work. Such a population is said to be in **Hardy-Weinberg equilibrium**, named for the British mathematician and German physician, respectively, who independently developed this idea in 1908.

To determine whether a population is in Hardy-Weinberg equilibrium, it is helpful to think about genetic crosses in a new way. Previously, we used Punnett squares to determine the genotypes of offspring in a genetic cross (see Figure 14.5). Here, instead of considering the possible allele combinations from one cross, we'll consider the combination of alleles in *all* of the crosses in a population.

Imagine that all the alleles for a given locus from all the individuals in a population are placed in a large bin (**Figure 23.7**). We can think of this bin as holding the population's gene pool for that locus. "Reproduction" occurs by selecting alleles at random from the bin; somewhat similar events occur in nature when fish release sperm and eggs into the water or when pollen (containing plant

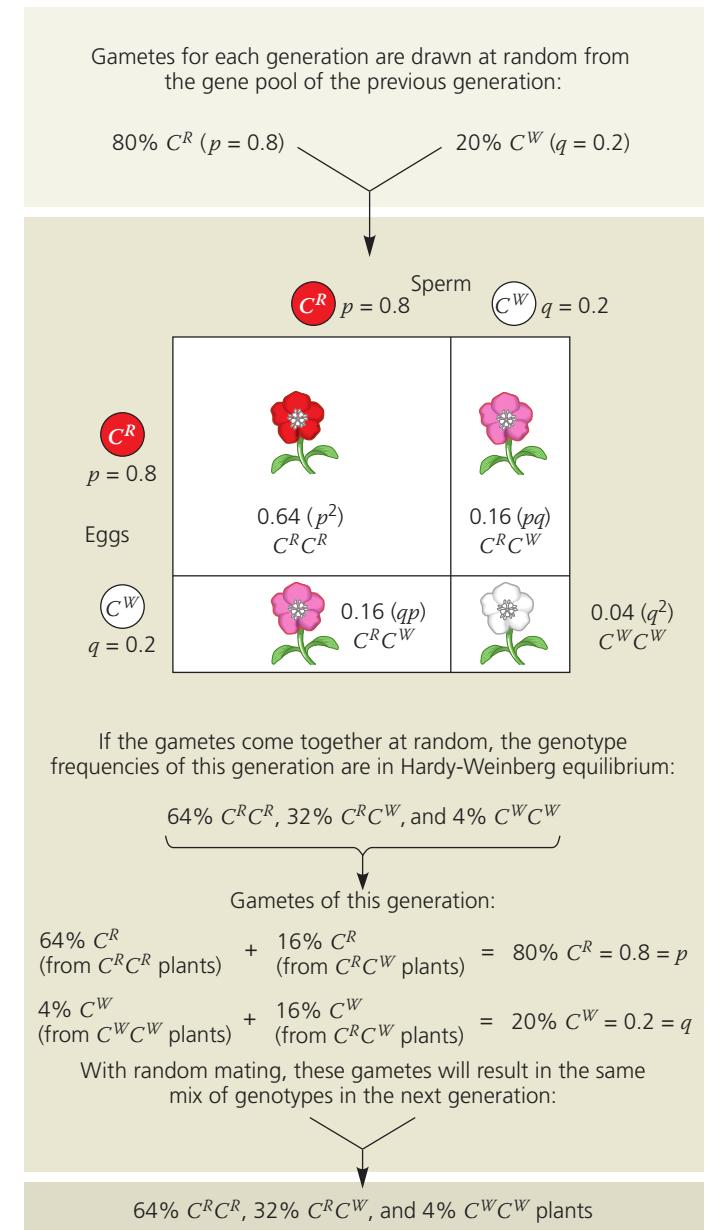


▲ **Figure 23.7** Selecting alleles at random from a gene pool.

sperm) is blown about by the wind. By viewing reproduction as a process of randomly selecting and combining alleles from the bin (the gene pool), we are in effect assuming that mating occurs at random—that is, that all male-female matings are equally likely.

Let's apply the bin analogy to the hypothetical wild-flower population discussed earlier. In that population of 500 flowers, the frequency of the allele for red flowers (C^R) is $p = 0.8$, and the frequency of the allele for white flowers (C^W) is $q = 0.2$. In other words, a bin holding all 1,000 copies of the flower-color gene in the population would contain 800 C^R alleles and 200 C^W alleles. Assuming that gametes are formed by selecting alleles at random from the bin, the probability that an egg or sperm contains a C^R or C^W allele is equal to the frequency of these alleles in the bin. Thus, as shown in Figure 23.7, each egg has an 80% chance of containing a C^R allele and a 20% chance of containing a C^W allele; the same is true for each sperm.

Using the rule of multiplication (see Figure 14.9), we can now calculate the frequencies of the three possible genotypes, assuming random unions of sperm and eggs. The probability that two C^R alleles will come together is $p \times p = p^2 = 0.8 \times 0.8 = 0.64$. Thus, about 64% of the plants in the next generation will have the genotype $C^R C^R$. The frequency of $C^W C^W$ individuals is expected to be $q \times q = q^2 =$



▲ **Figure 23.8** The Hardy-Weinberg principle. In our wildflower population, the gene pool remains constant from one generation to the next. Mendelian processes alone do not alter frequencies of alleles or genotypes.

? If the frequency of the C^R allele is 0.6, predict the frequencies of the $C^R C^R$, $C^R C^W$, and $C^W C^W$ genotypes.

$0.2 \times 0.2 = 0.04$, or 4%. $C^R C^W$ heterozygotes can arise in two different ways. If the sperm provides the C^R allele and the egg provides the C^W allele, the resulting heterozygotes will be $p \times q = 0.8 \times 0.2 = 0.16$, or 16% of the total. If the sperm provides the C^W allele and the egg the C^R allele, the heterozygous offspring will make up $q \times p = 0.2 \times 0.8 = 0.16$, or 16%. The frequency of heterozygotes is thus the sum of these possibilities: $pq + qp = 2pq = 0.16 + 0.16 = 0.32$, or 32%.

As shown in Figure 23.8, the genotype frequencies in the next generation must add up to 1 (100%). Thus, the equation

for Hardy-Weinberg equilibrium states that at a locus with two alleles, the three genotypes will appear in the following proportions:

$$\begin{array}{cccccc} p^2 & + & 2pq & + & q^2 & = 1 \\ \text{Expected} & & \text{Expected} & & \text{Expected} & \\ \text{frequency} & & \text{frequency} & & \text{frequency} & \\ \text{of genotype} & & \text{of genotype} & & \text{of genotype} & \\ C^R C^R & & C^R C^W & & C^W C^W & \end{array}$$

Note that for a locus with two alleles, only three genotypes are possible (in this case, $C^R C^R$, $C^R C^W$, and $C^W C^W$). As a result, the sum of the frequencies of the three genotypes must equal 1 (100%) in *any* population—regardless of whether the population is in Hardy-Weinberg equilibrium. A population is in Hardy-Weinberg equilibrium only if the genotype frequencies are such that the actual frequency of one homozygote is p^2 , the actual frequency of the other homozygote is q^2 , and the actual frequency of heterozygotes is $2pq$. Finally, as suggested by Figure 23.8, if a population such as our wildflowers is in Hardy-Weinberg equilibrium and its members continue to mate randomly generation after generation, allele and genotype frequencies will remain constant. The system operates somewhat like a deck of cards: No matter how many times the deck is reshuffled to deal out new hands, the deck itself remains the same. Aces do not grow more numerous than jacks. And the repeated shuffling of a population's gene pool over the generations cannot, in itself, change the frequency of one allele relative to another.

Conditions for Hardy-Weinberg Equilibrium

The Hardy-Weinberg approach describes a hypothetical population that is not evolving. But in real populations, the allele and genotype frequencies often *do* change over time. Such changes can occur when at least one of the following five conditions of Hardy-Weinberg equilibrium is not met:

- No mutations.** The gene pool is modified if mutations alter alleles or if entire genes are deleted or duplicated.
- Random mating.** If individuals tend to mate within a subset of the population, such as their near neighbors or close relatives (inbreeding), random mixing of gametes does not occur, and genotype frequencies change.
- No natural selection.** Differences in the survival and reproductive success of individuals carrying different genotypes can alter allele frequencies.
- Extremely large population size.** The smaller the population, the more likely it is that allele frequencies will fluctuate by chance from one generation to the next (a process called genetic drift).
- No gene flow.** By moving alleles into or out of populations, gene flow can alter allele frequencies.

Departure from these conditions usually results in evolutionary change, which, as we've already described, is common in natural populations. But it is also common for natural populations to be in Hardy-Weinberg equilibrium for specific genes. This can occur if selection alters allele frequencies at some loci but not others. In addition, some populations evolve so slowly that the changes in their allele and genotype frequencies are difficult to distinguish from those predicted for a non-evolving population.

Applying the Hardy-Weinberg Equation

The Hardy-Weinberg equation is often used as an initial test of whether evolution is occurring in a population (Concept Check 23.2, question 3 is an example). The equation also has medical applications, such as estimating the percentage of a population carrying the allele for an inherited disease. For example, consider phenylketonuria (PKU), a metabolic disorder that results from homozygosity for a recessive allele and occurs in about one out of every 10,000 babies born in the United States. Left untreated, PKU results in mental disability and other problems. (As described in Concept 14.4, newborns are now tested for PKU, and symptoms can be largely avoided with a diet very low in phenylalanine.)

To apply the Hardy-Weinberg equation, we must assume that no new PKU mutations are being introduced into the population (condition 1) and that people neither choose their mates on the basis of whether or not they carry this gene nor generally mate with close relatives (condition 2). We must also ignore any effects of differential survival and reproductive success among PKU genotypes (condition 3) and assume that there are no effects of genetic drift (condition 4) or of gene flow from other populations into the United States (condition 5). These assumptions are reasonable: The mutation rate for the PKU gene is low, inbreeding and other forms of nonrandom mating are not common in the United States, selection occurs only against the rare homozygotes (and then only if dietary restrictions are not followed), the U.S. population is very large, and populations outside the country have PKU allele frequencies similar to those seen in the United States.

If all these assumptions hold, then the frequency of individuals in the population born with PKU will correspond to q^2 in the Hardy-Weinberg equation (q^2 = frequency of homozygotes). Because the allele is recessive, we must estimate the number of heterozygotes rather than counting them directly as we did with the pink flowers. Since we know there is one PKU occurrence per 10,000 births ($q^2 = 0.0001$), the frequency (q) of the recessive allele for PKU is

$$q = \sqrt{0.0001} = 0.01$$

and the frequency of the dominant allele is

$$p = 1 - q = 1 - 0.01 = 0.99$$

The frequency of carriers, heterozygous people who do not have PKU but may pass the PKU allele to offspring, is

$$2pq = 2 \times 0.99 \times 0.01 = 0.0198$$

(approximately 2% of the U.S. population)

Remember, the assumption of Hardy-Weinberg equilibrium yields an approximation; the real number of carriers may differ. Still, our calculations suggest that harmful recessive alleles at this and other loci can be concealed in a population because they are carried by healthy heterozygotes. The **Scientific Skills Exercise** provides another opportunity for you to apply the Hardy-Weinberg equation to allele data.

CONCEPT CHECK 23.2

1. A population has 700 individuals, 85 of genotype AA, 320 of genotype Aa, and 295 of genotype aa. What are the frequencies of alleles A and a ?
2. The frequency of allele a is 0.45 for a population in Hardy-Weinberg equilibrium. What are the expected frequencies of genotypes AA, Aa, and aa?
3. **WHAT IF?** A locus that affects susceptibility to a degenerative brain disease has two alleles, V and v. In a population, 16 people have genotype VV, 92 have genotype Vv, and 12 have genotype vv. Is this population evolving? Explain.

For suggested answers, see Appendix A.

SCIENTIFIC SKILLS EXERCISE

Using the Hardy-Weinberg Equation to Interpret Data and Make Predictions

Is Evolution Occurring in a Soybean Population? One way to test whether evolution is occurring in a population is to compare the observed genotype frequencies at a locus with those expected for a non-evolving population based on the Hardy-Weinberg equation. In this exercise, you'll test whether a soybean population is evolving at a locus with two alleles, C^G and C^Y , that affect chlorophyll production and hence leaf color.

How the Experiment Was Done Students planted soybean seeds and then counted the number of seedlings of each genotype at day 7 and again at day 21. Seedlings of each genotype could be distinguished visually because the C^G and C^Y alleles show incomplete dominance: $C^G C^G$ seedlings have green leaves, $C^G C^Y$ seedlings have green-yellow leaves, and $C^Y C^Y$ seedlings have yellow leaves.

Data from the Experiment

Time (days)	Number of Seedlings			
	Green ($C^G C^G$)	Green-yellow ($C^G C^Y$)	Yellow ($C^Y C^Y$)	Total
7	49	111	56	216
21	47	106	20	173

Interpret the Data

1. Use the observed genotype frequencies from the day 7 data to calculate the frequencies of the C^G allele (p) and the C^Y allele (q).

CONCEPT 23.3

Natural selection, genetic drift, and gene flow can alter allele frequencies in a population

Note again the five conditions required for a population to be in Hardy-Weinberg equilibrium. A deviation from any of these conditions is a potential cause of evolution. New mutations (violation of condition 1) can alter allele frequencies, but because mutations are rare, the change from one generation to the next is likely to be very small. Non-random mating (violation of condition 2) can affect the frequencies of homozygous and heterozygous genotypes but by itself has no effect on allele frequencies in the gene pool. (Allele frequencies can change if individuals with certain inherited traits are more likely than other individuals to obtain mates. However, such a situation not only causes a deviation from random mating, but also violates condition 3, no natural selection.)

For the rest of this section we will focus on the three mechanisms that alter allele frequencies directly and cause most evolutionary change: natural selection, genetic drift, and gene flow (violations of conditions 3–5).



2. Next, use the Hardy-Weinberg equation ($p^2 + 2pq + q^2 = 1$) to calculate the expected frequencies of genotypes $C^G C^G$, $C^G C^Y$, and $C^Y C^Y$ for a population in Hardy-Weinberg equilibrium.
3. Calculate the observed frequencies of genotypes $C^G C^G$, $C^G C^Y$, and $C^Y C^Y$ at day 7. Compare these frequencies to the expected frequencies calculated in step 2. Is the seedling population in Hardy-Weinberg equilibrium at day 7, or is evolution occurring? Explain your reasoning and identify which genotypes, if any, appear to be selected for or against.
4. Calculate the observed frequencies of genotypes $C^G C^G$, $C^G C^Y$, and $C^Y C^Y$ at day 21. Compare these frequencies to the expected frequencies calculated in step 2 and the observed frequencies at day 7. Is the seedling population in Hardy-Weinberg equilibrium at day 21, or is evolution occurring? Explain your reasoning and identify which genotypes, if any, appear to be selected for or against.
5. Homozygous $C^Y C^Y$ individuals cannot produce chlorophyll. The ability to photosynthesize becomes more critical as seedlings age and begin to exhaust the supply of food that was stored in the seed from which they emerged. Develop a hypothesis that explains the data for days 7 and 21. Based on this hypothesis, predict how the frequencies of the C^G and C^Y alleles will change beyond day 21.



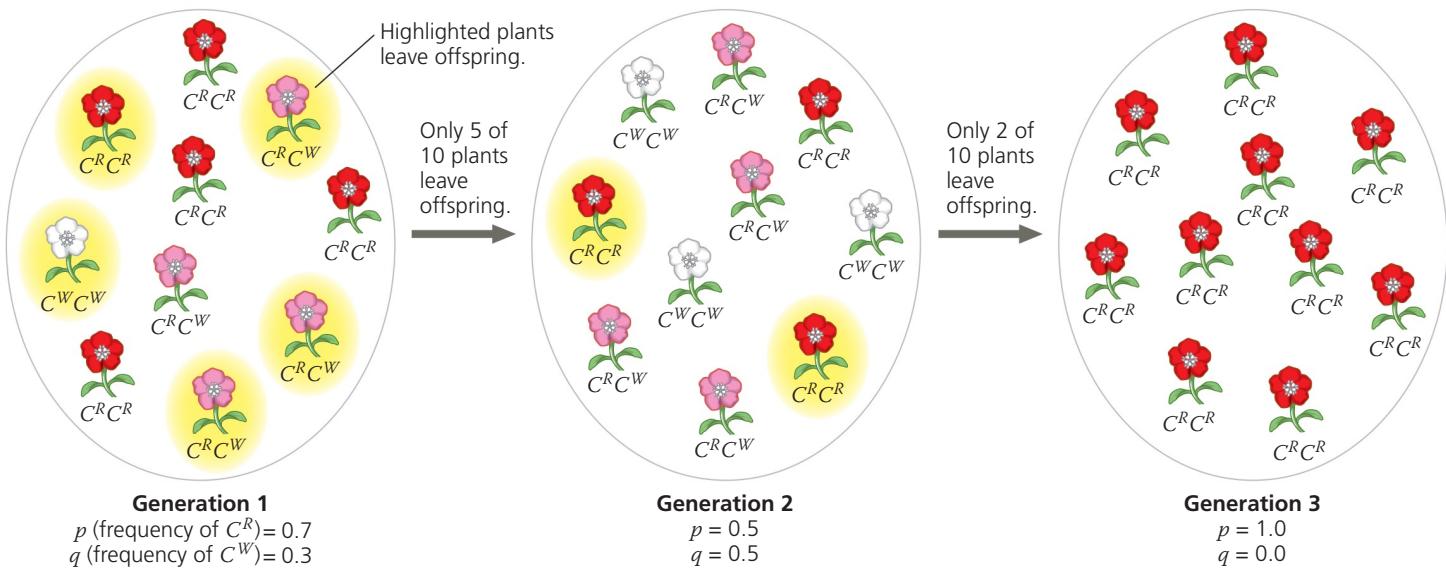
A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

Natural Selection

The concept of natural selection is based on differential success in survival and reproduction: Individuals in a population exhibit variations in their heritable traits, and those with traits that are better suited to their environment tend to produce more offspring than those with traits that are not as well suited (see Chapter 22).

In genetic terms, selection results in alleles being passed to the next generation in proportions that differ from those in the present generation. For example, the fruit fly *D. melanogaster* has an allele that confers resistance to several insecticides, including DDT. This allele has a frequency of 0% in laboratory strains of *D. melanogaster* established from flies collected in the wild in the early 1930s, prior to DDT use. However, in strains established from flies collected after 1960 (following 20 or more years of DDT use), the allele frequency is 37%. We can infer that this allele either arose by mutation between 1930 and 1960 or was present in 1930, but very rare. In any case, the rise in frequency of this allele most likely occurred because DDT is a powerful poison that is a strong selective force in exposed fly populations.

As the *D. melanogaster* example suggests, an allele that confers resistance to an insecticide will increase in frequency in a population exposed to that insecticide. Such changes are not coincidental. By consistently favoring some alleles over others, natural selection can cause **adaptive evolution** (evolution that results in a better match between organisms and their environment). We'll explore this process in more detail later in this chapter.



▲ Figure 23.9 Genetic drift. This small wildflower population has a stable size of ten plants. Suppose that by chance only five plants of generation 1 (those highlighted in yellow) produce fertile offspring. (This could occur, for example, if only those plants happened to grow in a location that provided enough nutrients to support the production of offspring.) Again by chance, only two plants of generation 2 leave fertile offspring. As a result, by chance the frequency of the C^W allele first increases in generation 2, then falls to zero in generation 3.

Genetic Drift

If you flip a coin 1,000 times, a result of 700 heads and 300 tails might make you suspicious about that coin. But if you flip a coin only 10 times, an outcome of 7 heads and 3 tails would not be surprising. The smaller the number of coin flips, the more likely it is that chance alone will cause a deviation from the predicted result. (In this case, the prediction is an equal number of heads and tails.) Chance events can also cause allele frequencies to fluctuate unpredictably from one generation to the next, especially in small populations—a process called **genetic drift**.

Figure 23.9 models how genetic drift might affect a small population of our wildflowers. In this example, drift leads to the loss of an allele from the gene pool, but it is a matter of chance that the C^W allele is lost and not the C^R allele. Such unpredictable changes in allele frequencies can be caused by chance events associated with survival and reproduction. Perhaps a large animal such as a moose stepped on the three $C^W C^W$ individuals in generation 2, killing them and increasing the chance that only the C^R allele would be passed to the next generation. Allele frequencies can also be affected by chance events that occur during fertilization. For example, suppose two individuals of genotype $C^R C^W$ had a small number of offspring. By chance alone, every egg and sperm pair that generated offspring could happen to have carried the C^R allele and not the C^W allele.

Certain circumstances can result in genetic drift having a significant impact on a population. Two examples are the founder effect and the bottleneck effect.

ANIMATION

BioFlix Visit the Study Area in **MasteringBiology** for the BioFlix® 3-D Animation on Mechanisms of Evolution.

The Founder Effect

When a few individuals become isolated from a larger population, this smaller group may establish a new population whose gene pool differs from the source population; this is called the **founder effect**. The founder effect might occur, for example, when a few members of a population are blown by a storm to a new island. Genetic drift, in which chance events alter allele frequencies, will occur in such a case if the storm indiscriminately transports some individuals (and their alleles), but not others, from the source population.

The founder effect probably accounts for the relatively high frequency of certain inherited disorders among isolated human populations. For example, in 1814, 15 British colonists founded a settlement on Tristan da Cunha, a group of small islands in the Atlantic Ocean midway between Africa and South America. Apparently, one of the colonists carried a recessive allele for retinitis pigmentosa, a progressive form of blindness that afflicts homozygous individuals. Of the founding colonists' 240 descendants on the island in the late 1960s, 4 had retinitis pigmentosa. The frequency of the allele that causes this disease is ten times higher on Tristan da Cunha than in the populations from which the founders came.

The Bottleneck Effect

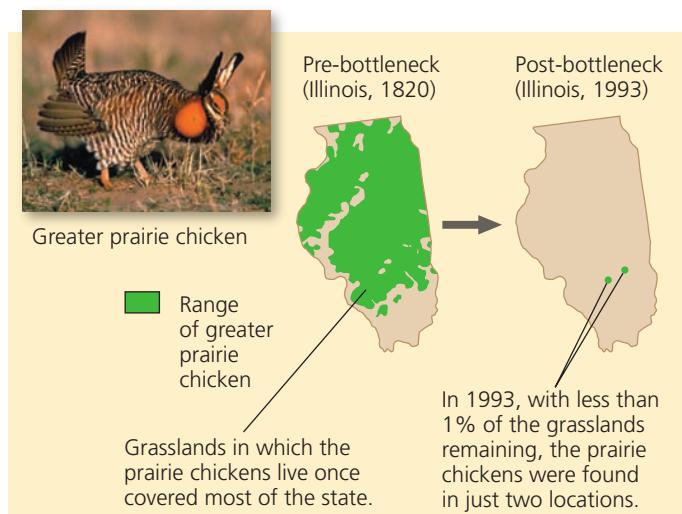
A sudden change in the environment, such as a fire or flood, may drastically reduce the size of a population. A severe drop in population size can cause the **bottleneck effect**, so named because the population has passed through a “bottleneck” that reduces its size (Figure 23.10). By chance alone, certain alleles may be overrepresented among the survivors, others may be underrepresented, and some may be absent altogether. Ongoing genetic drift is likely to have substantial effects on the gene pool until the population becomes large enough that chance events have less impact. But even if a population that has passed through a bottleneck ultimately

recovers in size, it may have low levels of genetic variation for a long period of time—a legacy of the genetic drift that occurred when the population was small.

Human actions sometimes create severe bottlenecks for other species, as the following example shows.

Case Study: Impact of Genetic Drift on the Greater Prairie Chicken

Millions of greater prairie chickens (*Tympanuchus cupido*) once lived on the prairies of Illinois. As these prairies were converted to farmland and other uses during the 19th and 20th centuries, the number of greater prairie chickens plummeted (Figure 23.11a). By 1993 fewer than 50 birds remained. These few surviving birds had low levels of genetic variation, and less than 50% of their eggs hatched, compared with much higher hatching rates of the larger populations in Kansas and Nebraska (Figure 23.11b).

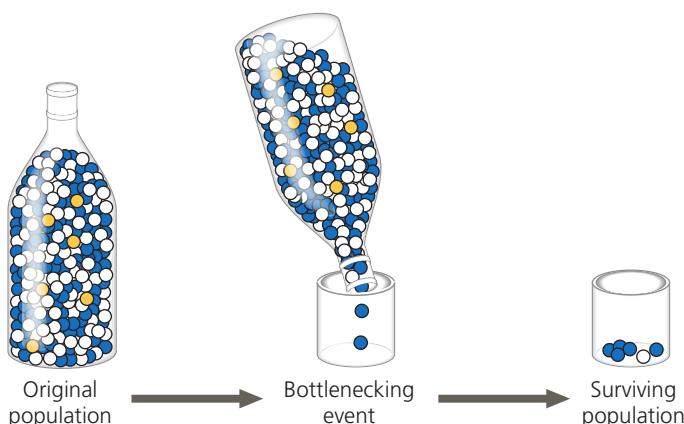


(a) The Illinois population of greater prairie chickens dropped from millions of birds in the 1800s to fewer than 50 birds in 1993.

Location	Population size	Number of alleles per locus	Percentage of eggs hatched
Illinois			
1930–1960s	1,000–25,000	5.2	93
1993	<50	3.7	<50
Kansas, 1998 (no bottleneck)	750,000	5.8	99
Nebraska, 1998 (no bottleneck)	75,000–200,000	5.8	96

(b) In the small Illinois population, genetic drift led to decreases in the number of alleles per locus and the percentage of eggs hatched.

▲ **Figure 23.10** The bottleneck effect. Shaking just a few marbles through the narrow neck of a bottle is analogous to a drastic reduction in the size of a population. By chance, blue marbles are overrepresented in the surviving population and gold marbles are absent.



These data suggest that genetic drift during the bottleneck may have led to a loss of genetic variation and an increase in the frequency of harmful alleles. To investigate this hypothesis, researchers extracted DNA from 15 museum specimens of Illinois greater prairie chickens. Of the 15 birds, 10 had been collected in the 1930s, when there were 25,000 greater prairie chickens in Illinois, and 5 had been collected in the 1960s, when there were 1,000 greater prairie chickens in Illinois. By studying the DNA of these specimens, the researchers were able to obtain a minimum, baseline estimate of how much genetic variation was present in the Illinois population *before* the population shrank to extremely low numbers. This baseline estimate is a key piece of information that is not usually available in cases of population bottlenecks.

The researchers surveyed six loci and found that the 1993 population had fewer alleles per locus than the pre-bottleneck Illinois or the current Kansas and Nebraska populations (see Figure 23.11b). Thus, as predicted, drift had reduced the genetic variation of the small 1993 population. Drift may also have increased the frequency of harmful alleles, leading to the low egg-hatching rate. To counteract these negative effects, 271 birds from neighboring states were added to the Illinois population over four years. This strategy succeeded: New alleles entered the population, and the egg-hatching rate improved to over 90%. Overall, studies on the Illinois greater prairie chicken illustrate the powerful effects of genetic drift in small populations and provide hope that in at least some populations, these effects can be reversed.

Effects of Genetic Drift: A Summary

The examples we've described highlight four key points:

- 1. Genetic drift is significant in small populations.** Chance events can cause an allele to be disproportionately over- or underrepresented in the next generation. Although chance events occur in populations of all sizes, they tend to alter allele frequencies substantially only in small populations.
- 2. Genetic drift can cause allele frequencies to change at random.** Because of genetic drift, an allele may increase in frequency one year, then decrease the next; the change from year to year is not predictable. Thus, unlike natural selection, which in a given environment consistently favors some alleles over others, genetic drift causes allele frequencies to change at random over time.
- 3. Genetic drift can lead to a loss of genetic variation within populations.** By causing allele frequencies to fluctuate randomly over time, genetic drift can eliminate alleles from a population. Because evolution depends on genetic variation, such losses can influence how effectively a population can adapt to a change in the environment.

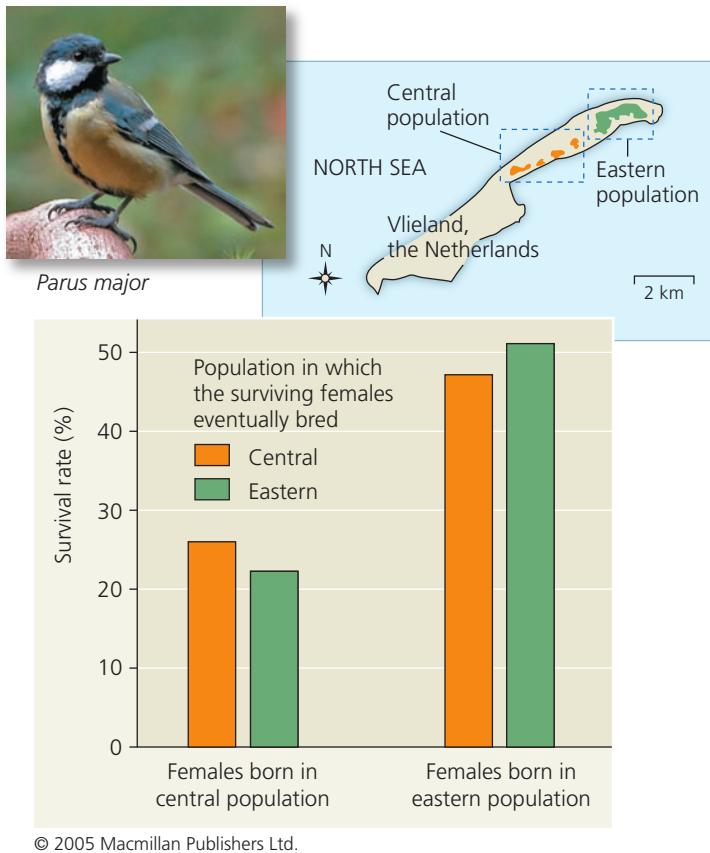
- 4. Genetic drift can cause harmful alleles to become fixed.** Alleles that are neither harmful nor beneficial can be lost or become fixed by chance through genetic drift. In very small populations, genetic drift can also cause alleles that are slightly harmful to become fixed. When this occurs, the population's survival can be threatened (as in the case of the greater prairie chicken).

Gene Flow

Natural selection and genetic drift are not the only phenomena affecting allele frequencies. Allele frequencies can also change by **gene flow**, the transfer of alleles into or out of a population due to the movement of fertile individuals or their gametes. For example, suppose that near our original hypothetical wildflower population there is another population consisting primarily of white-flowered individuals ($C^W C^W$). Insects carrying pollen from these plants may fly to and pollinate plants in our original population. The introduced C^W alleles would modify our original population's allele frequencies in the next generation. Because alleles are transferred between populations, gene flow tends to reduce the genetic differences between populations. In fact, if it is extensive enough, gene flow can result in two populations combining into a single population with a common gene pool.

Alleles transferred by gene flow can also affect how well populations are adapted to local environmental conditions. Researchers studying the songbird *Parus major* (great tit) on the small Dutch island of Vlieland noted survival differences between two populations on the island. The survival rate of females born in the eastern population is twice that of females born in the central population, regardless of where the females eventually settle and raise offspring (Figure 23.12). This finding suggests that females born in the eastern population are better adapted to life on the island than females born in the central population. But field studies also showed that the two populations are connected by high levels of gene flow (mating), which should reduce genetic differences between them. So how can the eastern population be better adapted to life on Vlieland than the central population?

The answer lies in the unequal amounts of gene flow from the mainland. In any given year, 43% of the first-time breeders in the central population are immigrants from the mainland, compared with only 13% in the eastern population. Birds with mainland genotypes survive and reproduce poorly on Vlieland, and in the eastern population, selection reduces the frequency of these genotypes. In the central population, however, gene flow from the mainland is so high that it overwhelms the effects of selection. As a result, females born in the central population have many immigrant genes, reducing the degree to which members of that population are adapted to life on the island. Researchers are currently investigating why gene flow is so much higher in the



▲ Figure 23.12 Gene flow and local adaptation. In *Parus major* populations on Vlieland, the yearly survival rate of females born in the central population is lower than that of females born in the eastern population. Gene flow from the mainland is much higher to the central population than it is to the eastern population, and birds from the mainland are selected against in both populations. These data suggest that gene flow from the mainland has prevented the central population from adapting fully to its local conditions.

central population and why birds with mainland genotypes survive and reproduce poorly on Vlieland.

Gene flow can also transfer alleles that improve the ability of populations to adapt to local conditions. For example, gene flow has resulted in the worldwide spread of several insecticide-resistance alleles in the mosquito *Culex pipiens*, a vector of West Nile virus and other diseases. Each of these alleles has a unique genetic signature that allowed researchers to document that it arose by mutation in only one or a few geographic locations. In their population of origin, these alleles increased because they provided insecticide resistance. These alleles were then transferred to new populations, where again, their frequencies increased as a result of natural selection.

Finally, gene flow has become an increasingly important agent of evolutionary change in human populations. Humans today move much more freely about the world than in the past. As a result, mating is more common between members of populations that previously had very little contact, leading to an exchange of alleles and fewer genetic differences between those populations.

CONCEPT CHECK 23.3

1. In what sense is natural selection more “predictable” than genetic drift?
2. Distinguish genetic drift from gene flow in terms of (a) how they occur and (b) their implications for future genetic variation in a population.
3. **WHAT IF?** Suppose two plant populations exchange pollen and seeds. In one population, individuals of genotype AA are most common (9,000 AA, 900 Aa, 100 aa), while the opposite is true in the other population (100 AA, 900 Aa, 9,000 aa). If neither allele has a selective advantage, what will happen over time to the allele and genotype frequencies of these populations?

For suggested answers, see Appendix A.

CONCEPT 23.4

Natural selection is the only mechanism that consistently causes adaptive evolution

Evolution by natural selection is a blend of chance and “sorting”: chance in the creation of new genetic variations (as in mutation) and sorting as natural selection favors some alleles over others. Because of this favoring process, the outcome of natural selection is *not* random. Instead, natural selection consistently increases the frequencies of alleles that provide reproductive advantage, thus leading to adaptive evolution.

Natural Selection: A Closer Look

In examining how natural selection brings about adaptive evolution, we’ll begin with the concept of relative fitness and the different ways that an organism’s phenotype is subject to natural selection.

Relative Fitness

The phrases “struggle for existence” and “survival of the fittest” are commonly used to describe natural selection, but these expressions are misleading if taken to mean direct competitive contests among individuals. There *are* animal species in which individuals, usually the males, lock horns or otherwise do combat to determine mating privilege. But reproductive success is generally more subtle and depends on many factors besides outright battle. For example, a barnacle that is more efficient at collecting food than its neighbors may have greater stores of energy and hence be able to produce a larger number of eggs. A moth may have more offspring than other moths in the same population because its body colors more effectively conceal it from predators, improving its chance of surviving long enough to produce more offspring. These examples illustrate how in a given

environment, certain traits can lead to greater **relative fitness**: the contribution an individual makes to the gene pool of the next generation *relative to* the contributions of other individuals.

Although we often refer to the relative fitness of a genotype, remember that the entity that is subjected to natural selection is the whole organism, not the underlying genotype. Thus, selection acts more directly on the phenotype than on the genotype; it acts on the genotype indirectly, via how the genotype affects the phenotype.

Directional, Disruptive, and Stabilizing Selection

Natural selection can alter the frequency distribution of heritable traits in three ways, depending on which phenotypes in a population are favored. These three modes of selection are called directional selection, disruptive selection, and stabilizing selection.

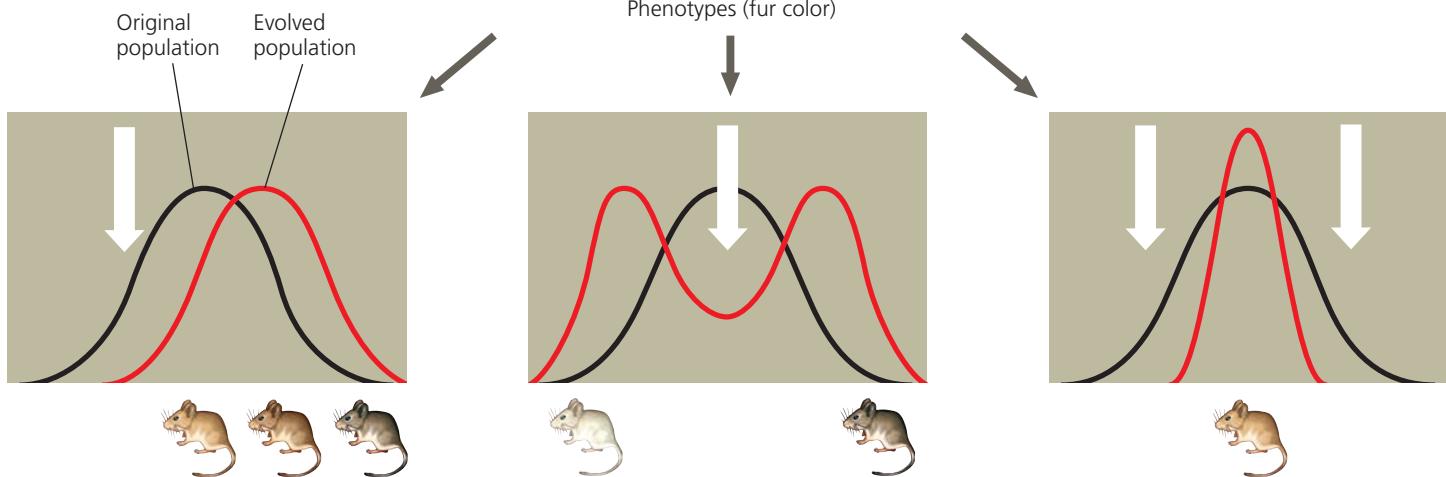
Directional selection occurs when conditions favor individuals exhibiting one extreme of a phenotypic range, thereby shifting a population's frequency curve for the phenotypic character in one direction or the other (**Figure 23.13a**).

► Figure 23.13 Modes of selection.

These cases describe three ways in which a hypothetical deer mouse population with heritable variation in fur coloration from light to dark might evolve. The graphs show how the frequencies of individuals with different fur colors change over time. The large white arrows symbolize selective pressures against certain phenotypes.

MAKE CONNECTIONS Review

Figure 22.13. Which mode of selection has occurred in soapberry bug populations that feed on the introduced goldenrain tree? Explain.



(a) Directional selection shifts the overall makeup of the population by favoring variants that are at one extreme of the distribution. In this case, lighter mice are selected against because they live among dark rocks, making it harder for them to hide from predators.

(b) Disruptive selection favors variants at both ends of the distribution. These mice have colonized a patchy habitat made up of light and dark rocks, with the result that mice of an intermediate color are selected against.

(c) Stabilizing selection removes extreme variants from the population and preserves intermediate types. If the environment consists of rocks of an intermediate color, both light and dark mice will be selected against.

Directional selection is common when a population's environment changes or when members of a population migrate to a new (and different) habitat. For instance, an increase in the relative abundance of large seeds over small seeds led to an increase in beak depth in a population of Galápagos finches (see Figure 23.2).

Disruptive selection (**Figure 23.13b**) occurs when conditions favor individuals at both extremes of a phenotypic range over individuals with intermediate phenotypes. One example is a population of black-bellied seedcracker finches in Cameroon whose members display two distinctly different beak sizes. Small-billed birds feed mainly on soft seeds, whereas large-billed birds specialize in cracking hard seeds. It appears that birds with intermediate-sized bills are relatively inefficient at cracking both types of seeds and thus have lower relative fitness.

Stabilizing selection (**Figure 23.13c**) acts against both extreme phenotypes and favors intermediate variants. This mode of selection reduces variation and tends to maintain the status quo for a particular phenotypic character. For example, the birth weights of most human babies lie in

the range of 3–4 kg (6.6–8.8 pounds); babies who are either much smaller or much larger suffer higher rates of mortality.

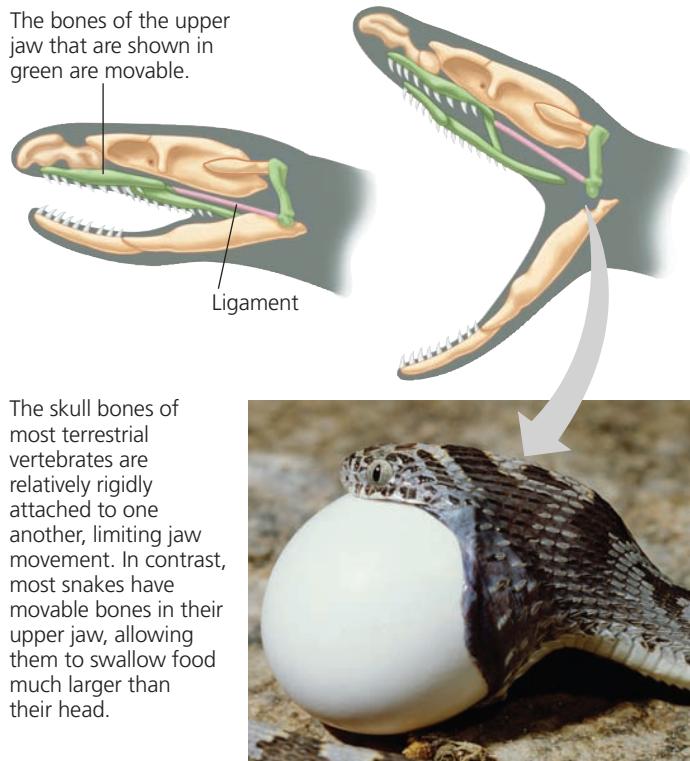
Regardless of the mode of selection, however, the basic mechanism remains the same. Selection favors individuals whose heritable phenotypic traits provide higher reproductive success than do the traits of other individuals.

The Key Role of Natural Selection in Adaptive Evolution

The adaptations of organisms include many striking examples. Certain octopuses, for example, have the ability to change color rapidly, enabling them to blend into different backgrounds. Another example is the remarkable jaws of snakes (Figure 23.14), which allow them to swallow prey much larger than their own head (a feat analogous to a person swallowing a whole watermelon). Other adaptations, such as a version of an enzyme that shows improved function in cold environments, may be less visually dramatic but just as important for survival and reproduction.

Such adaptations can arise gradually over time as natural selection increases the frequencies of alleles that enhance survival and reproduction. As the proportion of individuals that have favorable traits increases, the match between a species and its environment improves; that is, adaptive evolution occurs. However, the physical and biological components of an organism's environment may change over time. As a result, what constitutes a "good match" between an organism and its environment can be a moving target, making adaptive evolution a continuous, dynamic process.

And what about genetic drift and gene flow? Both can, in fact, increase the frequencies of alleles that improve the match between organisms and their environment, but neither does so consistently. Genetic drift can cause the frequency of a slightly beneficial allele to increase, but it also can cause the frequency of such an allele to decrease.



▲ Figure 23.14 Movable jaw bones in snakes.

Similarly, gene flow may introduce alleles that are advantageous or ones that are disadvantageous. Natural selection is the only evolutionary mechanism that consistently leads to adaptive evolution.

Sexual Selection

Charles Darwin was the first to explore the implications of **sexual selection**, a form of natural selection in which individuals with certain inherited characteristics are more likely than other individuals to obtain mates. Sexual selection can result in **sexual dimorphism**, a difference in secondary sexual characteristics between males and females of the same species (Figure 23.15). These distinctions include differences in size, color, ornamentation, and behavior.

How does sexual selection operate? There are several ways. In **intrasexual selection**, meaning selection within the same sex, individuals of one sex compete directly for mates of the opposite sex. In many species, intrasexual selection occurs among males. For example, a single male may patrol a group of females and prevent other males from mating with them. The patrolling male may defend his status by defeating smaller, weaker, or less fierce males in combat. More often, this male is the psychological victor in ritualized displays that discourage would-be competitors but do not risk injury that would reduce his own fitness (see Figure 51.16). Intrasexual selection also occurs among females in a variety of species, including ring-tailed lemurs and broad-nosed pipefish.

In **intersexual selection**, also called *mate choice*, individuals of one sex (usually the females) are choosy in selecting their mates from the other sex. In many cases, the female's choice depends on the showiness of the male's appearance or behavior (see Figure 23.15). What intrigued Darwin about mate choice is that male showiness may not seem adaptive in any other way and may in fact pose some risk. For



▲ Figure 23.15 Sexual dimorphism and sexual selection. Peacocks (above left) and peahens (above right) show extreme sexual dimorphism. There is intrasexual selection between competing males, followed by intersexual selection when the females choose among the showiest males.

example, bright plumage may make male birds more visible to predators. But if such characteristics help a male gain a mate, and if this benefit outweighs the risk from predation, then both the bright plumage and the female preference for it will be reinforced because they enhance overall reproductive success.

How do female preferences for certain male characteristics evolve in the first place? One hypothesis is that females prefer male traits that are correlated with “good genes.” If the trait preferred by females is indicative of a male’s overall genetic quality, both the male trait and female preference for it should increase in frequency. **Figure 23.16** describes one experiment testing this hypothesis in gray tree frogs.

Other researchers have shown that in several bird species, the traits preferred by females are related to overall male health. Here, too, female preference appears to be based on traits that reflect “good genes,” in this case alleles indicative of a robust immune system.

Balancing Selection

As we’ve seen, genetic variation is often found at loci affected by selection. What prevents natural selection from reducing the variation at those loci by culling all unfavorable alleles? As mentioned earlier, in diploid organisms, many unfavorable recessive alleles persist because they are hidden from selection when in heterozygous individuals. In addition, selection itself may preserve variation at some loci, thus maintaining two or more forms in a population. Known as **balancing selection**, this type of selection includes heterozygote advantage and frequency-dependent selection.

Heterozygote Advantage

If individuals who are heterozygous at a particular locus have greater fitness than do both kinds of homozygotes, they exhibit **heterozygote advantage**. In such a case, natural selection tends to maintain two or more alleles at that locus. Note that heterozygote advantage is defined in terms of *genotype*, not phenotype. Thus, whether heterozygote advantage represents stabilizing or directional selection depends on the relationship between the genotype and the phenotype. For example, if the phenotype of a heterozygote is intermediate to the phenotypes of both homozygotes, heterozygote advantage is a form of stabilizing selection.

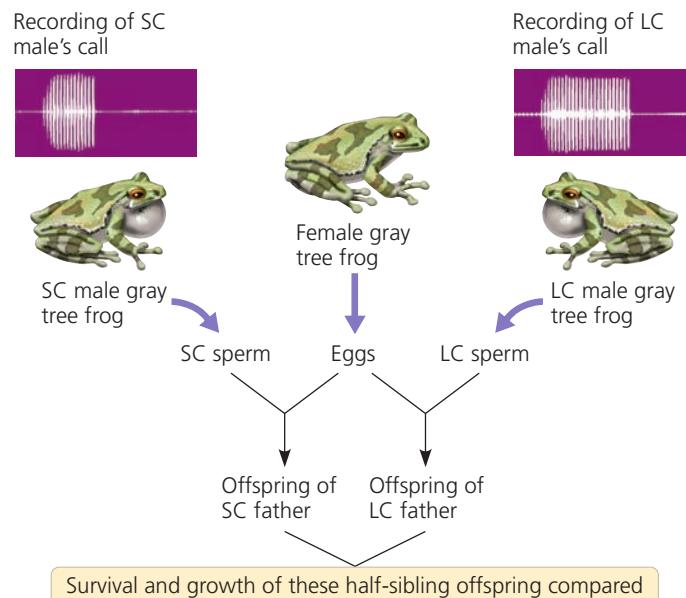
An example of heterozygote advantage occurs at the locus in humans that codes for the β polypeptide subunit of hemoglobin, the oxygen-carrying protein of red blood cells. In homozygous individuals, a certain recessive allele at that locus causes sickle-cell disease. The red blood cells of people with sickle-cell disease become distorted in shape, or *sickled*, under low-oxygen conditions (see Figure 5.19), as occurs in the capillaries. These sickled cells can clump together and block the flow of blood in the capillaries, resulting in serious

▼ Figure 23.16

Inquiry

Do females select mates based on traits indicative of “good genes”?

Experiment Female gray tree frogs (*Hyla versicolor*) prefer to mate with males that give long mating calls. Allison Welch and colleagues, at the University of Missouri, tested whether the genetic makeup of long-calling (LC) males is superior to that of short-calling (SC) males. The researchers fertilized half the eggs of each female with sperm from an LC male and fertilized the remaining eggs with sperm from an SC male. In two separate experiments (one in 1995, the other in 1996), the resulting half-sibling offspring were raised in a common environment and their survival and growth were monitored.



Results

Offspring Performance	1995	1996
Larval survival	LC better	NSD
Larval growth	NSD	LC better
Time to metamorphosis	LC better (shorter)	LC better (shorter)

NSD = no significant difference; LC better = offspring of LC males superior to offspring of SC males.

Conclusion Because offspring fathered by an LC male outperformed their half-siblings fathered by an SC male, the team concluded that the duration of a male’s mating call is indicative of the male’s overall genetic quality. This result supports the hypothesis that female mate choice can be based on a trait that indicates whether the male has “good genes.”

Source: A. M. Welch et al., Call duration as an indicator of genetic quality in male gray tree frogs, *Science* 280:1928–1930 (1998).

Inquiry in Action Read and analyze the original paper in Inquiry in Action: Interpreting Scientific Papers.

WHAT IF? Why did the researchers split each female frog’s eggs into two batches for fertilization by different males? Why didn’t they mate each female with a single male frog?

damage to organs such as the kidney, heart, and brain. Although some red blood cells become sickled in heterozygotes, not enough become sickled to cause sickle-cell disease.

Heterozygotes for the sickle-cell allele are protected against the most severe effects of malaria, a disease caused by a parasite that infects red blood cells (see Figure 28.16). One reason for this partial protection is that the body destroys sickled red blood cells rapidly, killing the parasites they harbor. Protection against malaria is important in tropical regions where the disease is a major killer. In such regions, selection favors heterozygotes over homozygous dominant individuals, who are more vulnerable to the effects of malaria, and also over homozygous recessive individuals, who develop sickle-cell disease. As we explore further in **Figure 23.17**, on the next two pages, these selective pressures have caused the frequency of the sickle-cell allele to reach relatively high levels in areas where the malaria parasite is common.

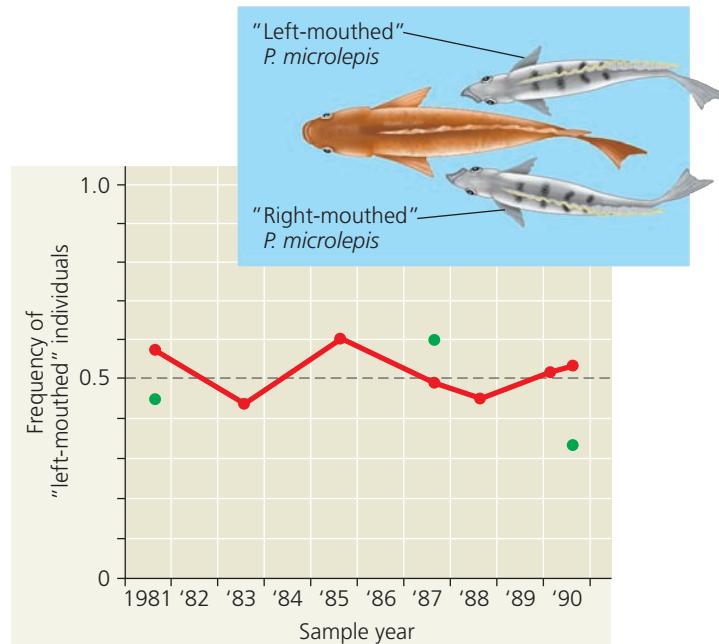
Frequency-Dependent Selection

In **frequency-dependent selection**, the fitness of a phenotype depends on how common it is in the population. Consider the scale-eating fish (*Perissodus microlepis*) of Lake Tanganyika, in Africa. These fish attack other fish from behind, darting in to remove a few scales from the flank of their prey. Of interest here is a peculiar feature of the scale-eating fish: Some are “left-mouthed” and some are “right-mouthed.” Simple Mendelian inheritance determines these phenotypes, with the right-mouthed allele being dominant to the left-mouthed allele. Because their mouth twists to the left, left-mouthed fish always attack their prey’s right flank (**Figure 23.18**). (To see why, twist your lower jaw and lips to the left and imagine trying to take a bite from the left side of a fish, approaching it from behind.) Similarly, right-mouthed fish always attack from the left. Prey species guard against attack from whatever phenotype of scale-eating fish is most common in the lake. Thus, from year to year, selection favors whichever mouth phenotype is least common. As a result, the frequency of left- and right-mouthed fish oscillates over time, and balancing selection (due to frequency dependence) keeps the frequency of each phenotype close to 50%.

Why Natural Selection Cannot Fashion Perfect Organisms

Though natural selection leads to adaptation, nature abounds with examples of organisms that are less than ideally suited for their lifestyles. There are several reasons why.

- Selection can act only on existing variations.** Natural selection favors only the fittest phenotypes among those currently in the population, which may not be the ideal traits. New advantageous alleles do not arise on demand.



© 1993 AAAS

▲ Figure 23.18 Frequency-dependent selection. In a population of the scale-eating fish, *Perissodus microlepis*, the frequency of left-mouthed individuals (red data points) rises and falls in a regular manner. The frequency of left-mouthed individuals among adults that reproduced was also recorded in three sample years (green data points).

INTERPRET THE DATA For 1981, 1987, and 1990, compare the frequency of left-mouthed individuals among breeding adults to the frequency of left-mouthed individuals in the entire population. What do the data suggest about when natural selection favors left-mouthed individuals over right-mouthed individuals (or vice versa)? Explain.

- Evolution is limited by historical constraints.** Each species has a legacy of descent with modification from ancestral forms. Evolution does not scrap the ancestral anatomy and build each new complex structure from scratch; rather, evolution co-opts existing structures and adapts them to new situations. We could imagine that if a terrestrial animal were to adapt to an environment in which flight would be advantageous, it might be best just to grow an extra pair of limbs that would serve as wings. However, evolution does not work this way; instead, it operates on the traits an organism already has. Thus, in birds and bats, an existing pair of limbs took on new functions for flight as these organisms evolved from nonflying ancestors.
- Adaptations are often compromises.** Each organism must do many different things. A seal spends part of its time on rocks; it could probably walk better if it had legs instead of flippers, but then it would not swim nearly as well. We humans owe much of our versatility and athleticism to our prehensile hands and flexible limbs, but these also make us prone to sprains, torn ligaments, and dislocations: Structural reinforcement has been compromised for agility.

▼ Figure 23.17

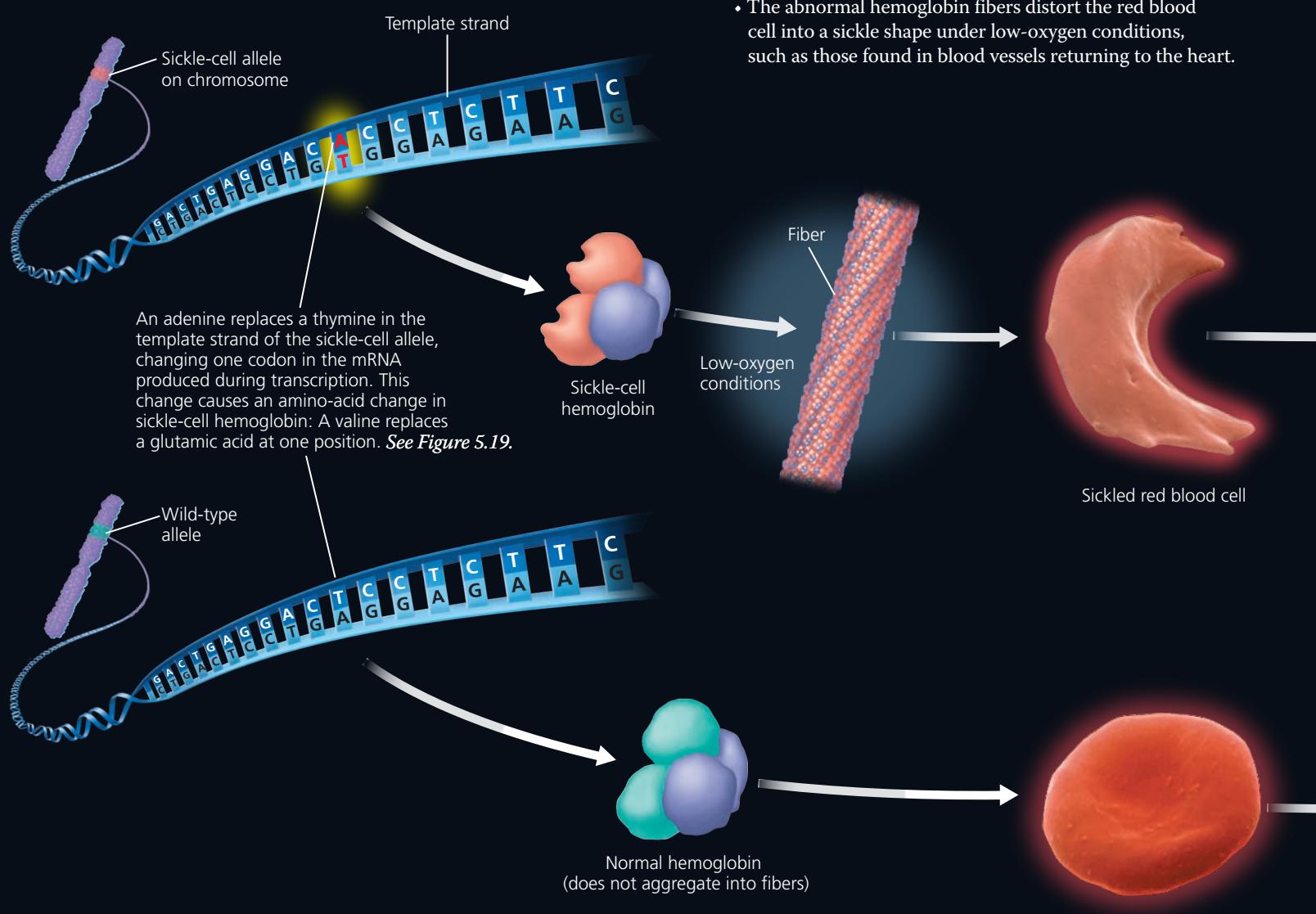
MAKE CONNECTIONS

The Sickle-Cell Allele

This child has sickle-cell disease, a genetic disorder that strikes individuals that have two copies of the sickle-cell allele. This allele causes an abnormality in the structure and function of hemoglobin, the oxygen-carrying protein in red blood cells. Although sickle-cell disease is lethal if not treated, in some regions the sickle-cell allele can reach frequencies as high as 15–20%. How can such a harmful allele be so common?

Events at the Molecular Level

- Due to a point mutation, the sickle-cell allele differs from the wild-type allele by a single nucleotide. See *Figure 17.25*.
- The resulting change in one amino acid leads to hydrophobic interactions between the sickle-cell hemoglobin proteins under low-oxygen conditions.
- As a result, the sickle-cell proteins bind to each other in chains that together form a fiber.



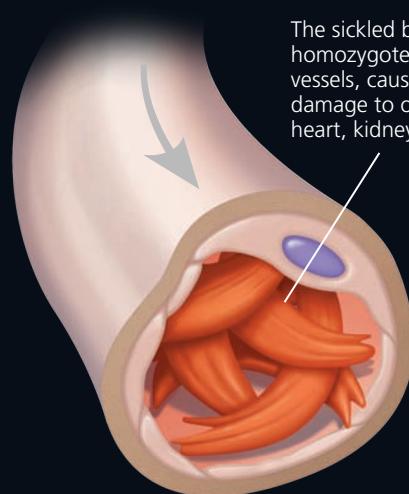


Infected mosquitos spread malaria when they bite people. See Figure 28.16.

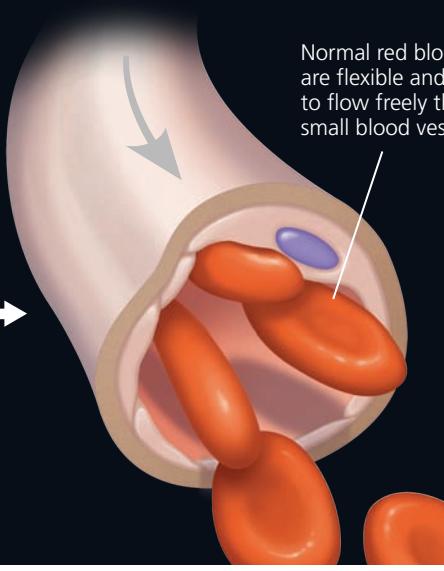
Effects on Individual Organisms

- The formation of sickled red blood cells causes homozygotes with two copies of the sickle-cell allele to have sickle-cell disease.
- Some sickling also occurs in heterozygotes, but not enough to cause the disease; they have sickle-cell trait. See Figure 14.17.

The sickled blood cells of a homozygote block small blood vessels, causing great pain and damage to organs such as the heart, kidney, and brain.



Normal red blood cells are flexible and are able to flow freely through small blood vessels.



Key

Frequencies of the sickle-cell allele

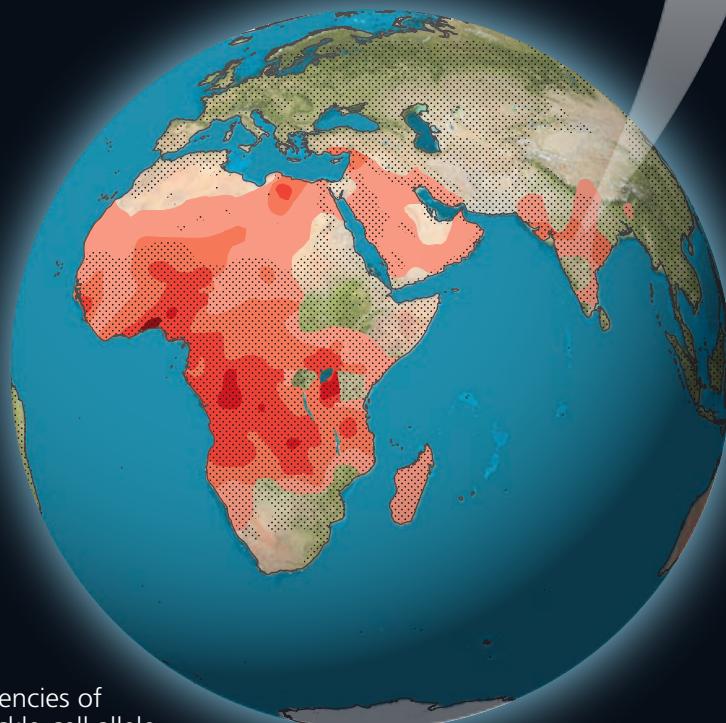
	3.0–6.0%
	6.0–9.0%
	9.0–12.0%
	12.0–15.0%
	>15.0%

Distribution of malaria caused by *Plasmodium falciparum* (a parasitic unicellular eukaryote)

MAKE CONNECTIONS In a region free of malaria, would individuals who are heterozygous for the sickle-cell allele be selected for or selected against? Explain.

Evolution in Populations

- Homozygotes with two sickle-cell alleles are strongly selected against because of mortality caused by sickle-cell disease. In contrast, heterozygotes experience few harmful effects from sickling yet are more likely to survive malaria than are homozygotes.
- In regions where malaria is common, the net effect of these opposing selective forces is heterozygote advantage. This has caused evolutionary change in populations—the products of which are the areas of relatively high frequencies of the sickle-cell allele shown in the map below.



4. Chance, natural selection, and the environment

interact. Chance events can affect the subsequent evolutionary history of populations. For instance, when a storm blows insects or birds hundreds of kilometers over an ocean to an island, the wind does not necessarily transport those individuals that are best suited to the new environment. Thus, not all alleles present in the founding population's gene pool are better suited to the new environment than the alleles that are "left behind." In addition, the environment at a particular location may change unpredictably from year to year, again limiting the extent to which adaptive evolution results in a close match between the organism and current environmental conditions.

With these four constraints, evolution does not tend to craft perfect organisms. Natural selection operates on a "better than" basis. We can, in fact, see evidence for evolution in the many imperfections of the organisms it produces.

CONCEPT CHECK 23.4

1. What is the relative fitness of a sterile mule? Explain.
2. Explain why natural selection is the only evolutionary mechanism that consistently leads to adaptive evolution.
3. **WHAT IF?** Consider a population in which heterozygotes at a certain locus have an extreme phenotype (such as being larger than homozygotes) that confers a selective advantage. Does such a situation represent directional, disruptive, or stabilizing selection? Explain.

For suggested answers, see Appendix A.

23 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 23.1

Genetic variation makes evolution possible (pp. 481–483)

- **Genetic variation** refers to genetic differences among individuals within a population.
- The nucleotide differences that provide the basis of genetic variation originate when mutation and gene duplication produce new alleles and new genes. New genetic variants are produced rapidly in organisms with short generation times. In sexually reproducing organisms, most of the genetic differences among individuals result from crossing over, the independent assortment of chromosomes, and fertilization

?

Typically, most of the nucleotide variability that occurs within a genetic locus does not affect the phenotype. Explain why.

CONCEPT 23.2

The Hardy-Weinberg equation can be used to test whether a population is evolving (pp. 483–487)

- A **population**, a localized group of organisms belonging to one species, is united by its **gene pool**, the aggregate of all the alleles in the population.
- For a population in **Hardy-Weinberg equilibrium**, the allele and genotype frequencies will remain constant if the population is large, mating is random, mutation is negligible, there is no gene flow, and there is no natural selection. For such a population, if p and q represent the frequencies of the only two possible alleles at a particular locus, then p^2 is the frequency of one kind of homozygote, q^2 is the frequency of the other kind of homozygote, and $2pq$ is the frequency of the heterozygous genotype.

?

Is it circular reasoning to calculate p and q from observed genotype frequencies and then use those values of p and q to test if the population is in Hardy-Weinberg equilibrium? Explain your answer.

CONCEPT 23.3

Natural selection, genetic drift, and gene flow can alter allele frequencies in a population (pp. 487–491)

- In natural selection, individuals that have certain inherited traits tend to survive and reproduce at higher rates than other individuals *because of* those traits.
- In **genetic drift**, chance fluctuations in allele frequencies over generations tend to reduce genetic variation.
- **Gene flow**, the transfer of alleles between populations, tends to reduce genetic differences between populations over time.

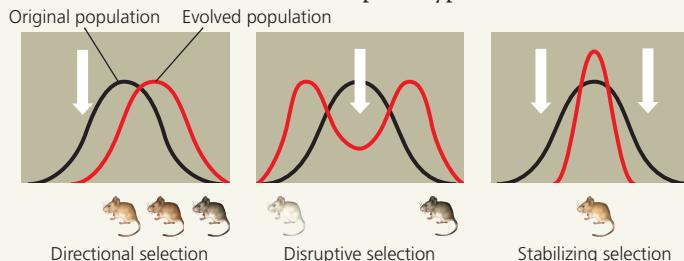
?

Would two small, geographically isolated populations in very different environments be likely to evolve in similar ways? Explain.

CONCEPT 23.4

Natural selection is the only mechanism that consistently causes adaptive evolution (pp. 491–498)

- One organism has greater **relative fitness** than another organism if it leaves more fertile descendants. The modes of natural selection differ in their effect on phenotype:



- Unlike genetic drift and gene flow, natural selection consistently improves the match between organisms and their environment.
- **Sexual selection** influences change in secondary sex characteristics that can give individuals advantages in mating.
- **Balancing selection** occurs when natural selection maintains two or more forms in a population.

- There are constraints to evolution: Natural selection can act only on available variation; structures result from modified ancestral anatomy; adaptations are often compromises; and chance, natural selection, and the environment interact.

? How might secondary sex characteristics differ between males and females in a species in which females compete for mates?

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

- Natural selection changes allele frequencies because some _____ survive and reproduce better than others.
 - alleles
 - loci
 - species
 - individuals
- No two people are genetically identical, except for identical twins. The main source of genetic variation among humans is
 - new mutations that occurred in the preceding generation.
 - genetic drift.
 - the reshuffling of alleles in sexual reproduction.
 - environmental effects.

LEVEL 2: APPLICATION/ANALYSIS

- If the nucleotide variability of a locus equals 0%, what is the gene variability and number of alleles at that locus?
 - gene variability = 0%; number of alleles = 0
 - gene variability = 0%; number of alleles = 1
 - gene variability = 0%; number of alleles = 2
 - gene variability > 0%; number of alleles = 2
- There are 25 individuals in population 1, all with genotype AA , and there are 40 individuals in population 2, all with genotype aa . Assume that these populations are located far from each other and that their environmental conditions are very similar. Based on the information given here, the observed genetic variation most likely resulted from
 - genetic drift.
 - nonrandom mating.
 - gene flow.
 - directional selection.
- A fruit fly population has a gene with two alleles, $A1$ and $A2$. Tests show that 70% of the gametes produced in the population contain the $A1$ allele. If the population is in Hardy-Weinberg equilibrium, what proportion of the flies carry both $A1$ and $A2$?
 - 0.7
 - 0.49
 - 0.42
 - 0.21

LEVEL 3: SYNTHESIS/EVALUATION

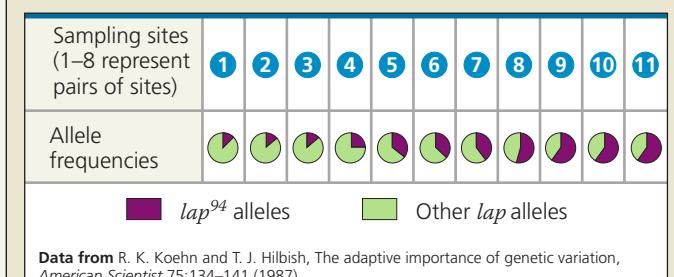
6. EVOLUTION CONNECTION

Using at least two examples, explain how the process of evolution is revealed by the imperfections of living organisms.

7. SCIENTIFIC INQUIRY

INTERPRET THE DATA Researchers studied genetic variation in the marine mussel *Mytilus edulis* around Long Island, New York. They measured the frequency of a particular allele (lap^{94}) for an enzyme involved in regulating the mussel's internal saltwater balance. The researchers presented their data as a series of pie charts linked to sampling sites within Long Island Sound, where the salinity is highly variable, and along the coast of the open ocean, where salinity is constant.

Create a data table for the 11 sampling sites by estimating the frequency of lap^{94} from the pie charts. (Hint: Think of each pie chart as a clock face to help you estimate the proportion of the shaded area.) Then graph the frequencies for sites 1–8 to show how the frequency of this allele changes with increasing salinity in Long Island Sound (from southwest to northeast). How do the data from sites 9–11 compare with the data from the sites within the Sound? Construct a hypothesis that explains the patterns you observe in the data and that accounts for the two observations listed below the map.



(1) The lap^{94} allele helps mussels maintain osmotic balance in water with a high salt concentration but is costly to use in less salty water; and (2) mussels produce larvae that can disperse long distances before they settle on rocks and grow into adults.

8. WRITE ABOUT A THEME: ORGANIZATION

Heterozygotes at the sickle-cell locus produce both normal and abnormal (sickle-cell) hemoglobin (see Concept 14.4). When hemoglobin molecules are packed into a heterozygote's red blood cells, some cells receive relatively large quantities of abnormal hemoglobin, making these cells prone to sickling. In a short essay (approximately 100–150 words), explain how these molecular and cellular events lead to emergent properties at the individual and population levels of biological organization.

9. SYNTHESIZE YOUR KNOWLEDGE



This kettle lake formed 14,000 years ago when a glacier that covered the surrounding area melted. Initially devoid of animal life, over time the lake was colonized by invertebrates and other animals. Hypothesize how mutation, natural selection, genetic drift, and gene flow may have affected populations that colonized the lake.

For suggested answers, see Appendix A.

MasteringBiology®

Students Go to **MasteringBiology** for assignments, the eText, and the Study Area with practice tests, animations, and activities.

Instructors Go to **MasteringBiology** for automatically graded tutorials and questions that you can assign to your students, plus Instructor Resources.

24

The Origin of Species

KEY CONCEPTS

- 24.1 The biological species concept emphasizes reproductive isolation
- 24.2 Speciation can take place with or without geographic separation
- 24.3 Hybrid zones reveal factors that cause reproductive isolation
- 24.4 Speciation can occur rapidly or slowly and can result from changes in few or many genes

▲ **Figure 24.1** How did this flightless bird come to live on the isolated Galápagos Islands?

That “Mystery of Mysteries”

When Darwin came to the Galápagos Islands, he noted that these volcanic islands were teeming with plants and animals found nowhere else in the world (**Figure 24.1**). Later he realized that these species had formed relatively recently. He wrote in his diary: “Both in space and time, we seem to be brought somewhat near to that great fact—that mystery of mysteries—the first appearance of new beings on this Earth.”

The “mystery of mysteries” that captivated Darwin is **speciation**, the process by which one species splits into two or more species. Speciation fascinated Darwin (and many biologists since) because it has produced the tremendous diversity of life, repeatedly yielding new species that differ from existing ones. Speciation also helps to explain the many features that organisms share (the unity of life).

When one species splits into two, the species that result share many characteristics because they are descended from this common ancestor. At the DNA sequence level, for example, such similarities indicate that the flightless cormorant (*Phalacrocorax harrisi*) in Figure 24.1 is closely related to flying cormorants found in the Americas. This suggests that the flightless cormorant originated from an ancestral cormorant species that flew from the mainland to the Galápagos.

◀ Galápagos giant tortoise, another species unique to the islands