How Populations Evolve

CHAPTER 13

What does actor George Clooney have in common with George Washington, Ernest Hemingway, Christopher Columbus, and Mother Teresa? They all survived bouts with malaria, a disease caused by a microscopic parasite that is one of the worst killers in human history. In the 1960s, the World Health Organization (WHO) launched a campaign to eradicate malaria. Their strategy focused on killing the mosquitoes that carry the parasite from person to person. DDT, a widely used pesticide, was deployed in massive spraying operations. But in one location after another, early success was followed by rebounding mosquito populations in which resistance to DDT had evolved. Malaria continued to spread. Today, malaria causes more than a million deaths and 250 million cases of miserable illness each year.

How does evolution hinder attempts to eradicate disease?

Evolution has also hindered efforts to help malaria victims. At the same time that DDT was being celebrated as a miracle pesticide in the war against malaria, a drug called chloroquine was hailed as the miracle cure. But its effectiveness has diminished over time, as resistance to the drug has evolved in parasite populations. In some regions, chloroquine is powerless against the disease. The most effective antimalarial drug now is artemisinin, a compound extracted from a plant used in traditional Chinese medicine. But the effectiveness of this drug will eventually succumb to the power of evolution, too. Cases of malaria that don't respond to artemisinin have already appeared in Southeast Asia. The girl in the photo on the right is being tested to ensure that her treatment was effective.

An understanding of evolution informs all of biology, from exploring life's molecules to analyzing ecosystems. Applications of evolutionary biology are transforming fields as diverse as medicine, agriculture, and conservation biology. In this chapter, we begin our study of evolution with the enduring legacy of Charles Darwin's explanation for the unity and diversity of life. We also delve into the nitty-gritty of natural selection, the mechanism for evolution that Darwin proposed.

BIG IDEAS

Darwin's Theory of Evolution

(13.1–13.7)

Darwin's theory of evolution explains the adaptations of organisms and the unity and diversity of life.

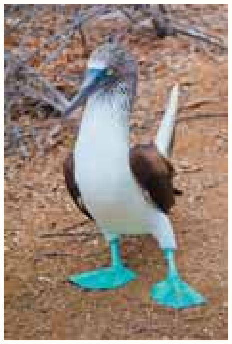
The Evolution of Populations

(13.8–13.11)

Genetic variation makes evolution possible within a population.

Mechanisms of Microevolution (13.12–13.18)

Natural selection, genetic drift, and gene flow can alter gene pools; natural selection leads to adaptive evolution.



Darwin's Theory of Evolution

13.1 A sea voyage helped Darwin frame his theory of evolution

If you have heard of the theory of evolution, you have probably heard of Charles Darwin. Although Darwin was born more than 200 years ago, his work had such an extraordinary impact that many biologists mark his birthday—February 12, the same as Abraham Lincoln's—with a celebration of his contributions to science. The publication of Darwin's best-known book, *On the Origin of Species by Means of Natural Selection*, commonly referred to as *The Origin of Species*, launched the era of evolutionary biology.

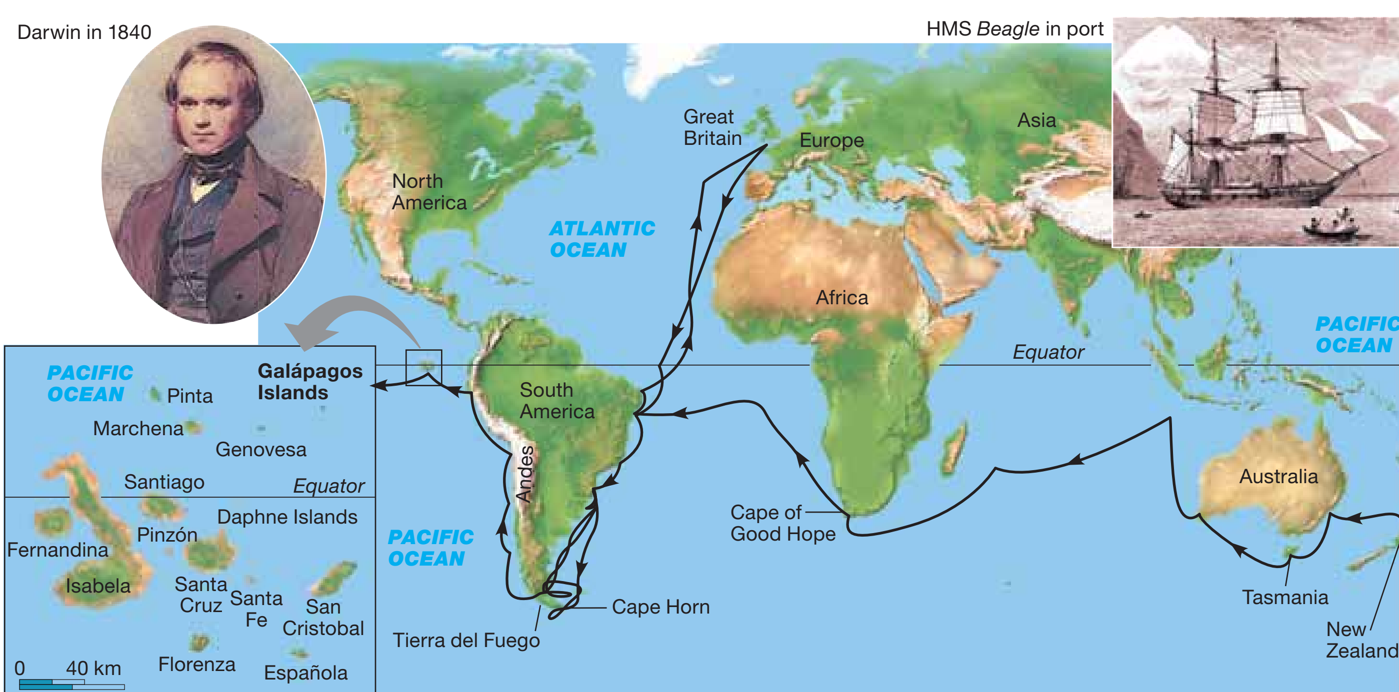
Darwin's Cultural and Scientific Context Darwin's early career gave no hint of his future fame. As a boy, he was fascinated with nature. When not reading books about nature, he was fishing, hunting, and collecting insects. His education was typical for a young man of his social class. Darwin's father, an eminent physician, could see no future for his son as a naturalist and sent him to medical school. But Darwin, finding medicine boring and surgery before the days of anesthesia horrifying, quit medical school. His father then enrolled him at Cambridge University with the intention that he should become a clergyman.

The cultural and scientific context of his time also instilled Darwin with a conventional view of Earth and its life. Most scientists accepted the views of the Greek philosopher Aristotle, who generally held that species are fixed, permanent forms that do not evolve. Judeo-Christian culture fortified this idea with a literal interpretation of the biblical book of Genesis, which tells the story of each form of life being individually created in its present-day form. In the 1600s, religious scholars used biblical accounts to estimate the age of Earth at 6,000 years. Thus, the idea that all living species came into being relatively recently and are unchanging in form dominated the intellectual climate of the Western world at the time.

Darwin's radical thinking stemmed from his postcollege life, when he returned to his childhood interests. At the age of 22, Darwin set sail on HMS *Beagle*, a survey ship preparing for a long expedition to chart poorly known stretches of the South American coast **(Figure 13.1A)**.

Darwin's Sea Voyage During the five-year voyage of the *Beagle*, Darwin spent most of his time on shore collecting thousands of specimens of fossils and living plants and animals. He also kept detailed journals of his observations. For a naturalist (field biologist) from a small, temperate country, seeing the glorious diversity of unfamiliar life-forms on other continents was a revelation. He carefully noted the characteristics of plants and animals that made them well suited to such diverse environments as the jungles of Brazil, the grasslands of Argentina, the towering peaks of the Andes, and the desolate and frigid lands at the southern tip of South America.

Many of Darwin's observations indicated that geographic proximity is a better predictor of relationships among organism than similarity of environment. For example, the plants and animals living in temperate regions of South America more closely resembled species living in tropical regions of that continent than species living in temperate regions



▲ **Figure 13.1A** The voyage of the *Beagle* (1831–1836), with insets showing a young Charles Darwin and the ship on which he sailed of Europe. And the South American fossils Darwin found, though clearly species different from living ones, were distinctly South American in their resemblance to the contemporary plants and animals of that continent. For instance, he collected fossilized armor plates resembling those of living armadillo species. Paleontologists later reconstructed the creature to which the armor belonged—an extinct armadillo the size of a Volkswagen Beetle.

Darwin was particularly intrigued by the geographic distribution of organisms on the Galápagos Islands. The Galápagos are relatively young volcanic islands about 900 kilometers (540 miles) off the Pacific coast of South America. Most of the animals that inhabit these remote islands are found nowhere else in the world, but they resemble South American species. For example, Darwin noticed that Galápagos marine iguanas—with a flattened tail that aids in swimming—are similar to, but distinct from, land-dwelling iguanas on the islands and on the South American mainland **(Figure 13.1B)**. Furthermore, each island had its own distinct variety of giant tortoise **(Figure 13.1C)**, the strikingly unique inhabitant for which the islands were named (galápago means "tortoise" in Spanish).

▲ **Figure 13.1B** A marine iguana in the waters around the Galápagos Islands

▲ **Figure 13.1C** A giant tortoise, one of the unique inhabitants of the Galápagos Islands

While on his voyage, Darwin was strongly influenced by the newly published *Principles of Geology*, by Scottish geologist Charles Lyell. The book presented the case for an ancient Earth sculpted over millions of years by gradual geologic processes that continue today. Having witnessed an earthquake that raised part of the coastline of Chile almost a meter, Darwin realized that natural forces gradually changed Earth's surface and that these forces still operate. Thus, the fossils of marine snails that Darwin found high up in the Andes could have been lifted from sea level by natural mountain-building forces such as earthquakes.

By the time Darwin returned to Great Britain, he had begun to seriously doubt that Earth and all its living organisms had been specially created only a few thousand years earlier. As he reflected on his observations, analyzed his collections, and discussed his work with colleagues, he concluded that the evidence was better explained by the hypothesis that present-day species are the descendants of ancient ancestors that they still resemble in some ways. Over time, differences gradually accumulated by a process that Darwin called "descent with modification," his phrase for evolution. Darwin did not originate the concept of evolution—other scientists had explored the idea that organisms had changed over time. Unlike the others, however, Darwin also proposed a scientific mechanism for how life evolves. In the process he called **natural selection**, individuals with certain traits are more likely to survive and reproduce than are individuals who do not have those traits. He hypothesized that as the descendants of ancestral populations spread into various habitats over millions and millions of years, they accumulated diverse modifications, or **adaptations**, that fit them to specific ways of life in their environment.

Darwin's Writings By the early 1840s, Darwin had composed a long essay describing the major features of his theory of evolution by natural selection. Realizing that his ideas would cause an uproar, however, he delayed publication. Even as he procrastinated, Darwin continued to compile evidence in support of his hypothesis. In 1858, Alfred Russel Wallace, a British naturalist doing fieldwork in Indonesia, conceived a hypothesis almost identical to Darwin's. Faced with the possibility that Wallace's work would be published first, Darwin finally released his essay to the scientific community.

The following year, Darwin published *The Origin of Species*, a book that supported his hypothesis with immaculate logic and hundreds of pages of evidence drawn from observations and experiments in biology, geology, and paleontology. The hypothesis of evolution set forth in *The Origin of Species* also generated predictions that have been tested and verified by more than 150 years of research. Consequently, scientists regard Darwin's concept of evolution by means of natural selection as a **theory**—a widely accepted explanatory idea that is broader in scope than a hypothesis, generates new hypotheses, and is supported by a large body of evidence.

Next, we examine lines of evidence for Darwin's theory of **evolution**, the idea that living species are descendants of ancestral species that were different from present-day ones. We then return to the second main point Darwin made in *The Origin of Species*, that natural selection is the mechanism for evolutionary change. With our current understanding of how this mechanism works, we extend Darwin's definition of evolution to include "genetic changes in a population from generation to generation."

? What was Darwin's phrase for evolution? What does it mean?

■ Descent with modification. An ancestral species could diversify into many descendant species by the accumulation of adaptations to various environments.

13.2 The study of fossils provides strong evidence for evolution

Fossils—imprints or remains of organisms that lived in the past—document differences between past and present organisms and the fact that many species have become extinct. The organic substances of a dead organism usually decay rapidly, but the hard parts of an animal that are rich in minerals, such as the bones and teeth of vertebrates and the shells of clams and snails, may remain as fossils. For example, the fossilized skull in **Figure 13.2A** is from one of our early relatives, *Homo erectus*, who lived some 1.5 million years ago in Africa.

▲ **Figure 13.2A** Skull of *Homo erectus*

▲ **Figure 13.2B** Ammonite casts

Some fossils are not the actual remnants of organisms. The 375-million-year-old fossils shown in **Figure 13.2B** are casts of ammonites, shelled marine animals related to the present-day nautilus (see Figure 18.9E). Casts form when a dead organism captured in sediment decomposes and leaves an empty mold that is later filled by minerals dissolved in water. The minerals harden, making a replica of the organism. Fossils may also be imprints that remain after the organism decays. Footprints, burrows, and fossilized feces (known as coprolites) provide evidence of an ancient organism's behavior.

In rare instances, an entire organism, including its soft parts, is encased in a medium that prevents bacteria and fungi from decomposing the body. Examples include insects trapped in amber (fossilized tree resin) and mammoths, bison, and even prehistoric humans frozen in ice or preserved in bogs.

Many fossils are found in fine-grained sedimentary rocks formed from the sand or mud that settles to the bottom of seas, lakes, swamps, and other aquatic habitats. New layers of sediment cover older ones and compress them into layers of rock called **strata** (singular, *stratum*). The fossils in a particular stratum provide a glimpse of some of the organisms that lived in the area at the time the layer formed. Because younger strata are on top of older ones, the relative ages of fossils can be determined by the layer in which they are found. Thus, the sequence in which fossils appear within layers of sedimentary rocks is a historical record of life on Earth.

Paleontologists (scientists who study fossils) sometimes gain access to very old fossils when erosion carves through upper (younger) strata, revealing deeper (older) strata that had been buried. **Figure 13.2C** shows strata of sedimentary rock at the Grand Canyon. The Colorado River has cut through more than 2,000 m (more than a mile) of rock, exposing sedimentary layers that can be read like huge pages from the book of life. Scan the canyon wall from rim to floor, and you look back through hundreds of millions of years. Each layer entombs fossils that represent some of the organisms from that period of Earth's history.

▲ **Figure 13.2C** Strata of sedimentary rock at the Grand Canyon

Of course, the **fossil record**—the chronicle of evolution over millions of years of geologic time engraved in the order in which fossils appear in rock strata—is incomplete. Many of Earth's organisms did not live in areas that favor fossilization. Many fossils that did form were in rocks later distorted or destroyed by geologic processes. Furthermore, not all fossils that have been preserved are accessible to paleontologists. Even with its limitations, however, the fossil record is remarkably detailed.

? What types of animals do you think would be most represented in the fossil record? Explain your answer.

■ Animals with hard parts, such as shells or bones that readily fossilize, and those that lived in areas where sedimentary rock may form

13.3 Fossils of transitional forms support Darwin's theory of evolution

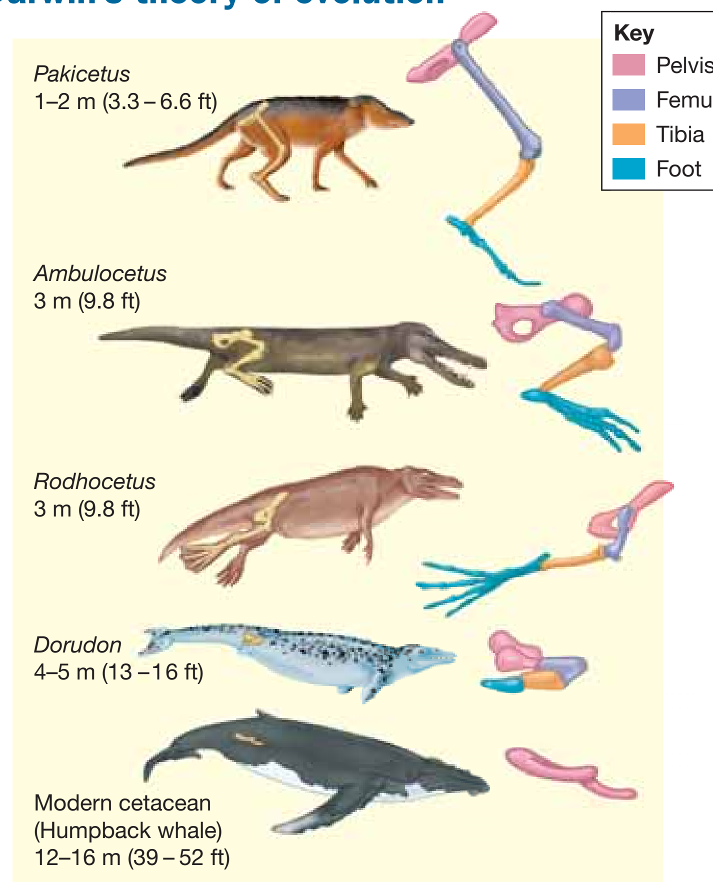
SCIENTIFIC THINKING

In *The Origin of Species*, Darwin predicted the existence of fossils of transitional forms linking very different groups of organisms. For example, he hypothesized that whales evolved from land-dwelling mammals. If this hypothesis was correct, then fossils should show a series of changes in a lineage of mammals adapted to a fully aquatic habitat. Although Darwin lacked evidence with which to test this prediction, thousands of fossil discoveries have since shed light on the evolutionary origins of many groups of plants and animals, including the transition of fish to amphibian (see Module 19.4), the origin of birds from a lineage of dinosaurs (see Module 19.7), and the evolution of mammals from a reptilian ancestor. If Darwin were alive today, he would surely be delighted to know that evidence discovered over the past few decades has made the origin of whales from terrestrial mammals one of the best-documented evolutionary transitions to date.

Whales are cetaceans, a group that also includes dolphins and porpoises. They have forelimbs in the form of flippers but lack hind limbs. If cetaceans evolved from four-legged land animals, then transitional forms should have reduced hind limb and pelvic bones. Based on the few fossils available in the 1960s, paleontologists hypothesized the ancestors of whales were hoofed, wolflike carnivores.

Beginning in the late 1970s, an extraordinary series of transitional fossils unearthed in Pakistan and Egypt provided the evidence paleontologists needed to test the hypothesis. **Figure 13.3** shows the progressive reduction in hind limb and pelvic bones in five of the fossil species. The 50-million-year-old *Pakicetus* ("whale of Pakistan") was a wolf-sized carnivore whose body shape and long limbs resembled those of land animals. However, other skeletal features, including distinctively cetacean middle ear structures, suggest adaptations to an aquatic environment. *Ambulocetus* ("walking whale"), roughly 48 million years old, was a perfect intermediate between modern whales and their land-dwelling ancestors: The joints of its forelimbs suggest mobility on land, while a powerful tail and large, paddle-like hind feet suggest the ability to swim. Adaptations for swimming are more apparent in the 46-million-year-old fossils of *Rodhocetus*, which had relatively short limbs and long-toed webbed feet. The fossil genus *Dorudon*, which lived between 40 and 35 million years ago, had completed the transition to aquatic life. The wrist and elbow joints of its paddle-like forelimbs could not have been used for walking. Its hind limbs were tiny, and as in modern whales, the remaining bit of its pelvis was not even connected to the vertebral column.

The new fossil discoveries were consistent with the earlier hypothesis, and paleontologists became more firmly convinced that whales did indeed arise from a wolflike carnivore. Meanwhile, molecular biologists were testing an alternative hypothesis using DNA analysis to infer relationships among living animals. They found a close relationship between whales and hippopotamuses, which are members of a group of mostly herbivorous, cloven-hoofed mammals that includes pigs, deer, and camels. Consequently, these researchers hypothesized that whales and hippos were both descendants of a cloven-hoofed ancestor. (A cloven hoof is a hoof split into two toes.)



▲ **Figure 13.3** **The transition to life in the sea; note positions of bones in animals (not drawn to scale)**

TRY THIS **List the animals shown, and describe how the structure of each animal's hind limbs reflects their function.**

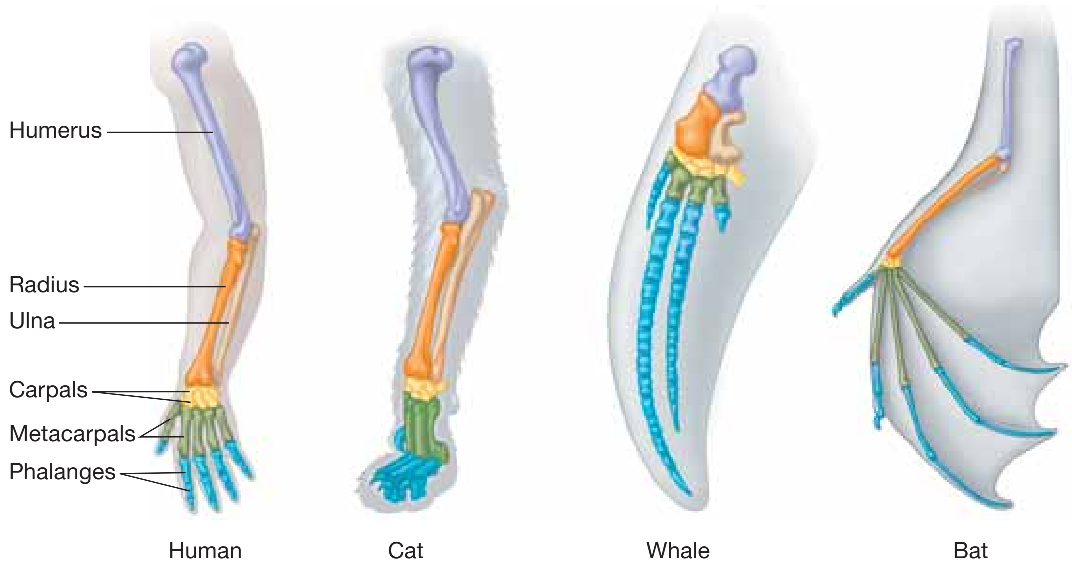
Paleontologists were taken aback by the contradictory results, but openness to new evidence is a hallmark of science. They turned their attention to seeking a fossil that would resolve the issue. Cloven-hoofed mammals have a unique ankle bone. If the ancestor of whales was a wolflike carnivore, then the shape of its ankle bone would be similar to most present-day mammals. Two fossils discovered in 2001 provided the answer. Both *Pakicetus* and *Rodhocetus* had the distinctive ankle bone of a cloven-hoofed mammal. Thus, as is often the case in science, scientists are becoming more certain about the evolutionary origin of whales as mounting evidence from different lines of inquiry converge.

? **What anatomical feature did scientists predict in fossils of species transitional between terrestrial and aquatic mammals?**

Reduced hind limb and pelvic bones

13.4 Homologies provide strong evidence for evolution

A second type of evidence for evolution comes from analyzing similarities among different organisms. Evolution is a process of descent with modification—characteristics present in an ancestral organism are altered over time by natural selection as its descendants face different environmental conditions. In other words, evolution is a remodeling process. 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**.



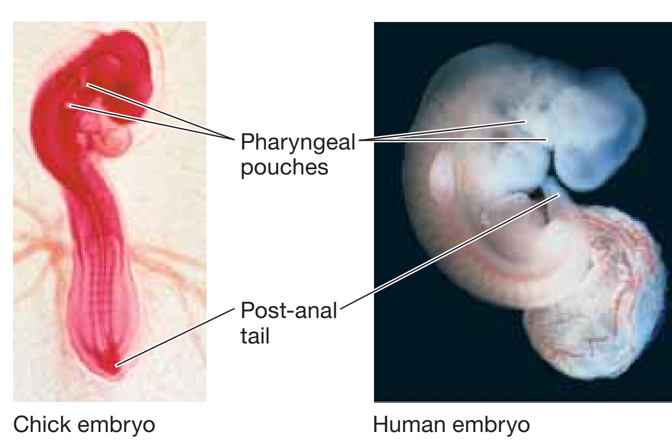
▲ **Figure 13.4A** **Homologous structures: vertebrate forelimbs**

Darwin cited the anatomical similarities among vertebrate forelimbs as evidence of common ancestry. As **Figure 13.4A** shows, the same skeletal elements make up the forelimbs of humans, cats, whales, and bats. The functions of these forelimbs differ. A whale's flipper does not do the same job as a bat's wing, so if these structures had been uniquely engineered, then we would expect that their basic designs would be very different. The logical explanation is that the arms, forelegs, flippers, and wings of these different mammals are variations on an anatomical structure of an ancestral organism that over millions of years has become adapted to different functions. Biologists call such anatomical similarities in different organisms **homologous structures**—features that often have different functions but are structurally similar because of common ancestry.

Because of advances in **molecular biology**, the study of the molecular basis of genes and gene expression, present-day scientists have a much deeper understanding of homologies than Darwin did. Just as your hereditary background is recorded in the DNA you inherit from your parents, the evolutionary history of each species is documented in the DNA inherited from its ancestral species. If two species have homologous genes with sequences that match closely, biologists conclude that these sequences must have been inherited from a relatively recent common ancestor. Conversely, the greater the number of sequence differences between species, the more distant is their last common ancestor. Molecular comparisons between diverse organisms have allowed biologists to develop hypotheses about the evolutionary divergence of major branches on the tree of life, as you learned in the previous module on the origin of whales.

Darwin's boldest hypothesis was that all life-forms are related. Molecular biology provides strong evidence for this claim: All forms of life use the same genetic language of DNA and RNA, and the genetic code—how RNA triplets are translated into amino acids—is essentially universal. Thus, it is likely that all species descended from common ancestors that used this code. Because of these homologies, bacteria engineered with human genes can produce human proteins such as insulin and human growth hormone (see Module 12.7). But molecular homologies go beyond a shared genetic code. For example, organisms as dissimilar as humans and bacteria share homologous genes inherited from a very distant common ancestor.

An understanding of homology can also explain observations that are otherwise puzzling. For example, comparing early stages of development in different animal species reveals similarities not visible in adult organisms. At some point in their development, all vertebrate embryos have a tail posterior to the anus, as well as structures called pharyngeal (throat) pouches. These pouches are homologous structures that ultimately develop to have very different functions, such as gills in fishes and parts of the ears and throat in humans. Note the pharyngeal pouches and tails of the bird embryo (left) and the human embryo (right) in **Figure 13.4B**.



▲ **Figure 13.4B** **Homologous structures in vertebrate embryos**

Some of the most interesting homologies are “leftover” structures that are of marginal or perhaps no importance to the organism. These **vestigial structures** are remnants of features that served important functions in the organism’s ancestors. For example, the small pelvis and hind-leg bones of ancient whales are vestiges (traces) of their walking ancestors. The eye remnants that are buried under scales in blind species of cave fishes—a vestige of their sighted ancestors—are another example.

Organisms may also retain genes that have lost their function, even though homologous genes in related species are fully functional. Researchers have identified many of these inactive “pseudogenes” in humans. One such gene encodes an enzyme known as GLO that is used in making vitamin C. Almost all mammals have a metabolic pathway to synthesize this essential vitamin from glucose. Although humans and other primates have functional genes for the first three steps in the pathway, the inactive GLO gene prevents vitamin C from being made—we must get sufficient amounts in our diet to maintain health.

Next we see how homologies help us trace evolutionary descent.

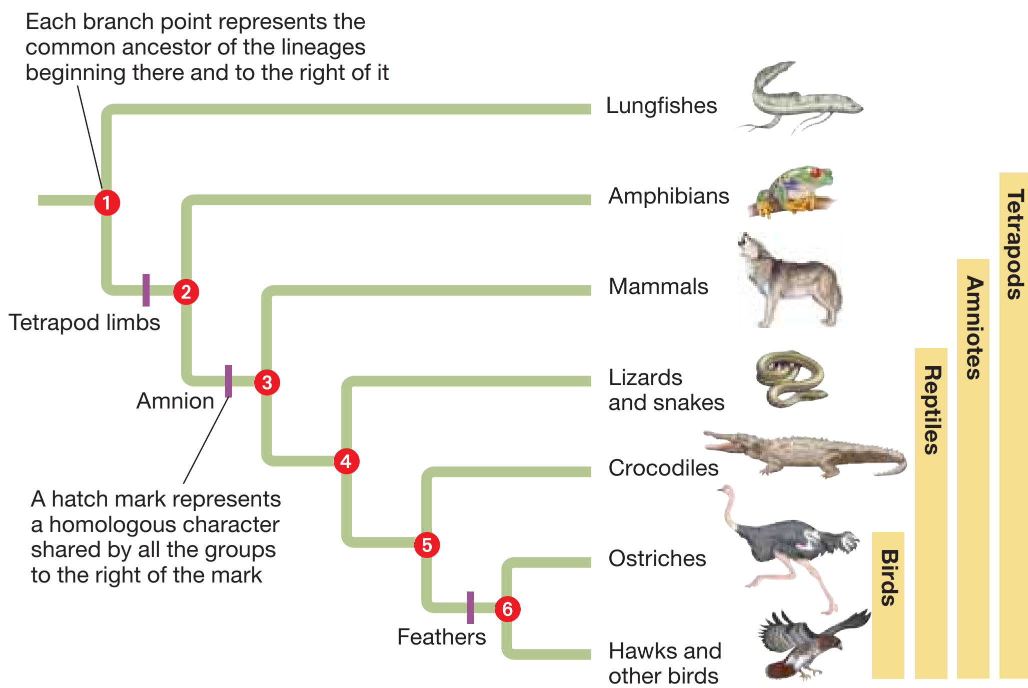
? What is homology? How does the concept of homology relate to molecular biology?

■ Homology is similarity in different species due to evolution from a common ancestor. Similarities in DNA sequences or proteins reflect the evolutionary relationship that is the basis of homology.

13.5 Homologies indicate patterns of descent that can be shown on an evolutionary tree

Darwin was the first to view the history of life as a tree, with multiple branchings from a common ancestral trunk to the descendant species at the tips of the twigs (see Figure 14.1). Biologists represent these patterns of descent with an **evolutionary tree**, although today they often turn the trees sideways.

Homologous structures, both anatomical and molecular, can be used to determine the branching sequence of such a tree. Some homologous characters, such as the genetic code, are shared by all species because they date to the deep ancestral past. In contrast, characters that evolved more recently are shared only within smaller groups of organisms. For example, all tetrapods (from the Greek *tetra*, four, and *pod*, foot) possess the same basic limb bone structure illustrated in Figure 13.4A, but their ancestors do not.



▲ **Figure 13.5** An evolutionary tree for tetrapods and their closest living relatives, the lungfishes

Figure 13.5 is an evolutionary tree of tetrapods (amphibians, mammals, and reptiles, including birds) 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 crocodiles and birds descended from ancestor 5. Three homologies are shown by the purple hatch marks on the tree—tetrapod limbs, the amnion (a protective embryonic membrane), and feathers. Tetrapod limbs were present in ancestor 2 and hence are found in all of its descendants. The amnion was present only in ancestor 3 and thus is shared only by mammals and reptiles. Feathers were present only in ancestor 6 and hence are found only in birds.

Evolutionary trees are hypotheses reflecting our current understanding of patterns of evolutionary descent. Some trees, such as the one in Figure 13.5, are supported by a strong combination of fossil, anatomical, and molecular data. Others are more speculative because few data are available.

Now that you have learned about Darwin’s view of evolution as descent with modification, let’s examine the mechanism he proposed for how life evolves—natural selection.

? Refer to the evolutionary tree in Figure 13.5. Are crocodiles more closely related to lizards or birds?

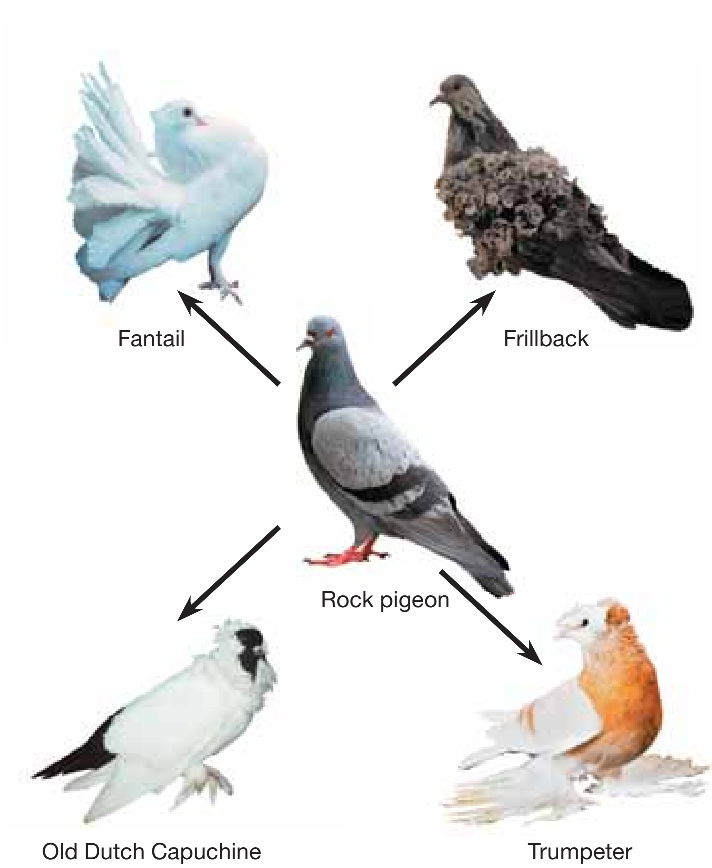
■ Look for the most recent common ancestor of these groups. Crocodiles are more closely related to birds because they share a more recent common ancestor with birds (ancestor 5) than with lizards (ancestor 4).

13.6 Darwin proposed natural selection as the mechanism of evolution

Darwin's greatest contribution to biology was his explanation of *how* life evolves. Because he thought that species formed gradually over long periods of time, he knew that he would not be able to study the evolution of new species by direct observation. But he did have a way to gain insight into the process of incremental change—the practices used by plant and animal breeders.

All domesticated plants and animals are the products of selective breeding from wild ancestors. For example, the baseball-size tomatoes grown today are very different from their Peruvian ancestors, which were not much larger than blueberries, and dachshunds bear little resemblance to the wolves from which they were bred. Having conceived the notion that **artificial selection**—the selective breeding of domesticated plants and animals to promote the occurrence of desirable traits in the offspring—was the key to understanding evolutionary change, Darwin bred fancy pigeons **(Figure 13.6)** to gain firsthand experience. He also talked to farmers about livestock breeding. He learned that artificial selection has two essential components, variation and heritability.

Variation among individuals—for example, differences in coat type in a litter of puppies, size of corn ears, or milk production by the individual cows in a herd—allows the breeder to select the animals or plants with the most desirable combination of characters as breeding stock for the next generation. Heritability refers to the transmission of a trait from parent to offspring. Despite their lack of knowledge of the underlying genetics, breeders had long understood the importance of heritability in artificial selection.



▲ **Figure 13.6** **Artificial selection: fancy pigeon varieties bred from the rock pigeon**

Unlike most naturalists, who sought consistency of traits in order to classify organisms, Darwin was a careful observer of variations between individuals. He knew that individuals in natural populations have small but measurable differences. But what forces in nature played the role of the breeder by choosing which individuals became the breeding stock for the next generation?

Darwin found inspiration in an essay written by economist Thomas Malthus, who contended that much of human suffering—disease, famine, and war—was the consequence of human populations increasing faster than food supplies and other resources. Darwin applied Malthus's idea to populations of plants and animals. He deduced that the production of more individuals than the limited resources can support leads to a struggle for existence, with only some offspring surviving in each generation. Of the many eggs laid, young born, and seeds spread, only a tiny fraction complete development and leave offspring. The rest are eaten, starved, diseased, unmated, or unable to reproduce for other reasons. The essence of natural selection is this unequal reproduction. Individuals whose traits better enable them to obtain food or escape predators or tolerate physical conditions will survive and reproduce more successfully, passing these adaptive traits to their offspring (see Module 1.9).

Darwin reasoned that if artificial selection can bring about so much change in a relatively short period of time, then natural selection could modify species considerably over hundreds or thousands of generations. Over vast spans of time, many traits that adapt a population to its environment will accumulate. If the environment changes, however, or if individuals move to a new environment, natural selection will select for adaptations to these new conditions, sometimes producing changes that result in the origin of a completely new species in the process.

It is important to emphasize three key points about evolution by natural selection. First, although natural selection occurs through interactions between individual organisms and the environment, individuals do not evolve. Rather, it is the population—the group of organisms—that evolves over time as adaptive traits become more common in the group and other traits change or disappear.

Second, natural selection can amplify or diminish only heritable traits. Certainly, an organism may become modified through its own interactions with the environment during its lifetime, and those acquired characteristics may help the organism survive. But unless coded for in the genes of an organism's gametes, such acquired characteristics cannot be passed on to offspring. Thus, a championship female bodybuilder will not give birth to a muscle-bound baby.

Third, evolution is not goal directed; it does not lead to perfectly adapted organisms. Whereas artificial selection is a deliberate attempt by humans to produce individuals with specific traits, natural selection is the result of environmental factors that vary from place to place and over time. A trait that is favorable in one situation may be useless—or even detrimental—in different circumstances. And as you will see, adaptations are often compromises. Now let's look at some examples of natural selection.

? **Compare artificial selection and natural selection.**

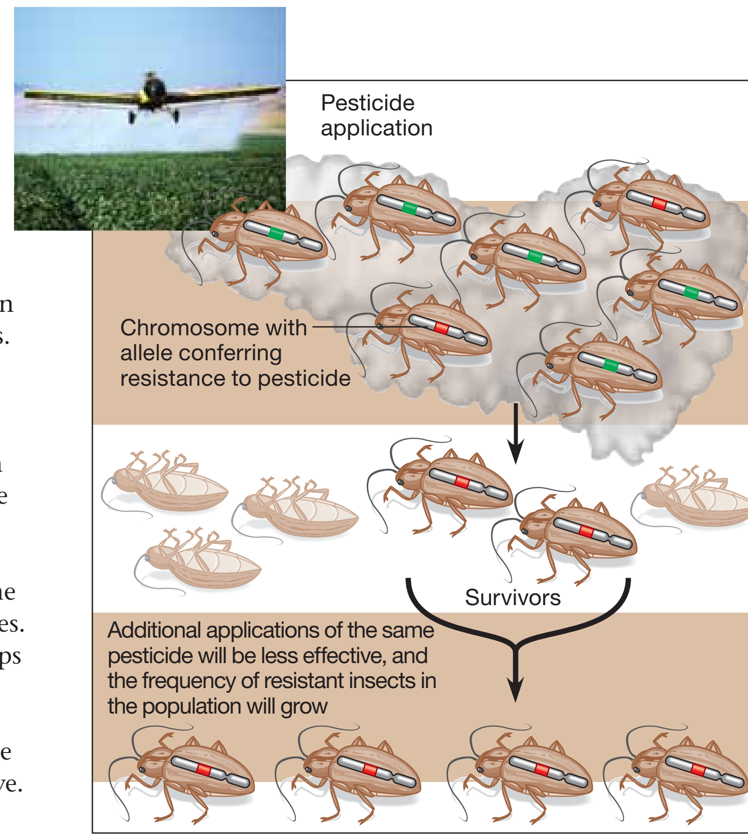
■ In artificial selection, humans choose the desirable traits and breed only organisms with those traits. In natural selection, the environment does the choosing: Individuals with traits best suited to the environment survive and reproduce most successfully, passing those adaptive traits to offspring.

13.7 Scientists can observe natural selection in action

Look at any natural environment, and you will see the products of natural selection—adaptations that suit organisms to their environment. But can we see natural selection in action?

Indeed, biologists have documented evolutionary change in thousands of scientific studies. A classic example comes from work that Peter and Rosemary Grant and their students did with finches in the Galápagos Islands over more than 30 years (see Module 14.9). As part of their research, they measured changes in beak size in a population of a ground finch species. These birds eat mostly small seeds. In dry years, when all seeds are in short supply, birds must eat more large seeds. Birds with larger, stronger beaks have a feeding advantage and greater reproductive success, and the Grants measured an increase in the average beak depth for the population. During wet years, smaller beaks are more efficient for eating the now abundant small seeds, and the Grants found a decrease in average beak depth.

An unsettling example of natural selection in action is the evolution of pesticide resistance in hundreds of insect species. Pesticides control insects and prevent them from eating crops or transmitting diseases. Whenever a new type of pesticide is used to control pests, the story is similar **(Figure 13.7)**: A relatively small amount of poison initially kills most of the insects, but subsequent applications are less and less effective. The few survivors of the first pesticide wave are individuals that are genetically resistant, carrying an allele (alternative form of a gene, colored red in the figure) that somehow enables them to survive the chemical attack. So the poison kills most members of the population, leaving the resistant survivors to reproduce and pass the alleles for pesticide resistance to their offspring. The proportion of pesticide-resistant individuals thus increases in each generation.



▲ **Figure 13.7** **Evolution of pesticide resistance in an insect population**

TRY THIS **Explain the failure of WHO's anti-malaria campaign by drawing a diagram similar to Figure 13.7.**

WHO's campaign against malaria described in the chapter introduction is a real-world example of the evolution of pesticide resistance. Some mosquitoes in the populations that were sprayed with DDT carried an allele that codes for an enzyme that detoxifies the pesticide. When the presence of DDT changed the environment, the individuals carrying that allele had an advantage. They survived to leave offspring, while nonresistant individuals did not. Thus, the process of natural selection defeated the efforts of WHO to control the spread of malaria by using DDT to kill mosquitoes.

These examples of evolutionary adaptation highlight two important points about natural selection. First, natural selection is more an editing process than a creative mechanism. A pesticide does not create new alleles that allow insects to survive. Rather, the presence of the pesticide leads to natural selection for insects in the population that already have those alleles. Second, natural selection is contingent on time and place: It favors those heritable traits in a varying population that fit the current, local environment. If the environment changes, different traits may be favored.

In the next few modules, we examine the genetic basis of evolution more closely.

? **In what sense is natural selection more an editing process than a creative process?**

■ Natural selection cannot create beneficial traits on demand but instead "edits" variation in a population by selecting for individuals with those traits that are best suited to the current environment.

The Evolution of Populations

13.8 Mutation and sexual reproduction produce the genetic variation that makes evolution possible

In *The Origin of Species*, Darwin provided evidence that life on Earth has evolved over time, and he proposed that natural selection, in favoring some heritable traits over others, was the primary mechanism for that change. But he could not explain the cause of variation among individuals, nor could he account for how those variations passed from parents to offspring.

Just a few years after the publication of *The Origin of Species*, Gregor Mendel wrote a groundbreaking paper on inheritance in pea plants (see Module 9.2). By breeding peas in his abbey garden, Mendel discovered the hereditary processes required for natural selection. Although the significance of Mendel's work was not recognized during his or Darwin's lifetime, its rediscovery in 1900 set the stage for understanding the genetic differences on which evolution is based.

Genetic Variation You have no trouble recognizing your friends in a crowd. The unique genome of each person is reflected in phenotypic variation, the expressed traits such as appearance that allow you to identify individuals. Indeed, individual variation occurs in all species, as illustrated by the garter snakes in **Figure 13.8**. All four of these snakes were captured in one Oregon field. In addition to obvious physical differences, such as the snakes' colors and patterns, most populations have a great deal of phenotypic variation that can be observed only at the molecular level, such as an enzyme that detoxifies DDT.

Of course, not all variation in a population is heritable. The phenotype results from a combination of the genotype, which is inherited, and many environmental influences. For instance, if you have dental work to straighten and whiten your teeth, you will not pass your environmentally produced smile to your offspring. Only the genetic component of variation is relevant to natural selection.

Many of the characters that vary in a population result from the combined effect of several genes. Polygenic inheritance produces characters that vary more or less continuously—in human height, for instance, from very short individuals to very tall ones (see Module 9.14). By contrast, other features, such as Mendel's purple and white pea flowers or human blood types, are determined by a single gene locus, with different alleles producing distinct phenotypes. But where do these alleles come from?

Mutation New alleles originate by **mutation**, a change in the genetic INFORMATION encoded in the nucleotide sequence of DNA. Thus, mutation is the ultimate source of the genetic variation that serves as raw material for evolution. In multicellular organisms, however, only mutations in cells that produce gametes can be passed to offspring and affect a population's genetic variability.

A change as small as a single nucleotide in a protein-coding gene can have a significant effect on phenotype, as in sickle-cell disease (see Module 9.13). An organism is a refined product of thousands of generations of past selection, and a random change in its DNA is not likely to improve its genome any more than randomly changing some letters on a page is likely to improve a story. In fact, mutation that affects a protein's function will probably be harmful. On rare occasions, however, a mutated allele may actually improve the adaptation of an individual to its environment and enhance its reproductive success. This kind of effect is more likely when the environment is changing in such a way that mutations that were once disadvantageous are favorable under the new conditions. For instance, mutations that endow houseflies with resistance to the pesticide DDT also reduce their growth rate. Before DDT was introduced, such mutations were a handicap to the flies that had them. But once DDT was part of the environment, the mutant alleles were advantageous, and natural selection increased their frequency in fly populations.

Chromosomal mutations that delete, disrupt, or rearrange many gene loci at once are almost certain to be harmful. But duplication of a gene or small pieces of DNA through errors in meiosis can provide an important source of genetic variation. If a repeated segment of DNA can persist over the generations, mutations may accumulate in the duplicate copies without affecting the function of the original gene, eventually leading to new genes with novel functions. This process may have played a major role in evolution.

▲ **Figure 13.8** Variation within a species of garter snakes

For example, the remote ancestors of mammals carried a single gene for detecting odors that has since been duplicated repeatedly. As a result, mice have about 1,300 different olfactory receptor genes. It is likely that such dramatic increases helped early mammals by enabling them to distinguish among many different smells. And repeated duplications of genes that control development are linked to the origin of vertebrate animals from an invertebrate ancestor.

In prokaryotes, mutations can quickly generate genetic variation. Because bacteria multiply so rapidly, a beneficial mutation can increase in frequency in a matter of hours or days. And because bacteria are haploid, with a single allele for each gene, a new allele can have an effect immediately.

Mutation rates in animals and plants average about one in every 100,000 genes per generation. For these organisms, low mutation rates, long time spans between generations, and diploid genomes prevent most mutations from significantly affecting genetic variation from one generation to the next.

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 inherits. (Of course, the origin of those allele variations is past mutations.)

Fresh assortments of existing alleles arise every generation from three random components of sexual reproduction: crossing over, independent orientation of homologous chromosomes at metaphase I of meiosis, and random fertilization (see Modules 8.15 and 8.17). During meiosis, pairs of homologous chromosomes, one set inherited from each parent, trade some of their genes by crossing over. These homologous chromosomes separate into gametes independently of other chromosome pairs. Thus, gametes from any individual vary extensively in their genetic makeup. Finally, each zygote made by a mating pair has a unique assortment of alleles resulting from the random union of sperm and egg.

Now let's see why genetic variation is such an essential element of evolution.

? What is the ultimate (original) source of genetic variation? What is the source of most genetic variation in a population that reproduces sexually?

Mutation; unique combinations of alleles resulting from sexual reproduction

13.9 Evolution occurs within populations

A common misconception about evolution is that individual organisms evolve during their lifetimes. It is true that natural selection acts on individuals: Each individual's combination of traits affects its survival and reproductive success. But the evolutionary impact of natural selection is only apparent in the changes in a population of organisms over time.

A **population** is a group of individuals of the same species that live in the same area and can potentially interbreed. We can measure evolution as a change in the prevalence of certain heritable traits in a population over a span of generations. The increasing proportion of resistant insects in areas sprayed with pesticide is one example. Natural selection favored insects with alleles for pesticide resistance; these insects left more offspring than nonresistant individuals, changing the genetic makeup of the population.

Different populations of the same species may be geographically isolated from each other to such an extent that an exchange of genetic material never or only rarely occurs. Such isolation is common in populations confined to different lakes, as shown in Figure 13.9, or islands. For example, each population of Galápagos tortoises is restricted to its own island. Not all populations have such sharp boundaries. However, members of a population typically breed with one another and are therefore more closely related to each other than they are to members of a different population.

In studying evolution at the population level, biologists focus on the **gene pool**, which consists of all copies of every type of allele at every locus in all members of the population. For many loci, there are two or more alleles in the gene pool. For example, in a mosquito population, there may be two alleles relating to DDT breakdown, one that codes for an enzyme that breaks down DDT and one for a version of the enzyme that does not. In populations living in fields sprayed with DDT, the allele for the enzyme conferring resistance will increase in frequency and the other allele will decrease in frequency. When the relative frequencies of alleles in a population change like this over a number of generations, evolution is occurring on its smallest scale. Such a change in a gene pool is often called **microevolution**.

In the next module, we'll explore how to test whether evolution is occurring in a population.

? Why can't an individual evolve?

Evolution involves changes in the genetic makeup of a population over time. An individual's genetic makeup rarely changes during its lifetime.

▲ Figure 13.9 Lakes in Alaska containing isolated populations

13.10 The Hardy-Weinberg equation can test whether a population is evolving

To understand how microevolution works, let's first examine a simple population in which evolution is not occurring and thus the gene pool is not changing. Consider an imaginary population of iguanas with individuals that differ in foot webbing (**Figure 13.10A**). Let's assume that foot webbing is controlled by a single gene and that the allele for nonwebbed feet (W) is completely dominant to the allele for webbed feet (w). The term *dominant* (see Module 9.3) may seem to suggest that over many generations, the W allele will somehow come to "dominate," becoming more and more common at the expense of the recessive allele. In fact, this is not what happens. The shuffling of alleles that accompanies sexual reproduction does not alter the genetic makeup of the population. In other words, no matter how many times alleles are segregated into different gametes and united in different combinations by fertilization, the frequency of each allele in the gene pool will remain constant unless other factors are operating. This condition is known as the **Hardy-Weinberg equilibrium** named for the two scientists who derived it independently in 1908.

▲ **Figure 13.10A** Imaginary iguanas, with and without foot webbing

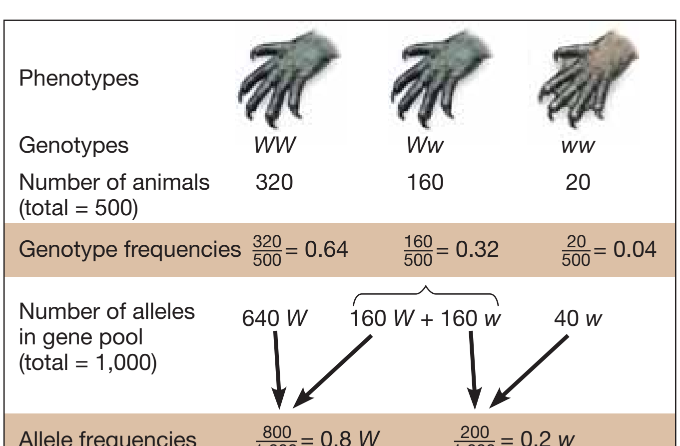
To test the Hardy-Weinberg equilibrium, let's look at two generations of our imaginary iguana population. **Figure 13.10B** shows the frequencies of alleles in the gene pool of the original population. We have a total of 500 animals; of these, 320 have the genotype WW (nonwebbed feet), 160 have the heterozygous genotype, Ww (also nonwebbed feet, because the nonwebbed allele W is dominant), and 20 have the genotype ww (webbed feet). The proportions or frequencies of the three genotypes are shown in the middle of Figure 13.10B: 0.64 for $WW\left(\frac{320}{500}\right)$, 0.32 for $Ww\left(\frac{160}{500}\right)$, and 0.04 for $ww\left(\frac{20}{500}\right)$.

From these genotype frequencies, we can calculate the frequency of each allele in the population. Because these are diploid organisms, this population of 500 has a total of 1,000 alleles for foot type. To determine the number of W alleles, we add the number in the WW iguanas, $2 \times 320 = 640$, to the number in the Ww iguanas, 160. The total number of W alleles is thus 800. The frequency of the W allele, which we will call p, is $\frac{800}{1,000}$, or 0.8. We can calculate the frequency of the w allele in a similar way; this frequency, called q, is 0.2.

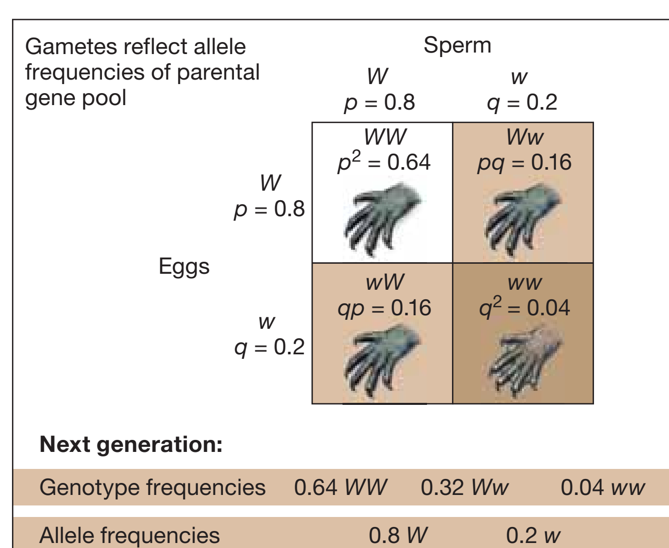
The letters p and q are often used to represent allele frequencies. Notice that $p + q = 1$. The combined frequencies of all alleles for a gene in a population must equal 1. If there are only two alleles and you know the frequency of one allele, you can calculate the frequency of the other.

What happens when the iguanas of this parent population form gametes? At the end of meiosis, each gamete has one allele for foot type, either W or w. The frequencies of the two alleles in the gametes will be the same as their frequencies in the gene pool of the parental population, 0.8 for W and 0.2 for w.

Figure 13.10C shows a Punnett square that uses these gamete allele frequencies and the rule of multiplication (see Module 9.7) to calculate the frequencies of the three genotypes in the next generation. The probability of producing a WW individual (by combining two W alleles from the pool of gametes) is $p \times p = p^2$, or $0.8 \times 0.8 = 0.64$. Thus, the frequency of WW iguanas in the next generation would be 0.64. Likewise, the frequency of ww individuals would be $q^2 = 0.04$. For heterozygous individuals, Ww, the genotype can form in two ways, depending on whether the sperm or egg supplies the dominant allele. In other words, the frequency of Ww would be $2pq = 2 \times 0.8 \times 0.2 = 0.32$. Do these frequencies look familiar? Notice that the three genotypes have the same frequencies in the next generation as they did in the parent generation.



▲ **Figure 13.10B** Gene pool of the original population of imaginary iguanas



▲ **Figure 13.10C** Gene pool of the next generation of imaginary iguanas

Finally, what about the frequencies of the alleles in this new generation? Because the genotype frequencies are the same as in the parent population, the allele frequencies p and q are also the same. In fact, we could follow the frequencies of alleles and genotypes through many generations, and the results would continue to be the same. Thus, the gene pool of this population is in a state of equilibrium—Hardy-Weinberg equilibrium.

Now let's write a general formula for calculating the frequencies of genotypes in a population from the frequencies of alleles in the gene pool. In our imaginary iguana population, the frequency of the *W* allele (p) is 0.8, and the frequency of the *w* allele (q) is 0.2. Again note that $p + q = 1$. Also notice in Figures 13.10B and 13.10C that the frequencies of the three possible genotypes in the populations also add up to 1 (that is, $0.64 + 0.32 + 0.04 = 1$). We can represent these relationships symbolically with the Hardy-Weinberg equation:

$$\underset{\text{Frequency of homozygous dominants}}{p^2} + \underset{\text{Frequency of heterozygotes}}{2pq} + \underset{\text{Frequency of homozygous recessives}}{q^2} = 1$$

If a population is in Hardy-Weinberg equilibrium, allele and genotype frequencies will remain constant generation after generation. Something other than the reshuffling processes of sexual reproduction is required to change allele frequencies in a population. One way to find out what factors *can* change a gene pool is to identify the conditions that must be met if genetic equilibrium is to be maintained.

For a population to be in Hardy-Weinberg equilibrium, it must satisfy five main conditions:

1. Very large population. The smaller the population, the more likely that allele frequencies will fluctuate by chance from one generation to the next.
2. No gene flow between populations. When individuals move into or out of populations, they add or remove alleles, altering the gene pool.
3. No mutations. By changing alleles or deleting or duplicating genes, mutations modify the gene pool.
4. Random mating. If individuals mate preferentially, such as with close relatives (inbreeding), random mixing of gametes does not occur, and genotype frequencies change.
5. No natural selection. The unequal survival and reproductive success of individuals (natural selection) can alter allele frequencies.

Because all five conditions are rarely met in real populations, allele and genotype frequencies often do change. The Hardy-Weinberg equation can be used to test whether evolution is occurring in a population. The equation also has medical applications, as we see next.

? Which is *least* likely to alter allele and genotype frequencies in a few generations of a large, sexually reproducing population: gene flow, mutation, or natural selection? Explain.

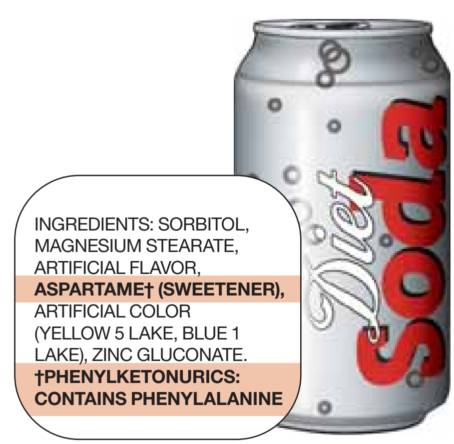
■ Mutation. Because mutations are rare, their effect on allele and genotype frequencies from one generation to the next is likely to be small.

13.11 The Hardy-Weinberg equation is useful in public health science

CONNECTION

Public health scientists use the Hardy-Weinberg equation to estimate how many people carry alleles for certain inherited diseases. Consider the case of phenylketonuria (PKU), an inherited inability to break down the amino acid phenylalanine that results in brain damage if untreated. Newborns are routinely screened for PKU, which occurs in about one out of 10,000 babies born in the United States. The health problems associated with PKU can be prevented by strict adherence to a diet that limits the intake of phenylalanine. Packaged foods with ingredients such as aspartame, a common artificial sweetener that contains phenylalanine, must be labeled clearly **(Figure 13.11)**.

PKU is due to a recessive allele, so the frequency of individuals born with PKU corresponds to the q^2 term in the Hardy-Weinberg equation. Given one PKU occurrence per 10,000 births, $q^2 = 0.0001$. Therefore, the frequency of the recessive allele for PKU in the population, q, equals the square root of 0.0001, or 0.01. And the frequency of the dominant allele, p, equals $1 - q$, or 0.99. The frequency of carriers, heterozygous people who do not have PKU but may pass the PKU allele on to offspring, is $2pq$, which equals $2 \times 0.99 \times 0.01$, or 0.0198. Thus, the equation tells us that about 2% (actually 1.98%) of the U.S. population are carriers of the PKU allele. Estimating the frequency of a harmful allele is part of any public health program dealing with genetic diseases.



▲ **Figure 13.11** A warning to individuals with PKU

? Which term in the Hardy-Weinberg equation—p^2, $2pq$, or q^2—corresponds to the frequency of individuals who have no alleles for the disease PKU?

■ The frequency of individuals with no PKU alleles is p^2.

Mechanisms of Microevolution

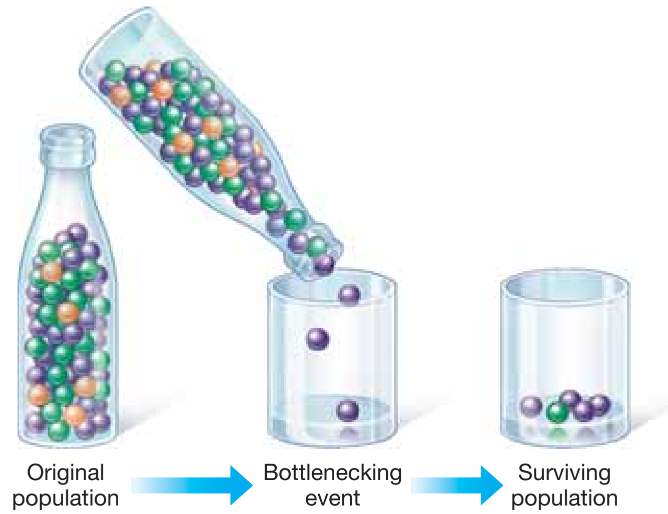
13.12 Natural selection, genetic drift, and gene flow can cause microevolution

Deviations from the five conditions named in Module 13.10 for Hardy-Weinberg equilibrium can alter allele frequencies in a population (microevolution). Although new genes and new alleles originate by mutation, these random and rare events probably change allele frequencies little within a population of sexually reproducing organisms. Nonrandom mating can affect the frequencies of homozygous and heterozygous genotypes, but by itself usually does not affect allele frequencies. The three main causes of evolutionary change are natural selection, genetic drift, and gene flow.

Natural Selection The condition for Hardy-Weinberg equilibrium that there be no natural selection—that all individuals in a population be equal in ability to reproduce—is probably never met in nature. Populations consist of varied individuals, and some variants leave more offspring than others. In our imaginary iguana population, individuals with webbed feet (genotype *ww*) might survive better and produce more offspring because they are more efficient at swimming and catching food than individuals that lack webbed feet. Genetic equilibrium would be disturbed as the frequency of the *w* allele increased in the gene pool from one generation to the next.

Genetic Drift Flip a coin a thousand times, and a result of 700 heads and 300 tails would make you suspicious about that coin. But flip a coin 10 times, and an outcome of 7 heads and 3 tails would seem within reason. The smaller the sample, the more likely that chance alone will cause a deviation from an idealized result—in this case, an equal number of heads and tails. Let's apply that logic to a population's gene pool. The frequencies of alleles will be more stable from one generation to the next when a population is large. In a process called **genetic drift**, chance events can cause allele frequencies to fluctuate unpredictably from one generation to the next. The smaller the population, the more impact genetic drift is likely to have. In fact, an allele can be lost from a small population by such chance fluctuations. Two situations in which genetic drift can have a significant impact on a population are those that produce the bottleneck effect and the founder effect.

Catastrophes such as hurricanes, floods, or fires may kill large numbers of individuals, leaving a small surviving population that is unlikely to have the same genetic makeup as the original population. Such a drastic reduction in population size is called a **bottleneck effect**. Analogous to shaking just a few marbles through a bottleneck (Figure 13.12A), certain alleles (purple marbles) may be present at higher frequency in the surviving population than in the original population, others (green marbles) may be present at lower frequency, and some (orange marbles) may not be present at all. After a population is drastically reduced, genetic drift may continue for many generations until the population is again large enough for fluctuations due to chance to have less of an impact. Even if a population that has passed through a bottleneck ultimately recovers its size, it may have low levels of genetic variation—a legacy of the genetic drift that occurred when the population was small.



▲ **Figure 13.12A** The bottleneck effect

One reason it is important to understand the bottleneck effect is that human activities such as overhunting and habitat destruction may create severe bottlenecks for other species. Examples of species affected by bottlenecks include the endangered Florida panther, the African cheetah, and the greater prairie chicken (Figure 13.12B). Millions of these birds once lived on the prairies of Illinois. But as their habitat was converted to farmland and other uses during the 19th and 20th centuries, the number of greater prairie chickens plummeted. By 1993, only two Illinois populations remained, with a total of fewer than 50 birds. Less than 50% of the eggs of these birds hatched. Researchers compared the DNA of the 1993 population with DNA extracted from museum specimens dating back to the 1930s. They surveyed six gene loci and found that the modern birds had lost 30% of the alleles that were present in

▲ **Figure 13.12B** Greater prairie chicken (*Tympanuchus cupido*) the museum specimens. Thus, genetic drift as a result of the bottleneck reduced the genetic variation of the population and may have increased the frequency of harmful alleles, leading to the low egg-hatching rate.

Genetic drift is also likely when a few individuals colonize an island or other new habitat, producing what is called the **founder effect**. The smaller the group, the less likely that the genetic makeup of the colonists will represent the gene pool of the larger population they left.

The founder effect explains the relatively high frequency of certain inherited disorders among some human populations established by small numbers of colonists. For example, in 1814, 15 people founded a colony on Tristan da Cunha, a group of small islands in the middle of the Atlantic Ocean. Apparently, one of the colonists carried a recessive allele for retinitis pigmentosa, a progressive form of blindness. Of the 240 descendants who still lived on the islands in the 1960s, four had retinitis pigmentosa, and at least nine others were known to be heterozygous carriers of the allele. The frequency of this allele is 10 times higher on Tristan da Cunha than in the British population from which the founders came.

Gene Flow Allele frequencies in a population can also change as a result of **gene flow**, by which a population may gain or lose alleles when fertile individuals move into or out of a population or when gametes (such as plant pollen) are transferred between populations. Gene flow tends to reduce differences between populations. For example, humans today move more freely about the world than in the past, and gene flow has become an important agent of microevolutionary change in previously isolated human populations.

Let's return to the Illinois greater prairie chickens and see how gene flow improved their fate. To counteract the lack of genetic diversity, researchers added a total of 271 birds from neighboring states to the Illinois populations. This strategy worked. New alleles entered the population, and the egg-hatching rate improved to more than 90%.

? How might gene flow between populations living in different habitats actually interfere with each population's adaptation to its local environment?

The introduction of alleles that may not be beneficial in a particular habitat prevents the population living there from becoming fully adapted to its local conditions.

13.13 Natural selection is the only mechanism that consistently leads to adaptive evolution

Genetic drift, gene flow, and even mutation can cause microevolution. But only by chance could these events result in improving a population's fit to its environment. In natural selection, on the other hand, only the events that produce genetic variation (mutation and sexual reproduction) are random. The process of natural selection, in which better-adapted individuals are more likely to survive and reproduce, is *not* random. Consequently, only natural selection consistently leads to adaptive evolution—evolution that results in a better fit between organisms and their environment.

The adaptations of organisms include many striking examples. Consider these examples of STRUCTURE AND FUNCTION that make the blue-footed booby suited to its home on the Galápagos Islands (Figure 13.13). The bird's body and bill are streamlined like a torpedo, minimizing friction as it dives from heights up to 24 m (more than 75 feet) into the shallow water below. To pull out of this high-speed dive once it hits the water, the booby uses its large tail as a brake. Its large, webbed feet make great flippers, propelling the bird through the water at high speeds—a huge advantage when hunting fish.

▲ **Figure 13.13** Blue-footed booby (*Sula nebouxii*)

Such adaptations are the result of natural selection. By consistently favoring some alleles over others, natural selection improves the match between organisms and their environment. However, the environment may change over time. As a result, what constitutes a "good match" between an organism and its environment is a moving target, making adaptive evolution a continuous, dynamic process.

Let's take a closer look at natural selection. The commonly used phrase "survival of the fittest" is misleading if we take it to mean direct competition between individuals. There are animal species in which individuals lock horns or otherwise do combat to determine mating privilege. But reproductive success is generally more subtle and passive. In a varied population of moths, certain individuals may produce more offspring than others because their wing colors hide them from predators better. Plants in a wildflower population may differ in reproductive success because the slight variations in color, shape, or fragrance of some flowers attract more pollinators. In a given environment, such 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. The fittest individuals in the context of evolution are those that produce the largest number of viable, fertile offspring and thus pass on the most genes to the next generation.

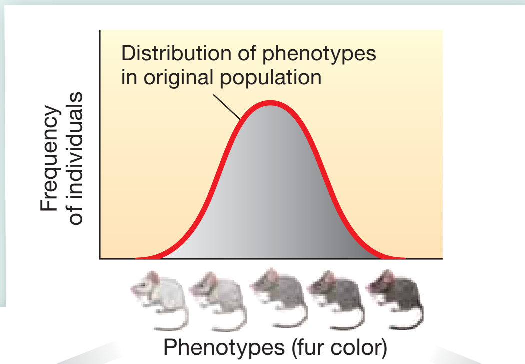
? Explain how the phrase "survival of the fittest" differs from the biological definition of relative fitness.

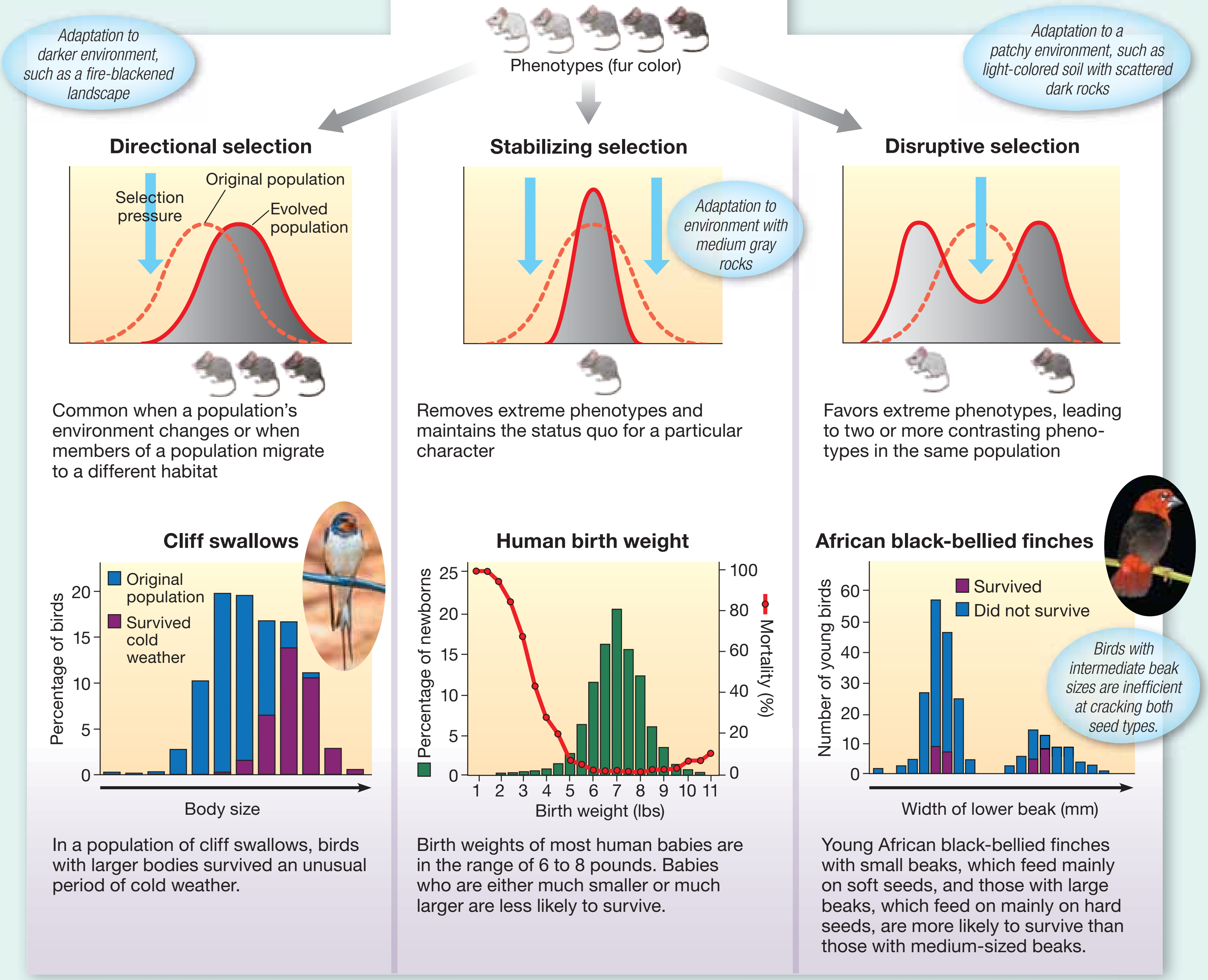
Survival alone does not guarantee reproductive success. An organism's relative fitness is determined by its number of fertile offspring and thus its relative contribution to the gene pool of the next generation.

VISUALIZING THE CONCEPT

13.14 Natural selection can alter variation in a population in three ways

Evolutionary fitness is related to genes, but it is an organism's phenotype—its physical traits, metabolism, and behavior—that is directly exposed to the environment. Depending on which phenotypes in a population are favored by natural selection, three general outcomes are possible. **Directional selection** shifts the overall makeup of the population by acting against individuals at one of the phenotypic extremes. **Stabilizing selection** favors intermediate phenotypes. **Disruptive selection** typically occurs when environmental conditions vary in a way that favors individuals at both ends of a phenotypic range over individuals with intermediate phenotypes. To visualize how each mode of selection affects the distribution of phenotypes, let's look at an imaginary mouse population that has a heritable variation in fur coloration. The graphs at the bottom of the page show an example of each mode of selection in a natural population.





? **What type of selection probably resulted in the color variations evident in the garter snakes in Figure 13.8?**

Disruptive selection

13.15 Sexual selection may lead to phenotypic differences between males and females

Darwin was the first to examine **sexual selection**, a form of natural selection in which individuals with certain traits are more likely than other individuals to obtain mates. The males and females of an animal species obviously have different reproductive organs. But they may also have secondary sexual characteristics, noticeable differences not directly associated with reproduction or survival. This distinction in appearance, called **sexual dimorphism**, is often manifested in a size difference, but it can also include forms of adornment, such as manes on lions or colorful plumage on birds **(Figure 13.15A)**. Males are usually the showier sex, at least among vertebrates.

In some species, individuals compete directly with members of the same sex for mates **(Figure 13.15B)**. This type of sexual selection is called intrasexual selection (within the same sex, most often the males). Contests may involve physical combat but are more often ritualized displays (see Module 35.19). Intrasexual selection is frequently found in species where the winning individual acquires a harem of mates.

In a more common type of sexual selection, called intersexual selection (between sexes) or mate choice, individuals of one sex (usually females) are choosy in selecting their mates. Males with the largest or most colorful adornments are often the most attractive to females. The extraordinary feathers of a peacock's tail are an example of this sort of "choose me" statement. What intrigued Darwin is that some of these mate-attracting features do not seem to be otherwise adaptive and may in fact pose some risks. For example, showy plumage may make male birds more visible to predators. But if such secondary sexual characteristics help a male gain a mate, then they will be reinforced over the generations for the most Darwinian of reasons—because they enhance reproductive success. Every time a female chooses a mate based on a certain appearance or behavior, she perpetuates the alleles that influenced her to make that choice and allows a male with that particular phenotype to perpetuate his alleles.

What is the advantage to females of being choosy? One hypothesis is that females prefer male traits that are correlated with "good genes." In several bird species, research has shown that traits preferred by females, such as bright beaks or long tails, are related to overall male health. The "good genes" hypothesis was also tested in gray tree frogs. Female frogs prefer to mate with males that give long mating calls **(Figure 13.15C)**. Researchers collected eggs from wild gray tree frogs. Half of each female's eggs were fertilized with sperm from long-calling males, and the others with sperm from short-calling males. The offspring of long-calling male frogs grew bigger, grew faster, and survived better than their half-siblings fathered by short-calling males. The duration of a male's mating call was shown to be indicative of the male's overall genetic quality, supporting the hypothesis that female mate choice can be based on a trait that indicates whether the male has "good genes."

Next we return to the concept of directional selection, focusing on the evolution of drug resistance in microorganisms that cause disease.

▲ **Figure 13.15A** Extreme sexual dimorphism (peacock and peahen)

▲ **Figure 13.15B** A contest for access to mates between two male elks

▲ **Figure 13.15C** A male gray tree frog calling for mates

? Males with the most elaborate ornamentation may garner the most mates. How might choosing such a mate be advantageous to a female?

■ An elaborate display may signal good health and therefore good genes, which in turn could be passed along to the female's offspring.

13.16 The evolution of drug-resistant microorganisms is a serious public health concern

EVOLUTION CONNECTION

As you probably know, antibiotics are drugs that kill infectious microorganisms. Before antibiotics, people often died from bacterial diseases such as whooping cough, and a minor wound—a razor nick or a scratch from a rose thorn—could result in a fatal infection. A new era in human health followed the introduction of penicillin, the first widely used antibiotic, in the 1940s. Suddenly, many diseases that had often been fatal could easily be cured.

Medical experts now fear that the process of evolution could end the era of antibiotics. In the same way that pesticides select for resistant insects, antibiotics select for resistant bacteria. A gene that codes for an enzyme that breaks down an antibiotic or a mutation that alters the binding site of an antibiotic can make a bacterium and its offspring resistant to that antibiotic. Again we see both the random and nonrandom aspects of natural selection—the random genetic mutations in bacteria and the nonrandom selective effects as the environment favors the antibiotic-resistant phenotype. The same explanation applies to the evolution of chloroquine resistance in populations of the parasitic microbe that causes malaria, which you learned about in the chapter introduction. It's only a matter of time before the effectiveness of artemisinin is also lost to natural selection.

The rapid evolution of antibiotic resistance has been fueled by their widespread use—and misuse. Livestock producers add antibiotics to animal feed as a growth promoter and to prevent illness, practices that may select for bacteria resistant to standard antibiotics. Doctors may overprescribe antibiotics. Patients may stop taking the medication as soon as they feel better. This allows mutant bacteria that are killed more slowly by the drug to survive and multiply. Subsequent mutations in such bacteria may lead to full-blown antibiotic resistance.

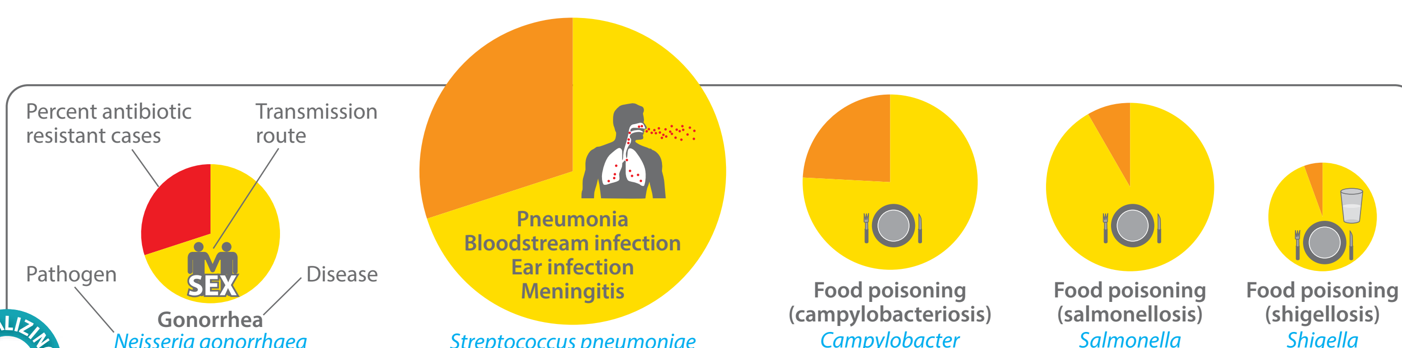
A formidable "superbug" known as MRSA (methicillin-resistant *Staphylococcus aureus*) was the first sign that the power of antibiotics might be fading. *S. aureus* ("staph") is common in health-care facilities, where natural selection for antibiotic resistance is strong because of the extensive use of antibiotics. Staph outbreaks also occur in community settings such as athletic facilities, schools, and military barracks. Some staph infections cause relatively minor skin disorders, but when bacteria invade the bloodstream, staph infections can be fatal. Although deaths from invasive MRSA acquired at health-care facilities have declined recently as a result of preventative measures, MRSA remains a serious threat to public health.

Medical and pharmaceutical researchers are engaged in a race against the powerful force of evolution on many fronts. In 2013, the Centers for Disease Control (CDC) reported that drug-resistant microorganisms infect more than 2 million people and cause 23,000 deaths in the United States each year. The CDC identified 15 microorganisms that pose urgent or serious threats to public health. Some of the infections are associated with health-care facilities; others are passed on by contaminated food and water, sexual contact, or droplets exhaled from the respiratory tract of an infected person. **Figure 13.16** shows the estimated percentage of infections by antibiotic-resistant strains for several diseases.

How does evolution hinder attempts to eradicate disease?

? **Explain why the following statement is incorrect: "Antibiotics have created resistant bacteria."**

■ The use of antibiotics did not cause bacteria to make new alleles. Rather, antibiotic use has increased the frequency of alleles for resistance that were already naturally present in bacterial populations.



VISUALIZING THE DATA

▲ **Figure 13.16** Urgent (red) and serious (orange) threats from antibiotic-resistant bacteria. Circle area represents the total numbers of infections; slices show the percent caused by antibiotic-resistant strains.

Data from Centers for Disease Control and Prevention, cdc.gov.

13.17 Diploidy and balancing selection preserve genetic variation

As natural selection acts on variants within a population, the population becomes better suited for life in its environment. But what prevents natural selection from eliminating all variation as it selects against unfavorable genotypes? Why aren't less adaptive alleles eliminated as the "best" alleles are passed to the next generation? It turns out that the tendency for natural selection to reduce variation in a population is countered by mechanisms that maintain variation.

Most eukaryotes are diploid. Having two sets of chromosomes helps to prevent populations from becoming genetically uniform. As you know, natural selection acts on the phenotype, and recessive alleles only influence the phenotype of a homozygous recessive individual. In a heterozygote, a recessive allele is, in effect, protected from natural selection. The "hiding" of recessive alleles in heterozygotes can maintain a huge pool of alleles that may not be favored under present conditions but that could be advantageous if the environment changes.

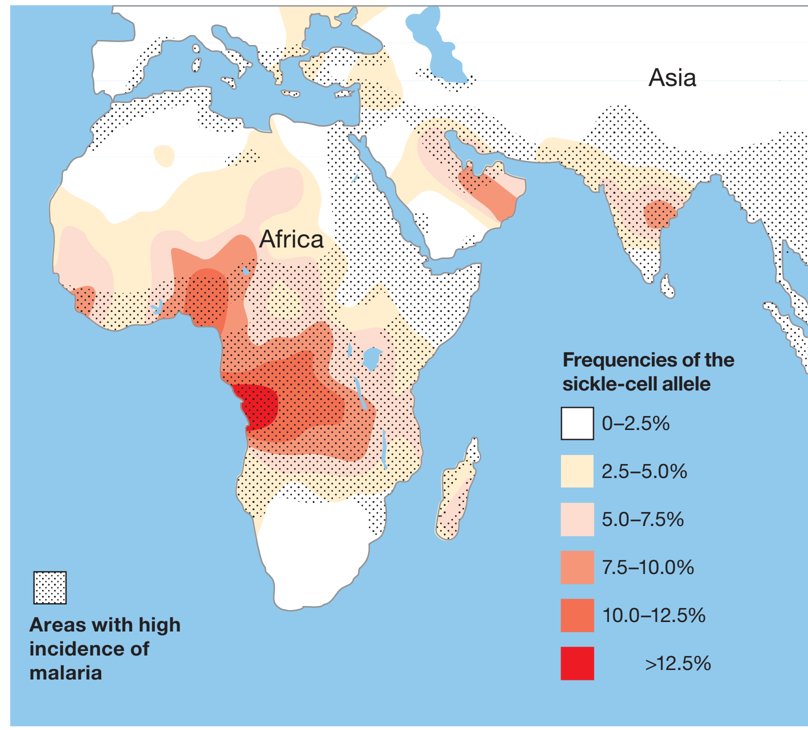
In some cases, genetic variation is preserved rather than reduced by natural selection. **Balancing selection** occurs when natural selection maintains stable frequencies of two or more phenotypic forms in a population.

Heterozygote advantage is a type of balancing selection in which heterozygous individuals have greater reproductive success than either type of homozygote, with the result that two or more alleles for a gene are maintained in the population. An example of heterozygote advantage is the protection from malaria conferred by sickle-cell hemoglobin (see Module 9.13). The frequency of the sickle-cell allele is generally highest in areas where malaria is a major cause of death, such as West Africa **(Figure 13.17)**. Heterozygotes are protected from the most severe effects of malaria. Individuals who are homozygous for the normal hemoglobin allele are selected against by malaria. Individuals homozygous for the sickle-cell allele are selected against by sickle-cell disease. Thus, sickle-cell hemoglobin is an evolutionary response to a fatal disease that first emerged in the environment of humans around 10,000 years ago. Notice that it is not an ideal solution—even heterozygotes may have health problems—but adaptations are often compromises.

Some of the genetic variation in a population probably has little or no impact on reproductive success. But even if only a fraction of the variation in a gene pool affects reproductive success, that is still an enormous resource of raw material for natural selection and the adaptive evolution it brings about.

? **Why would natural selection tend to reduce genetic variation more in populations of haploid organisms than in populations of diploid organisms?**

■ All alleles in a haploid organism are phenotypically expressed and are hence screened by natural selection.



Adapted from A.C. Allison, Abnormal hemoglobins and erythrovute enzyme-deficiency traits, Genetic variation in human populations, G.A. Harrison, ed. Oxford, *Elsevier Science* (1961).

▲ **Figure 13.17** **Map of malaria and sickle-cell allele**

13.18 Natural selection cannot fashion perfect organisms

Though natural selection leads to adaptation, there are several reasons why nature abounds with organisms that seem to be less than ideally "engineered" for their lifestyles.

1. *Selection can act only on existing variations*. Natural selection favors only the fittest variants from the phenotypes that are available, which may not be the ideal traits. New, advantageous alleles do not arise on demand.
2. *Evolution is limited by historical constraints*. Each species has a legacy of descent with modification from ancestral forms. Evolution does not scrap ancestral anatomy and build each new complex structure from scratch. Rather, it co-opts existing structures and adapts them to new situations. Thus, as birds and bats evolved from four-legged ancestors, their existing forelimbs took on new functions for flight and each lineage was left with only two limbs for walking.
3. *Adaptations are often compromises*. Each organism must do many different things. A blue-footed booby uses its webbed feet to swim after prey in the ocean, but these same feet make for clumsy travel on land.
4. *Chance, natural selection, and the environment interact*. Chance events often affect the genetic makeup of populations. When a storm blows insects over an ocean to an island, the wind does not necessarily transport the individuals that are best suited to the new environment. In small populations, genetic drift can result in the loss of beneficial alleles. In addition, the environment may change unpredictably from year to year, again limiting the extent to which adaptive evolution results in a close match between organisms and the environment.

With all these constraints, we cannot expect evolution to craft perfect organisms. Natural selection operates on a "better than" basis. Evidence for evolution is seen in the imperfections of the organisms it produces as well as in adaptations.

? **Humans owe much of their physical versatility and athleticism to their flexible limbs and joints. But we are prone to sprains, torn ligaments, and dislocations. Why?**

■ Adaptations are compromises: Structural reinforcement has been compromised as agility was selected for.

CHAPTER **13** REVIEW

For practice quizzes, BioFlix animations, MP3 tutorials, video tutors, and more study tools designed for this textbook, go to MasteringBiology™

REVIEWING THE CONCEPTS

Darwin's Theory of Evolution 13.1–13.7

13.1 A sea voyage helped Darwin frame his theory of evolution. Darwin's theory differed greatly from the long-held notion of a young Earth inhabited by unchanging species. Darwin called his theory descent with modification, which explains that all of life is connected by common ancestry and that descendants have accumulated adaptations to changing environments over vast spans of time.

13.2 The study of fossils provides strong evidence for evolution. The fossil record reveals the historical sequence in which organisms have evolved.

13.3 Fossils of transitional forms support Darwin's theory of evolution.

13.4 Homologies provide strong evidence for evolution. Structural and molecular homologies reveal evolutionary relationships.

13.5 Homologies indicate patterns of descent that can be shown on an evolutionary tree.

13.6 Darwin proposed natural selection as the mechanism of evolution.

Observations

Heritable variations in individuals → ← Overproduction of offspring

Inferences

Individuals well-suited to the environment tend to leave more offspring

and

Over time, favorable traits accumulate in the population

13.7 Scientists can observe natural selection in action.

The Evolution of Populations 13.8–13.11

13.8 Mutation and sexual reproduction produce the genetic variation that makes evolution possible.

13.9 Evolution occurs within populations. Microevolution is a change in the frequencies of alleles in a population's gene pool.

13.10 The Hardy-Weinberg equation can test whether a population is evolving. The Hardy-Weinberg equilibrium states that allele and genotype frequencies will remain constant if a population is large, mating is random, and there is no mutation, gene flow, or natural selection.

Allele frequencies	$p + q = 1$
Genotype frequencies	$\underbrace{p^2}_{\text{Dominant homozygotes}} + \underbrace{2pq}_{\text{Heterozygotes}} + \underbrace{q^2}_{\text{Recessive homozygotes}} = 1$

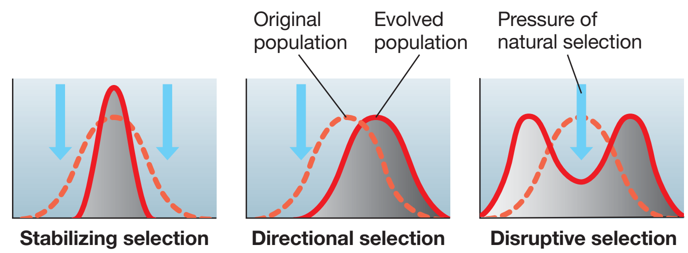
13.11 The Hardy-Weinberg equation is useful in public health science.

Mechanisms of Microevolution 13.12–13.18

13.12 Natural selection, genetic drift, and gene flow can cause microevolution. The bottleneck effect and founder effect lead to genetic drift.

13.13 Natural selection is the only mechanism that consistently leads to adaptive evolution. Relative fitness is the relative contribution an individual makes to the gene pool of the next generation. As a result of natural selection, favorable traits increase in a population.

13.14 Natural selection can alter variation in a population in three ways.



13.15 Sexual selection may lead to phenotypic differences between males and females. Secondary sex characteristics can give individuals an advantage in mating.

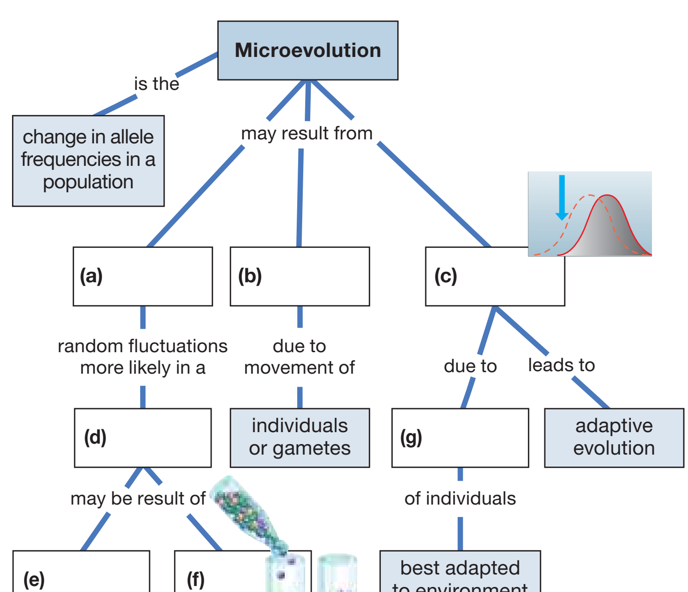
13.16 The evolution of drug-resistant microorganisms is a serious public health concern.

13.17 Diploidy and balancing selection preserve genetic variation. Diploidy preserves variation by "hiding" recessive alleles. Balancing selection may result from heterozygote advantage.

13.18 Natural selection cannot fashion perfect organisms. Natural selection can act only on available variation; anatomical structures result from modified ancestral forms; adaptations are often compromises; and chance, natural selection, and the environment interact.

CONNECTING THE CONCEPTS

1. Summarize the key points of Darwin's theory of descent with modification, including his proposed mechanism of evolution.
2. Complete this concept map describing potential causes of evolutionary change within populations.



TESTING YOUR KNOWLEDGE

Level 1: Knowledge/Comprehension

3. Which of the following did *not* influence Darwin as he synthesized the theory of evolution by natural selection?
   a. examples of artificial selection that produce large and relatively rapid changes in domesticated species
   b. Lyell's *Principles of Geology*, on gradual geologic changes
   c. comparisons of fossils with living organisms
   d. Mendel's paper describing the laws of inheritance
4. Natural selection is sometimes described as "survival of the fittest." Which of the following best measures an organism's fitness?
   a. how many fertile offspring it produces
   b. how strong it is when pitted against others of its species
   c. its ability to withstand environmental extremes
   d. how much food it is able to make or obtain
5. In an area of erratic rainfall, a biologist found that grass plants with alleles for curled leaves reproduced better in dry years, and plants with alleles for flat leaves reproduced better in wet years. This situation would tend to ________ . (*Explain your answer.*)
   a. cause genetic drift in the grass population.
   b. preserve genetic variation in the grass population.
   c. lead to stabilizing selection in the grass population.
   d. lead to uniformity in the grass population.
6. If an allele is recessive and lethal in homozygotes before they reproduce,
   a. the allele will be removed from the population by natural selection in approximately 1,000 years.
   b. the allele will likely remain in the population at a low frequency because it cannot be selected against in heterozygotes.
   c. the fitness of the homozygous recessive genotype is 0.
   d. both b and c are correct.
7. In a population with two alleles, *B* and *b*, the allele frequency of *b* is 0.4. *B* is dominant to *b*. What is the frequency of individuals with the dominant phenotype if the population is in Hardy-Weinberg equilibrium?
   a. 0.16
   b. 0.36
   c. 0.48
   d. 0.84
8. Within a few weeks of treatment with the drug 3TC, a patient's HIV population consists entirely of 3TC-resistant viruses. How can this result best be explained?
   a. HIV can change its surface proteins and resist vaccines.
   b. The patient must have become reinfected with a resistant virus.
   c. A few drug-resistant viruses were present at the start of treatment, and natural selection increased their frequency.
   d. HIV began making drug-resistant versions of its enzymes in response to the drug.

Level 2: Application/Analysis

9. In the late 1700s, machines that could blast through rock to build roads and railways were invented, exposing deep layers of rocks. How would you expect this development to aid the science of paleontology?
10. Write a paragraph briefly describing the kinds of scientific evidence for evolution.
11. In the early 1800s, French naturalist Jean Baptiste Lamarck suggested that the best explanation for the relationship of fossils to current organisms is that life evolves. He proposed that by using or not using its body parts, an individual may change its traits and then pass those changes on to its offspring. He suggested, for instance, that the ancestors of the giraffe had lengthened their necks by stretching higher and higher into the trees to reach leaves. Evaluate Lamarck's hypotheses from the perspective of present-day scientific knowledge.
12. Sickle-cell disease is caused by a recessive allele. Roughly one out of every 400 African Americans (0.25%) is afflicted with sickle-cell disease. Use the Hardy-Weinberg equation to calculate the percentage of African Americans who are carriers of the sickle-cell allele. (*Hint*: $q^2 = 0.0025$.)
13. It seems logical that natural selection would work toward genetic uniformity; the genotypes that are most fit produce the most offspring, increasing the frequency of adaptive alleles and eliminating less adaptive alleles. Yet there remains a great deal of genetic variation within populations. Describe factors that contribute to this variation.

Level 3: Synthesis/Evaluation

14. **SCIENTIFIC THINKING** Cetaceans are fully aquatic mammals that evolved from terrestrial ancestors. Gather information about the respiratory system of cetaceans and describe how it illustrates the statement made in Module 13.18 that "Evolution is limited by historical constraints."
15. A population of snails is preyed on by birds that break the snails open on rocks, eat the soft bodies, and leave the shells. The snails occur in both striped and unstriped forms. In one area, researchers counted both live snails and broken shells. Their data are summarized below:

	Striped	Unstriped	Total	Percent Striped
Living	264	296	560	47.1
Broken	486	377	863	56.3

Which snail form seems better adapted to this environment? Why? Predict how the frequencies of striped and unstriped snails might change in the future.

16. Advocates of "scientific creationism" and "intelligent design" lobby school districts for such things as a ban on teaching evolution, equal time in science classes to teach alternative versions of the origin and history of life, or disclaimers in textbooks stating that evolution is "just a theory." They argue that it is only fair to let students evaluate both evolution and the idea that all species were created by God as the Bible relates or that, because organisms are so complex and well adapted, they must have been created by an intelligent designer. Do you think that alternative views of evolution should be taught in science courses? Why or why not?

Answers to all questions can be found in Appendix 4.