

# Unit 4 MECHANISMS OF EVOLUTION



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the same subject area from Universidad Autónoma de Madrid, Spain. After completing two postdoctoral fellowships (one in Greece, the other in the United Kingdom), she worked for several years as a Research Associate at Cambridge University, UK, before joining the faculty at Harvard. Dr. Extavour is a dedicated advocate for women and underrepresented groups in science, and she also has performed worldwide as a professional soprano.

## AN INTERVIEW WITH

### Cassandra Extavour

#### How did you first become interested in science?

Although my first love was music, and music remains an essential part of my life, toward the end of high school I also became quite interested in biology. My conversations with a friend who was fascinated by human behavior led me to wonder how the brain causes people to exhibit different behaviors. But how could I learn about that? My parents did not go to college. I didn't even know that there were careers in science that were not in medicine. I thought the only way to learn about the brain was to be a doctor. So I entered university as a pre-med. But by the time I was finishing my undergraduate studies, I had learned about research labs. I got a summer internship in a developmental genetics lab, and I loved it—it was like entering

a new world where I could figure out the answers to questions that interested me.

#### What are the main questions you are asking in your research?

I'm interested in understanding the genes that control embryonic development and how the function of those genes has changed in different organisms due to evolution. Take a human, for example. Our bodies have many different types of cells. The instructions for everything that each of our cells needs to do are contained in the cell's DNA. All of our cells have exactly same DNA. What's mysterious is, since every cell in the body has the same set of instructions, why aren't they all doing the same thing? I work mostly with insects, but the same question applies to them (and to all multicellular organisms). We're trying to figure out how the same set of genes is used in different ways by different cells. We're also interested in where these genes came from in the first place and how they have evolved over time.

#### Much of your research has been on "evo-devo." Say more about what that means.

Evo-devo stands for evolutionary developmental biology. Scientists in this field try to understand the difference in development between, let's say, a coconut and a rose. They're both plants, they both make seeds, they both make pollen, but they don't look the same at all. Why is that? Or the fact that, when you compare the development of a monkey and a human, you can't detect many differences in their

embryos or their genes. How can they be similar in so many ways and yet end up as such different organisms? In my lab, we are particularly interested in egg and sperm cells—known as germ cells. We're trying to figure out how an embryo determines which cells become germ cells and how it tells those cells, "Okay, listen: When the animal you are part of becomes an adult, you will need to make eggs and sperm." We've found that in some cases, the same genes are used by a variety of different species to make germ cells. But in other cases, we've been surprised to find that a gene used to produce germ cells in one organism is used to make a completely different type of cell in another closely related organism.

#### What do you find most rewarding about your job?

When I was in high school, I never would have thought that I could get paid to think of interesting questions and then try to answer them. I love doing that, and I love the amazing freedom that comes with my job—I get to decide what I'm going to do each day. But the best part is working with students as they gain the independence, knowledge, and confidence to listen to my suggestions and then say,

"I'm not sure that's the best experiment. Here's an experiment that I think would be better, and here's why." That is a great moment. What they are really saying is, "I'm not learning to be a scientist anymore—I am a scientist."

They've come to understand what scientists do: We make the best proposal we can, we test it as best we can, and we say, "This is what I think the results from my experiments mean."



▲ Embryo of the crustacean *Parhyale hawaiiensis* showing cells (in red) that will develop into germ cells

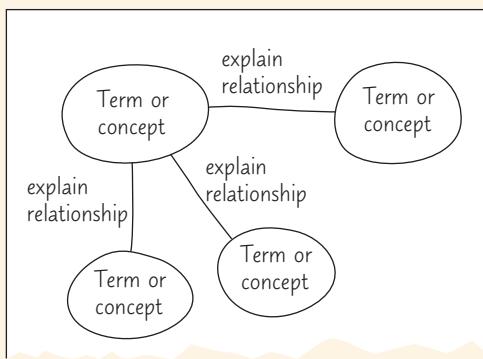
# 22 Descent with Modification: A Darwinian View of Life

## KEY CONCEPTS

- 22.1** The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species p. 469
- 22.2** Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life p. 471
- 22.3** Evolution is supported by an overwhelming amount of scientific evidence p. 476

## Study Tip

**Make a word cloud:** This chapter covers key topics related to evolution, such as descent with modification, heritable characteristics, natural selection, adaptation, convergent evolution, homology, and unity of life. Draw a “word cloud” of these terms: As you read the chapter, draw a line between terms that affect or relate to one another. Next to that line, briefly explain how those terms are connected.



## Go to Mastering Biology

### For Students (in eText and Study Area)

- Get Ready for Chapter 22
- Figure 22.17 Walkthrough: Tree Thinking
- Figure 22.20 Walkthrough: Transition to Life in the Sea
- BBC Video: A Future Without Antibiotics?

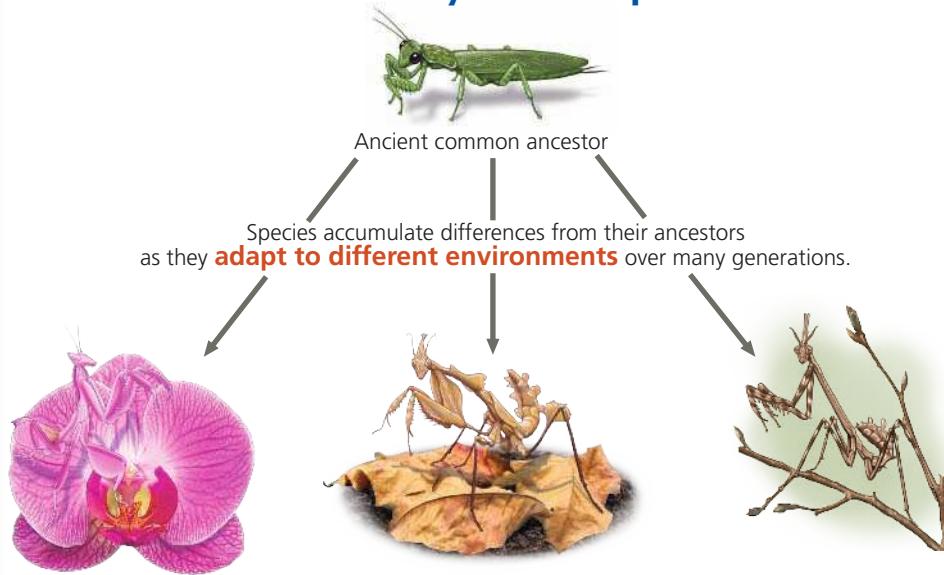
### For Instructors to Assign (in Item Library)

- HHMI Video: The Making of the Fittest: Natural Selection and Adaptation (Pocket Mouse)



**Figure 22.1** This Malaysian orchid mantis (*Hymenopus coronatus*) closely resembles the flower on which it rests, waiting for unwary prey to come within its reach. Other mantises have diverse shapes and colors that have evolved in different environments—yet all mantises also share certain features, such as grasping forelimbs, large eyes, and six legs.

## What causes the similarities and differences among Earth's many different species?



While different in some ways, these species share many similar features because they descended from a common ancestor. This process of

### descent with modification

shared ancestry, resulting in shared characteristics      accumulation of differences

has given rise to the **diversity of life**.

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

More than a century and a half ago, Charles Darwin was inspired to develop a scientific explanation for the *diversity of life*, the great number and remarkable variety of species on Earth. When he published his hypothesis in his book *The Origin of Species*, Darwin ushered in a scientific revolution—the era of evolutionary biology. As we'll see, Darwin developed his revolutionary ideas over time, influenced by the work of others and his travels (Figure 22.2).

## Endless Forms Most Beautiful

To set the stage for our study of Darwin and evolutionary biology, let's return to the well-hidden orchid mantis in Figure 22.1. This species is a member of a diverse group of

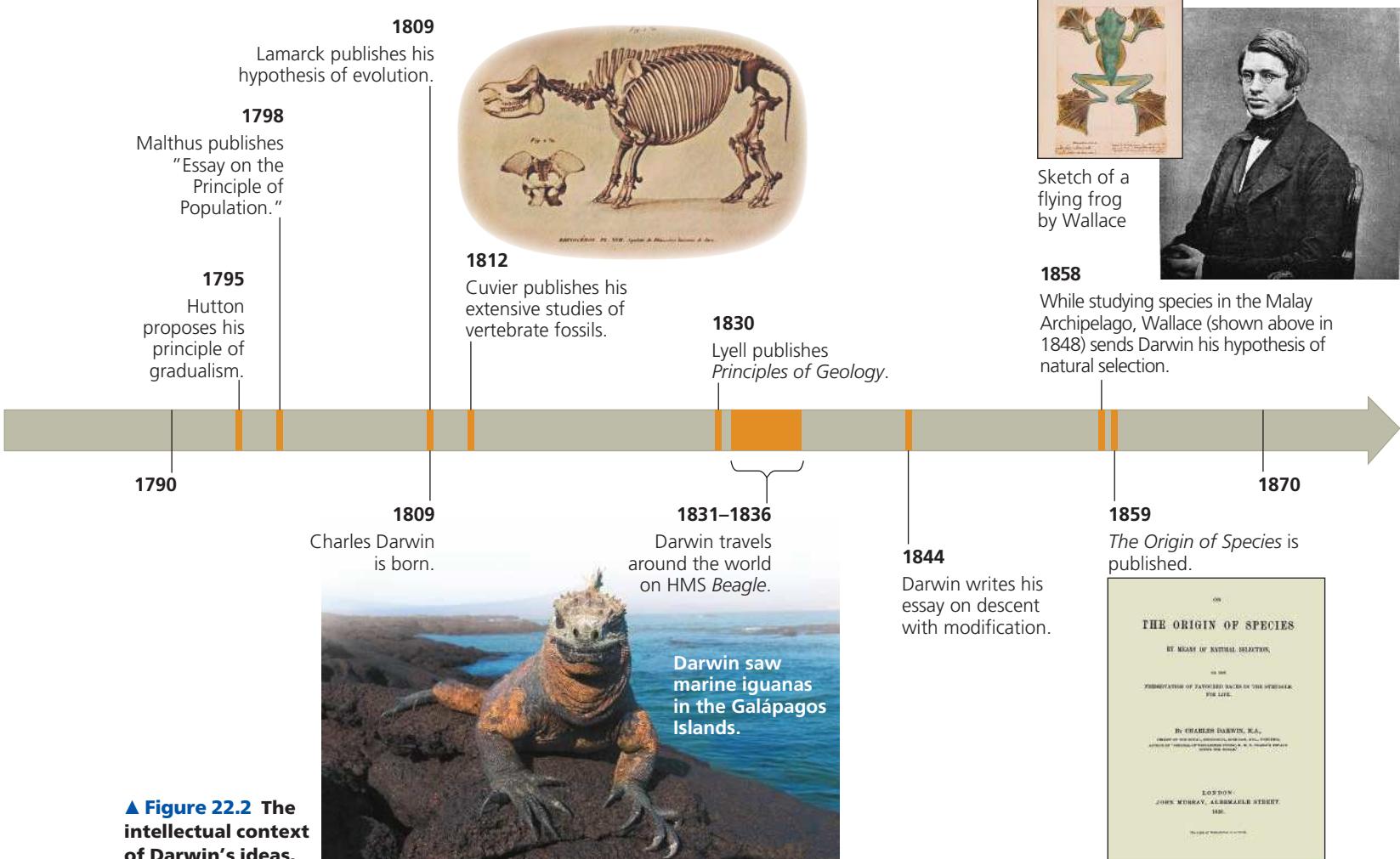
insects, the Mantodea, which includes 2,300 species in 430 genera. All these mantises share certain features, such as three pairs of legs, triangular heads with bulging eyes, and a flexible “neck.” Such shared features illustrate the unity of life, a phrase that highlights the fact that all organisms share characteristics.

But Earth's many different species also differ from one another. The mantises, for example, differ in features such as their size, shape, and color. Overall, the orchid mantis and its many close relatives illustrate three key observations about life:

- organisms are well suited (adapted) for life in their environments (Here and throughout this text, the term *environment* refers to other organisms as well as to the physical aspects of an organism's surroundings.)
- the many shared characteristics (unity) of life
- the rich diversity of life

Darwin, a keen observer of nature since childhood, set out to explain these three broad observations—an effort that eventually led him to conclude that life evolves over time.

For now, we will define **evolution** as *descent with modification*, a phrase Darwin used to summarize the process



by which species accumulate differences from their ancestors as they adapt to different environments over time. Evolution can also be defined as a change in the genetic composition of a population from generation to generation (see Concept 23.3).

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

As with all general theories in science, we continue to test our understanding of evolution by examining whether it can account for new observations and experimental results. In this and the following chapters, we'll examine how ongoing discoveries shape what we know about the pattern and process of evolution.

We'll begin our exploration of these discoveries by retracing Darwin's quest to explain the adaptations, unity, and diversity of what he called life's "endless forms most beautiful."

## Scala Naturae and Classification of Species

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

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

One such scientist was Carolus Linnaeus (1707–1778), a Swedish physician and botanist who sought to classify life's diversity, in his words, "for the greater glory of God." In the 1750s, Linnaeus developed the two-part, or *binomial*, format for naming species (such as *Homo sapiens* for humans) that is still used today. In contrast to the linear hierarchy of the *scala naturae*, Linnaeus used a nested classification system, grouping similar species into increasingly inclusive categories. For example, similar species are grouped in the same genus,

similar genera (plural of genus) are grouped in the same family, and so on.

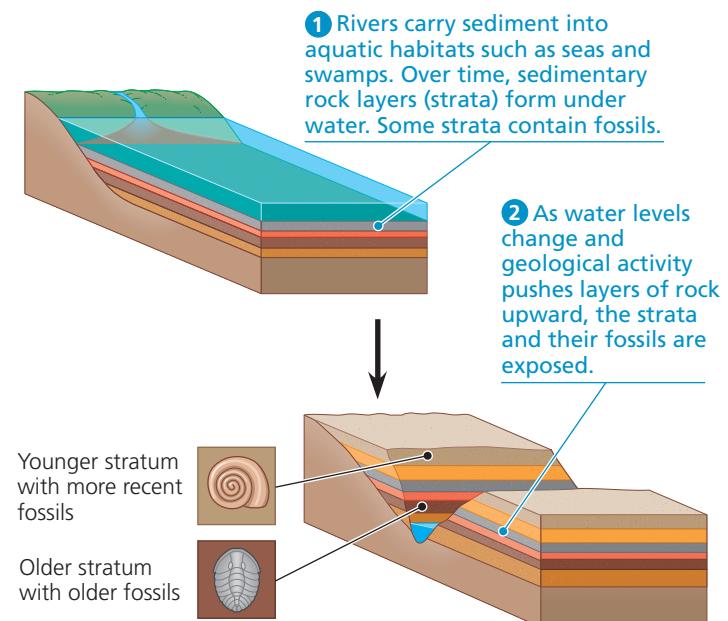
Linnaeus did not ascribe the resemblances among species to evolutionary kinship, but rather to the pattern of their creation. A century later, however, Darwin argued that classification should be based on evolutionary relationships. He also noted that scientists using the Linnaean system often grouped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

## Ideas About Change over Time

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

**Paleontology**, the study of fossils, was developed in large part by French scientist Georges Cuvier (1769–1832). In examining strata near Paris, Cuvier noted that the older the stratum, the more dissimilar its fossils were to current life-forms. He also observed that from one layer to the next, some new species appeared while others disappeared. He inferred that extinctions must have been a common occurrence, but he staunchly opposed the idea of evolution. Cuvier speculated that each boundary between strata represented a sudden catastrophic

▼ Figure 22.3 Formation of sedimentary strata with fossils.



→ Mastering Biology Video: Grand Canyon

event, such as a flood, that had destroyed many of the species living in that area. Such regions, he reasoned, were later repopulated by different species immigrating from other areas.

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

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

## Lamarck's Hypothesis of Evolution

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

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

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

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



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

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

### CONCEPT CHECK 22.1

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

*For suggested answers, see Appendix A.*

### CONCEPT 22.2

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

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

### Darwin's Research

Charles Darwin (1809–1882) was born in Shrewsbury, in western England. Even as a boy, he had a consuming interest in nature. When he was not reading nature books, he was fishing, hunting, riding, and collecting insects. However,

Darwin's father, a physician, could see no future for his son as a naturalist and sent him to medical school in Edinburgh. But Charles found medicine boring and surgery before the days of anesthesia horrifying. He quit medical school and enrolled at Cambridge University, intending to become a clergyman. (At that time, many scholars of science belonged to the clergy.)

At Cambridge, Darwin became the protégé of John Henslow, a botany professor. Soon after Darwin graduated, Henslow recommended him to Captain Robert FitzRoy, who was readying the survey ship HMS *Beagle* for a voyage around the world. Darwin would pay his own way and serve as a conversation partner to the young captain. FitzRoy, who was himself an adept scientist, accepted Darwin because he was a skilled naturalist and they were of similar age and social class.

### The Voyage of the Beagle

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

Darwin also spent much time thinking about geology. Despite repeated bouts of seasickness, he read Lyell's *Principles*

of Geology during the voyage. He experienced geologic change firsthand when a violent earthquake shook the coast of Chile, and he observed afterward that rocks along the coast had been thrust upward by several meters. Finding fossils of ocean organisms high in the Andes, Darwin inferred that the rocks containing the fossils must have been raised there by many similar earthquakes. These observations reinforced what he had learned from Lyell: Physical evidence did not support the traditional view that Earth was only a few thousand years old.

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

### Darwin's Focus on Adaptation

During the voyage of the *Beagle*, Darwin observed many examples of **adaptations**, inherited characteristics of organisms that enhance their survival and reproduction in specific environments. Later, as he reassessed his observations, he began to perceive adaptation to the environment and the origin of new species as closely related processes. Could a new species arise

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



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



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



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



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

**MAKE CONNECTIONS** Review Figure 1.20. Circle the most recent common ancestor shared by the three species that eat insects. Are all of the descendants of that ancestor insect-eaters?

from an ancestral form by the gradual accumulation of adaptations to a different environment? From studies made years after Darwin's voyage, biologists have concluded that this is indeed what happened to a diverse group of finches found on the Galápagos Islands (see Figure 1.20). The finches' various beaks and behaviors are adapted to the specific foods available on their home islands (Figure 22.6). Darwin realized that explaining such adaptations was essential to understanding evolution. His explanation of how adaptations arise centered on **natural selection**, a process in which individuals that have certain inherited traits tend to survive and reproduce at higher rates than do other individuals *because of* those traits. By the early 1840s, Darwin had worked out the major features of his hypothesis. He set these ideas on paper in 1844, when he wrote a long essay on descent with modification and its underlying mechanism, natural selection. Yet he was still reluctant to publish his ideas, in part because he anticipated the uproar they would cause. During this time, Darwin continued to compile evidence in support of his hypothesis. By the mid-1850s, he had described his ideas to Lyell and a few others. Lyell, who was not yet convinced of evolution, nevertheless urged Darwin to publish on the subject before someone else came to the same conclusions and published first.

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

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

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

→ **Mastering Biology HHMI Video: The Origin of Species: The Making of a Theory**



## Ideas from *The Origin of Species*

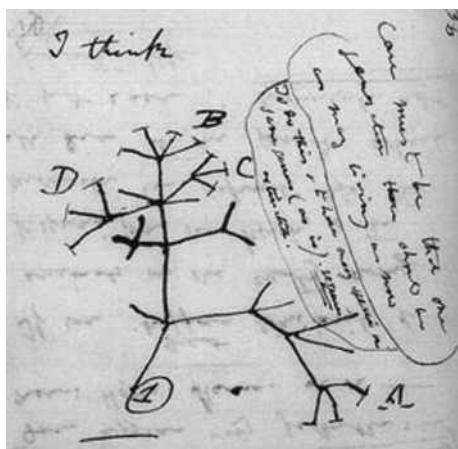
In his book, Darwin amassed evidence that descent with modification by natural selection explains three broad observations about nature—the unity of life, the diversity of life, and the striking ways in which organisms are suited for life in their environments.

### Descent with Modification

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

**► Figure 22.7**  
“I think . . .”  
In this 1837  
sketch, Darwin  
envisioned the  
branching pattern  
of evolution.

Branches that end in twigs labeled A–D represent particular groups of living organisms; all other branches represent extinct groups.



Darwin reasoned that over a long period of time, descent with modification eventually led to the rich diversity of life we see today. He viewed the history of life as a tree, with multiple branchings from a common trunk out to the tips of the youngest twigs (**Figure 22.7**). In his diagram, the tips of the twigs that are labeled A–D represent several groups of organisms living in the present day, while the unlabeled branches represent groups that are extinct. Each fork of the tree represents the most recent common ancestor of all the lines of evolution that subsequently branch from that point.

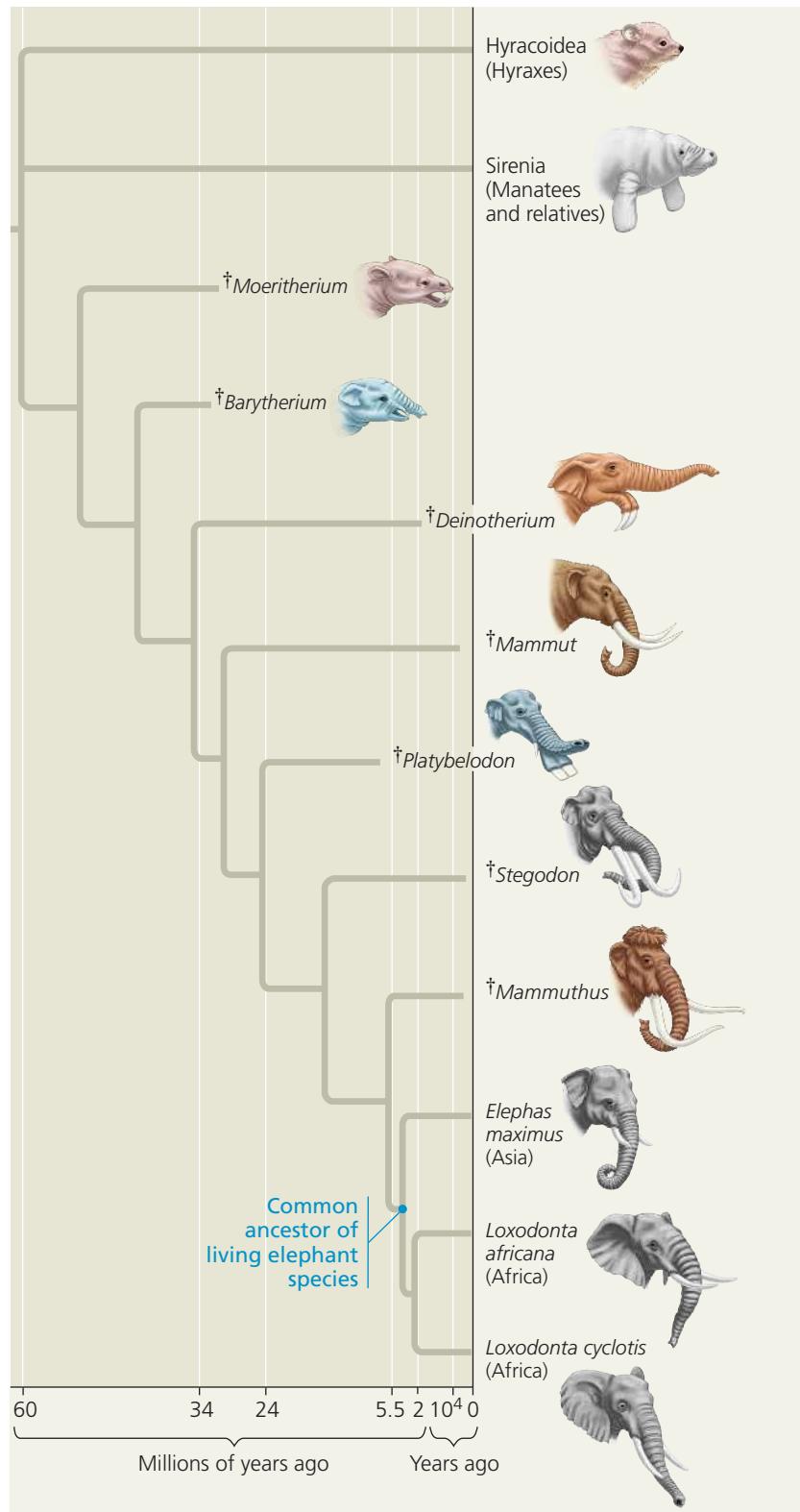
Darwin thought that such a branching process, along with past extinction events, could explain the large morphological gaps that sometimes exist between related groups of organisms. As an example, let's consider the three living species of elephants: the Asian elephant (*Elephas maximus*) and two species of African elephants (*Loxodonta africana* and *L. cyclotis*). These closely related species are very similar because they shared the same line of descent until a relatively recent split from their common ancestor, as shown in the tree diagram in **Figure 22.8**. Note that seven lineages related to elephants have become extinct over the past 32 million years. As a result, there are no living species that fill the morphological gap between the elephants and their nearest relatives today, the hyraxes and manatees.

Extinctions like those in Figure 22.8 are common. In fact, many evolutionary branches, even some major ones, are dead ends: Scientists estimate that over 99% of all species that have ever lived are now extinct. As in Figure 22.8, fossils of extinct species can document the divergence of present-day groups by “filling in” gaps between them.

### Artificial Selection, Natural Selection, and Adaptation

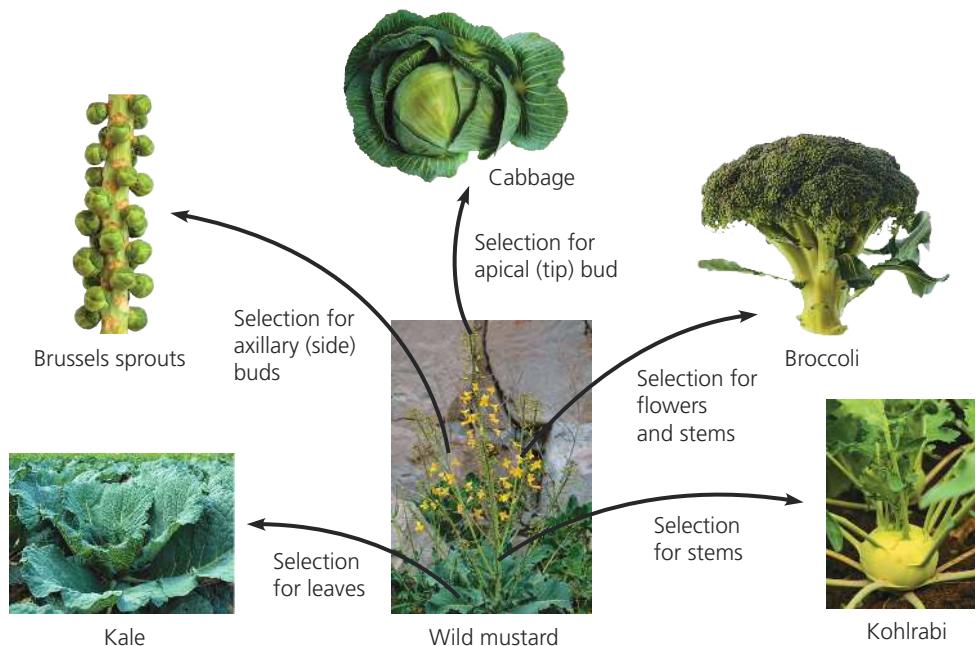
Darwin proposed the mechanism of natural selection to explain the observable patterns of evolution. He crafted his argument carefully, hoping to persuade even the most skeptical readers. First he discussed familiar examples of selective breeding of domesticated plants and animals. Humans have modified other species over many generations by selecting and breeding individuals that possess desired traits, a process

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



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

► **Figure 22.9 Artificial selection.** These different vegetables have all been selected from one species of wild mustard (*Brassica oleracea*). By selecting variations in different parts of the plant, breeders have obtained these divergent results.



called **artificial selection** (Figure 22.9). As a result of artificial selection, crops, livestock animals, and pets often bear little resemblance to their wild ancestors.

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

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

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

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

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

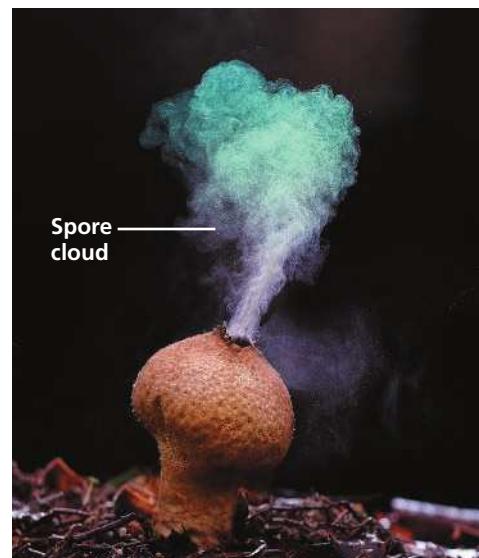
As these two inferences suggest, Darwin saw a connection between natural selection and the capacity of organisms to “over-reproduce.” He began to make this connection after reading an essay by economist Thomas Malthus, who contended that much of human suffering—disease, famine, and war—resulted from the human population’s potential to increase faster than food supplies and other resources. Darwin similarly realized that the capacity to overreproduce was typical of all species. Of the many eggs laid, young born, and seeds spread, only a fraction complete their development and leave offspring of their own. The rest are starved, eaten, diseased, unmated, or unable to tolerate physical conditions of the environment such as salinity or temperature.

An organism’s heritable traits can influence not only its own performance, but also how well its offspring cope with

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



► **Figure 22.11 Overproduction of offspring.** A single puffball fungus can produce billions of spores that give rise to offspring. If all of these offspring and their descendants survived to maturity, they would carpet the surrounding land surface.



environmental challenges. For example, an organism might have a trait that gives its offspring an advantage in escaping predators, obtaining food, or tolerating physical conditions. When such advantages increase the number of offspring that survive and reproduce, the traits that are favored will likely appear at a greater frequency in the next generation. Thus, over time, natural selection resulting from factors such as predators, lack of food, or adverse physical conditions can lead to an increase in the proportion of favorable traits in a population.

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

## Key Features of Natural Selection

Let's now summarize some of the main ideas of natural selection:

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

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

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

Third, environmental factors vary from place to place and over time. A trait that is favorable in one place or time may be useless—or even detrimental—in other places or times. Natural selection is always operating, but which traits are favored depends on the context in which a species lives and mates.

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



**▲ Figure 22.12 Camouflage as an example of evolutionary adaptation.** Related species of moths have diverse shapes and colors that evolved in different environments, as seen in this dead-leaf moth (*Oxytenis modestia*) in Peru (a) and buff-end moth (*Phalera bucephala*) in Scotland (b).

### CONCEPT CHECK 22.2

1. How does the concept of descent with modification explain both the unity and diversity of life?
2. **WHAT IF?** If you discovered a fossil of an extinct mammal that lived high in the Andes, would you predict that it would more closely resemble present-day mammals from South American jungles or present-day mammals that live high in Asian mountains? Explain.
3. **MAKE CONNECTIONS** Review the relationship between genotype and phenotype (see Figures 14.5 and 14.6). Suppose that in a particular pea population, flowers with the white phenotype are favored by natural selection. Predict what would happen over time to the frequency of the white-flower allele (the *p* allele) in the population.

For suggested answers, see Appendix A.

### CONCEPT 22.3

## Evolution is supported by an overwhelming amount of scientific evidence

In *The Origin of Species*, Darwin marshaled a broad range of evidence to support the concept of descent with modification. Still—as he readily acknowledged—there were instances

in which key evidence was lacking. For example, Darwin referred to the origin of flowering plants as an “abominable mystery,” and he lamented the lack of fossils showing how earlier groups of organisms gave rise to new groups.

In the last 150 years, new discoveries have filled many of the gaps that Darwin identified. The origin of flowering plants, for example, is much better understood (see Concept 30.3), and many fossils have been discovered that signify the origin of new groups of organisms (see Concept 25.2). In this section, we’ll consider four types of data that document the pattern of evolution and illuminate how it occurs: direct observations, homology, the fossil record, and biogeography.

## Direct Observations of Evolutionary Change

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

### Natural Selection in Response to Introduced Species

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

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

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

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

The observed changes in beak lengths had important consequences. In Australia, for example, the increase in beak

▼ Figure 22.13 Inquiry

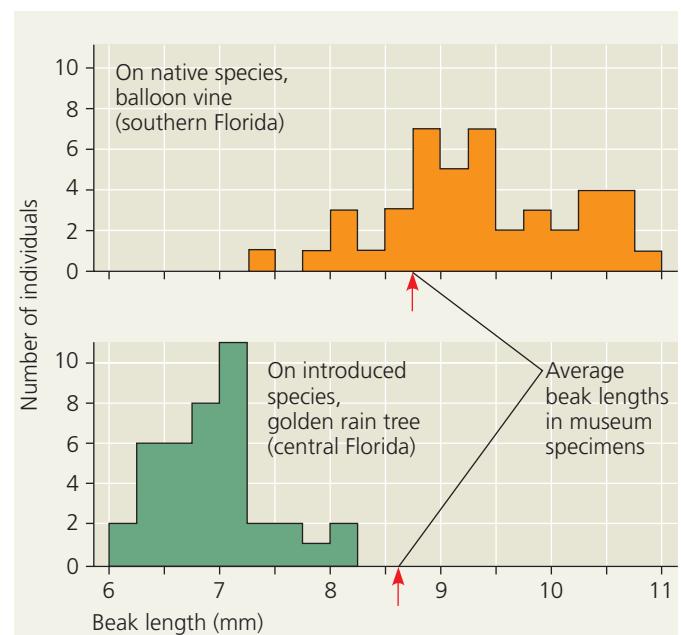
Can a change in a population’s food source result in evolution by natural selection?

**Field Study** Soapberry bugs feed most effectively when the length of their “beak” is similar to the depth of the seeds within the fruit. Researchers measured beak lengths in soapberry bug populations feeding on the native balloon vine. They also measured beak lengths in populations feeding on the introduced golden rain tree. The researchers then compared the measurements with those of museum specimens collected in the two areas before the golden rain tree was introduced.



Soapberry bug with beak inserted in balloon vine fruit

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



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

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

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

length nearly doubled the success with which soapberry bugs could eat the seeds of the introduced species. Furthermore, since historical data show that the golden rain tree reached central Florida just 35 years before the scientific studies were initiated, the results demonstrate that natural selection can cause rapid evolution in a wild population.

### The Evolution of Drug-Resistant Bacteria

An example of ongoing natural selection that dramatically affects humans is the evolution of drug-resistant pathogens (disease-causing organisms and viruses). This is a particular problem with bacteria and viruses because they can produce new generations in a short period of time; as a result, resistant strains of these pathogens can proliferate very quickly.

Consider the evolution of drug resistance in the bacterium *Staphylococcus aureus*. About one in three people harbor this species on their skin or in their nasal passages with no negative effects. However, certain genetic varieties (strains) of this species, known as methicillin-resistant *S. aureus* (MRSA), are formidable pathogens. Most MRSA infections are caused by recently appearing strains such as clone USA300, which can cause “flesh-eating disease” and potentially fatal infections (Figure 22.14). How did clone USA300 and other strains of MRSA become so dangerous?

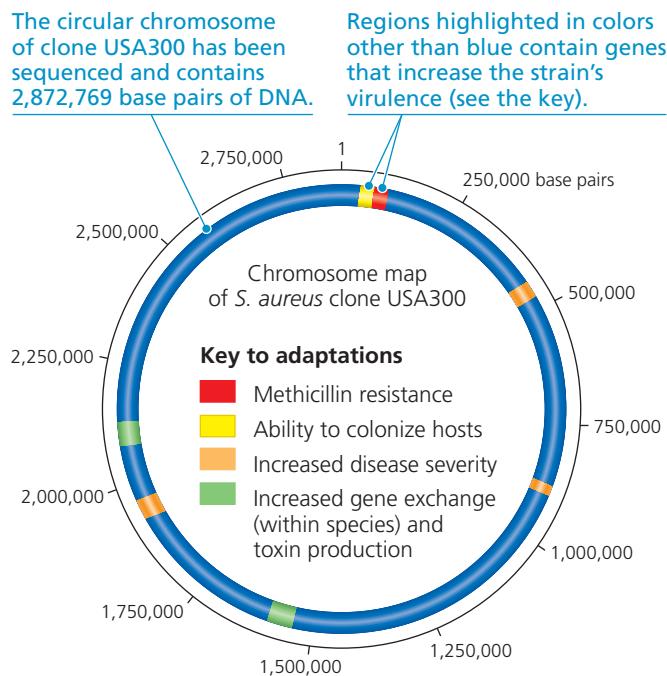
The story begins in 1943, when penicillin became the first widely used antibiotic. Since then, penicillin and other antibiotics have saved millions of lives. However, by 1945, more than 20% of the *S. aureus* strains seen in hospitals were already resistant to penicillin. These bacteria had an enzyme,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

For example, a promising new antibiotic, methicillin, was introduced in 1959. But by 1961, methicillin-resistant strains of *S. aureus* were observed. How did these resistant strains emerge? Methicillin works by deactivating an enzyme that bacteria use to synthesize their cell walls. However, some *S. aureus* populations included individuals that were able to synthesize their cell walls using a different enzyme that was not affected by methicillin. These individuals survived the methicillin treatments and reproduced at higher rates than did other individuals. Over time, these resistant individuals became increasingly common, leading to the spread of MRSA.

Initially, MRSA could be controlled by antibiotics that work differently from the way methicillin works. But this has become less effective because some MRSA strains are resistant to multiple antibiotics—probably because bacteria can exchange genes with members of their own and other species. Thus, the multidrug-resistant strains of today may have emerged over time as MRSA strains that were resistant to different antibiotics exchanged genes.

Finally, it is important to note that *S. aureus* is not the only pathogenic bacterium that has evolved resistance to multiple antibiotics. Furthermore, in recent decades, antibiotic resistance has spread much faster than new antibiotics have been

▼ **Figure 22.14 Clone USA300: a virulent strain of methicillin-resistant *Staphylococcus aureus* (MRSA).** Resistant to multiple antibiotics and highly contagious, this strain and its close relatives can cause lethal infections of the skin, lungs, and blood. As shown here, researchers have identified key areas of the USA300 genome that code for adaptations that cause its virulent properties.



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

discovered—a problem of great public health concern. Hope may loom on the horizon, however. For example, scientists recently reported the discovery of “teixobactin,” a new antibiotic that shows promise for treating MRSA and other pathogens. In addition, as we’ll describe in the Scientific Skills Exercise in Chapter 27, the methods used in the discovery of teixobactin may lead to the discovery of other new antibiotics as well.

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

→ **Mastering Biology BBC Video: A Future Without Antibiotics?**

## Homology

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

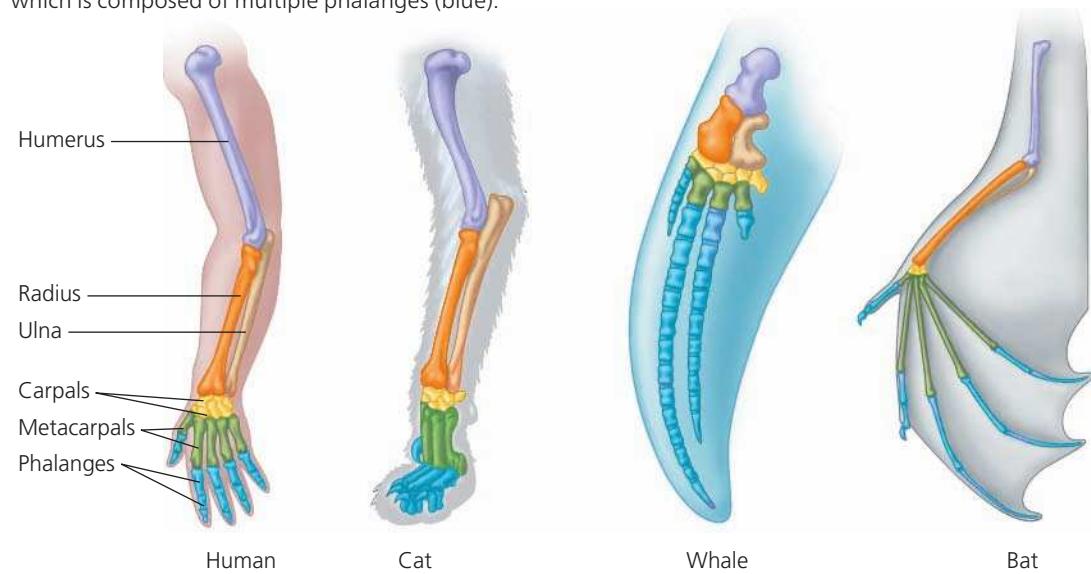
### Anatomical and Molecular Homologies

The view of evolution as a remodeling process leads to the prediction that closely related species should share similar features—and they do. Of course, closely related species share the features used to determine their relationship, but they also share many other features. Some of these shared features make little sense except in the context of evolution. For example, the forelimbs of all mammals—including humans, cats, whales, and bats—show the same arrangement of bones from the shoulder to the tips of the digits, even though the appendages have very different functions: lifting, walking, swimming, and flying (Figure 22.15). Such striking anatomical resemblances would be highly unlikely if these structures had arisen anew in each species. Rather, the underlying skeletons of the arms, forelegs, flippers, and wings of different mammals are **homologous structures** that represent variations on a structural theme that was present in their common ancestor.

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

Some of the most intriguing homologies concern “leftover” structures of marginal, if any, importance to the organism. These **vestigial structures** are remnants of features that served a

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

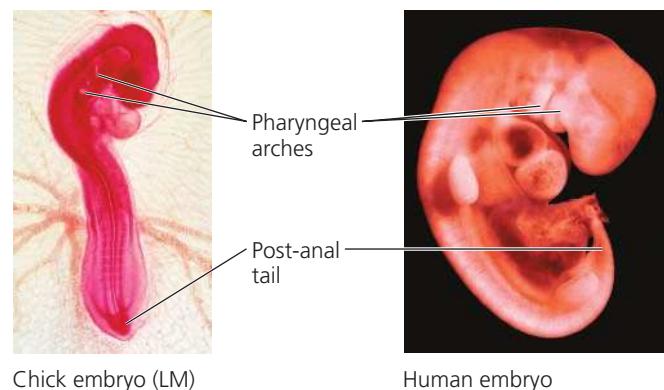


function in the organism's ancestors. For instance, snakes arose from ancestors with legs, and the skeletons of some snakes retain vestiges of the pelvis and leg bones of their ancestors. Likewise, blind species of cave fishes descended from ancestors with eyes—which explains why these blind fishes have eye remnants buried under their scales. We would not expect to see these vestigial structures if snakes and blind cave fishes had origins separate from those of other vertebrate animals.

Biologists also observe similarities among organisms at the molecular level. All forms of life use essentially the same genetic code, suggesting that all species descended from common ancestors that used this code. But molecular homologies go beyond a shared code. For example, organisms as dissimilar as humans and bacteria share genes inherited from a very distant common ancestor. Some of these homologous genes

### ▼ Figure 22.16 Anatomical similarities in vertebrate embryos.

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



have acquired new functions, while others, such as those coding for the ribosomal subunits used in protein synthesis (see Figure 17.18), have retained their original functions. It is also common for organisms to have genes that have lost their function, even though the homologous genes in related species may be fully functional. Like vestigial structures, it appears that such inactive “pseudogenes” may be present simply because a common ancestor had them.

### Homologies and “Tree Thinking”

Some homologous characteristics, such as the genetic code, are shared by all species because they date to the deep ancestral past. In contrast, homologous characteristics that evolved more recently are shared only within smaller groups of organisms.

Consider the *tetrapods* (from the Greek *tetra*, four, and *pod*, foot), the vertebrate group that consists of amphibians, mammals, and reptiles. Like all vertebrates, tetrapods have a backbone. But unlike other vertebrates, tetrapods also have limbs with digits (see Figure 22.15). As suggested by this example, homologous characteristics form a nested pattern: All life shares the deepest layer (in this case, all vertebrates have a backbone), and each successive smaller group adds its own homologies to those it shares with larger groups (in this case, all tetrapods have a backbone *and* limbs with digits). This nested pattern is exactly what we would expect to result from descent with modification from a common ancestor.

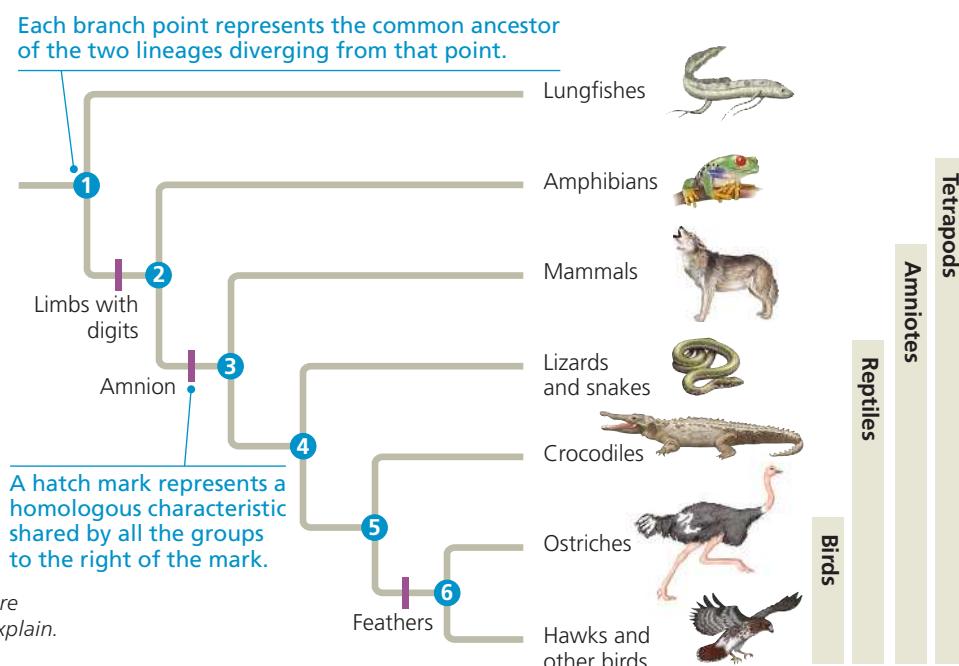
Biologists often represent the pattern of descent from common ancestors with an **evolutionary tree**, a diagram that reflects evolutionary relationships among groups of organisms. We will explore evolutionary trees in more detail in Chapter 26, but for now, let’s consider how we can interpret and use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

**Figure 22.17** is an evolutionary tree of tetrapods and their closest living relatives, the lungfishes. In this diagram, each branch point represents the most recent common ancestor of the two lineages diverging from that point. For example, lungfishes and all tetrapods

descended from ancestor **1**, whereas mammals, lizards and snakes, crocodiles, and birds all descended from ancestor **3**. As expected, the three homologies shown on the tree—limbs with digits, the amnion (a protective embryonic membrane), and feathers—form a nested pattern. Limbs with digits were present in common ancestor **2** and hence are found in all of the descendants of that ancestor (the tetrapods). The amnion was present only in ancestor **3** and hence is shared only by some tetrapods (mammals and reptiles). Feathers were present only in ancestor **6** and hence are found only in birds.

To explore “tree thinking” further, note that in Figure 22.17 mammals are positioned closer to amphibians than to birds. As a result, you might conclude that mammals are more closely related to amphibians than they are to birds. However, mammals are actually more closely related to birds than to amphibians because mammals and birds share a more recent common ancestor (ancestor **3**) than do mammals and amphibians (ancestor **2**). Ancestor **2** is also the most recent common ancestor of birds and amphibians, making mammals and birds equally related to amphibians. Finally, note that the tree in Figure 22.17 shows the relative timing of events but not their actual dates. Thus, we can conclude that ancestor **2** lived before ancestor **3**, but we do not know when that was.

Evolutionary trees are hypotheses that summarize our current understanding of patterns of descent. Our confidence in these relationships, as with any hypothesis, depends on the strength of the supporting data. In the case of Figure 22.17, the tree is supported by many different data sets, including both anatomical and DNA sequence data. As a result, biologists are confident that it accurately reflects evolutionary history. Scientists can use such well-supported evolutionary trees to make specific and sometimes surprising predictions about organisms (see Figure 26.17).



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

**VISUAL SKILLS** Based on this evolutionary tree, are crocodiles more closely related to lizards or birds? Explain.

→ Mastering Biology Figure Walkthrough

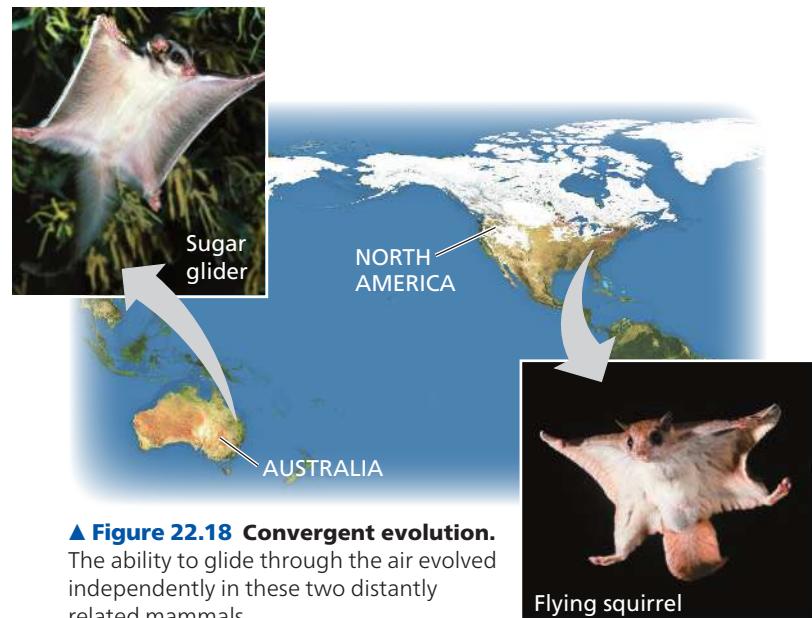
## A Different Cause of Resemblance: Convergent Evolution

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

## The Fossil Record

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

Fossils can also shed light on the origins of new groups of organisms. An example is the fossil record of cetaceans, the mammalian order that includes whales, dolphins, and porpoises. Some of these fossils (**Figure 22.19**) provided strong support for a hypothesis based on DNA sequence data: that cetaceans are



▲ **Figure 22.18** **Convergent evolution.**

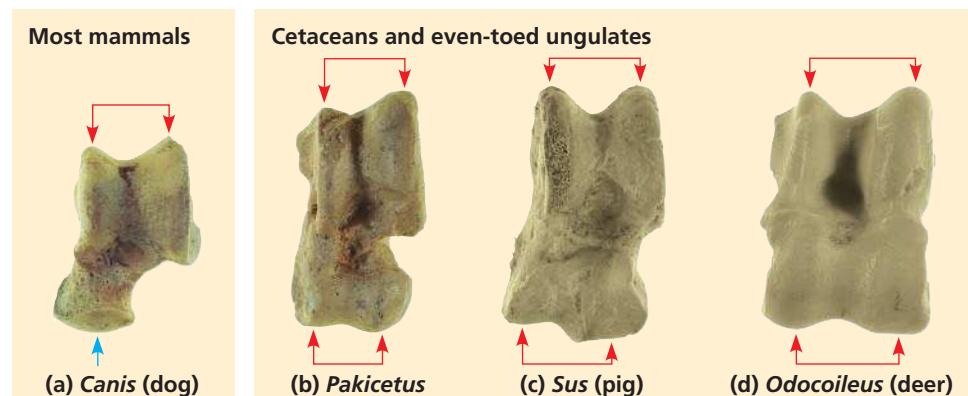
The ability to glide through the air evolved independently in these two distantly related mammals.

closely related to even-toed ungulates, a group that includes hippopotamuses, pigs, deer, and cows.

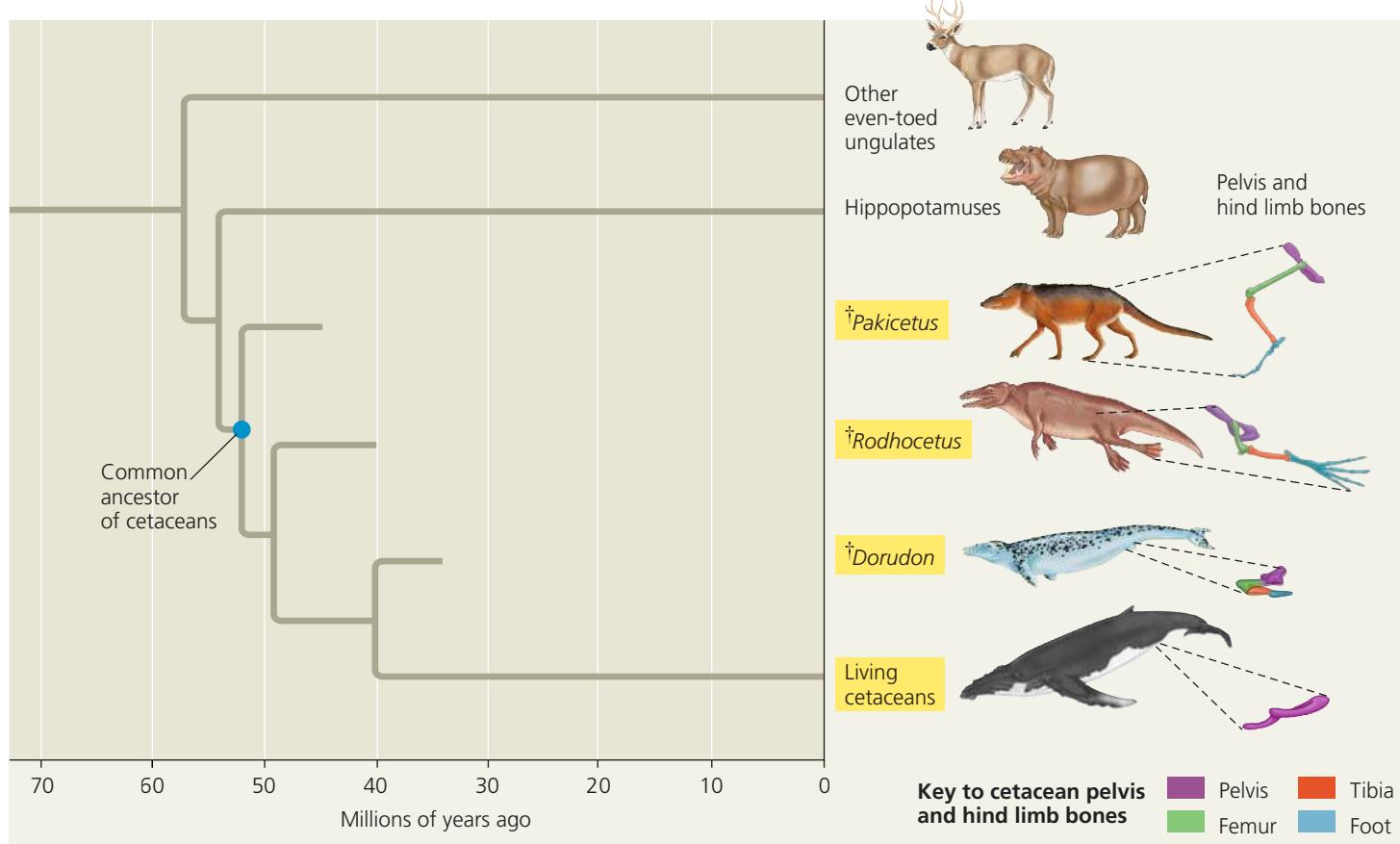
What else can fossils tell us about cetacean origins? The earliest cetaceans lived 50–60 million years ago. The fossil record indicates that prior to that time, most mammals were terrestrial. Although scientists had long realized that whales and other cetaceans originated from land mammals, few fossils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

Finally, although living cetaceans look very different from living even-toed ungulates, the fossil discoveries show that extinct early cetaceans such as *Pakicetus* looked fairly similar

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



▼ **Figure 22.20** **The transition to life in the sea.** Multiple lines of evidence support the hypothesis that cetaceans (yellow labels) evolved from terrestrial mammals. Fossils document the reduction over time in the pelvis and hind limb bones of extinct ( $\dagger$ ) cetacean ancestors, including *Pakicetus*, *Rodhocetus*, and *Dorudon*. DNA sequence data support the hypothesis that cetaceans are most closely related to hippopotamuses.

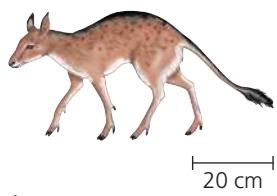


**VISUAL SKILLS** Use the diagram to determine which happened first during the evolution of cetaceans: changes in hind limb structure or the origin of tail flukes (the lobes on a whale's tail). Explain.

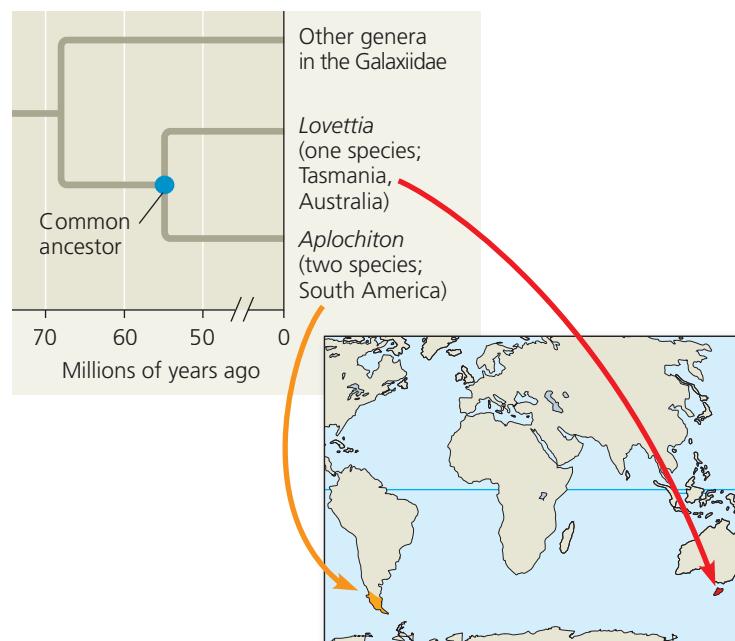
→ **Mastering Biology** **Figure Walkthrough**

to deer and other living even-toed ungulates. The extinct early cetaceans also looked very similar to extinct early even-toed ungulates, such as *Diacodexis* (Figure 22.19). Similar patterns are seen in fossils documenting the origins of other groups of organisms, including mammals (see Figure 25.7), flowering plants (see Concept 30.3), and tetrapods (see Figure 34.21). In each of these cases, the fossil record shows that over time, descent with modification produced increasingly large differences among related groups of organisms, ultimately resulting in the diversity of life today.

▼ **Figure 22.21**  
*Diacodexis*, an early even-toed ungulate.



▼ **Figure 22.22** **Closely related freshwater fish separated by 9,000 km of ocean.** There are three species in these two closely related genera of freshwater fish within the family Galaxiidae.



## Biogeography

A fourth type of evidence comes from **biogeography**, the scientific study of the geographic distributions of species. These distributions are influenced by many factors, including *continental drift*, the slow movement of Earth's continents over time. About 250 million years ago, these movements united all of Earth's landmasses into a single large continent called **Pangaea**.

(see Figure 25.16). Roughly 200 million years ago, Pangaea began to break apart; by 20 million years ago, the continents were within a few hundred kilometers of their present locations.

We can use our understanding of evolution and continental drift to predict where fossils of different groups of organisms might be found. For example, scientists have constructed evolutionary trees for horses based on anatomical data. These trees and the ages of fossils of horse ancestors suggest that the genus that includes present-day horses (*Equus*) originated 5 million years ago in North America. Geologic evidence indicates that at that time, North and South America were not yet connected, making it difficult for horses to travel between them. Thus, we would predict that the oldest *Equus* fossils should be found only on the continent on which the group originated—North America. This prediction and others like it for different groups of organisms have been upheld, providing more evidence for evolution.

Evolution also explains biogeographic data. For example, a group of three species of freshwater fish in the family Galaxiidae are found in regions separated by wide stretches of open ocean (Figure 22.22). None of these three species can

survive in salt water, so how can we explain their geographic distributions? These three species represent all known living descendants of a common ancestor. Since all of the living species cannot survive in salt water, it is likely that their common ancestor also was restricted to freshwater habitats. At first glance, this only deepens the mystery—how could that ancestor or its descendants have swum across vast stretches of ocean? A clue comes from genetic analyses indicating that the evolutionary lineages leading to these three species began to diverge about 55 million years ago. By that time, the southernmost portion of Pangaea was breaking apart into what would eventually become South America, Australia, and Antarctica. This suggests that their ancestors had spread across southern Pangaea before it broke apart. At later times, these three freshwater species originated on the continental regions where they currently live, resulting in their present-day geographic distribution.

## What Is Theoretical About Darwin's View of Life?

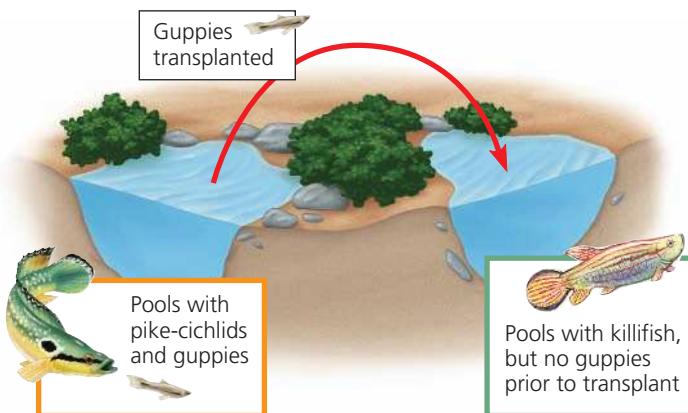
Some people dismiss Darwin's ideas as "just a theory." But the pattern of evolution—the observation that life has evolved

### Scientific Skills Exercise

#### Making and Testing Predictions

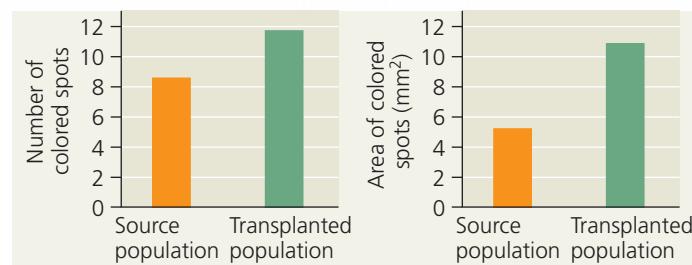
**Can Predation Result in Natural Selection for Color Patterns in Guppies?** Our understanding of evolution changes constantly as new observations lead to new hypotheses—and hence to new ways to test our understanding of evolutionary theory. Consider the wild guppies (*Poecilia reticulata*) that live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

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



**How the Experiment Was Done** Researchers transplanted 200 adult guppies from pools containing pike-cichlid fish, predators of adult guppies, to pools with only killifish, predators of juvenile guppies. They tracked the number of bright-colored spots and the total area of those spots on adult male guppies in each generation.

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



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

#### INTERPRET THE DATA

- Identify the following elements of hypothesis-based science in this example: (a) question, (b) hypothesis, (c) prediction, (d) control group, and (e) experimental group. (For additional information about hypothesis-based science, see Concept 1.3 and the Scientific Skills Review in Appendix D.)
- Explain how the types of data the researchers chose to collect enabled them to test their prediction.
- What conclusion do you draw from the data presented above?
- (a) Predict what would happen if, after 22 months, guppies from the transplanted population were returned to the source pool. (b) Describe an experiment to test your prediction.

→ **Instructors:** A version of this Scientific Skills Exercise can be assigned in *Mastering Biology*.

over time—is supported by a great deal of evidence. In addition, Darwin's explanation of the *process* of evolution—that natural selection is the primary cause of the observed pattern of evolutionary change—makes sense of massive amounts of data. As the **Scientific Skills Exercise** describes, the effects of natural selection also can be observed and tested in nature.

What, then, is theoretical about evolution? Keep in mind that the scientific meaning of the term *theory* is very different from its meaning in everyday use. The colloquial use of the word *theory* comes close to what scientists mean by a hypothesis. In science, a theory is much more comprehensive than a hypothesis. A theory, such as the theory of evolution by natural selection, accounts for many observations and explains and integrates a great variety of phenomena. Such a unifying theory does not become widely accepted unless its predictions stand up to thorough and continual testing by experiment and additional observation (see Concept 1.3). As the rest of this unit demonstrates, this has certainly been the case with the theory of evolution by natural selection.

The skepticism of scientists as they continue to test theories prevents these ideas from becoming dogma. For example, although Darwin thought that evolution was a very slow process, we now know that this isn't always true. Populations can evolve rapidly, and new species can form in relatively short

periods of time: a few thousand years or less. Furthermore, evolutionary biologists now recognize that natural selection is not the only mechanism responsible for evolution. Indeed, the study of evolution today is livelier than ever as scientists use a wide range of experimental approaches and genetic analyses to test predictions based on natural selection and other evolutionary mechanisms.

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

### CONCEPT CHECK 22.3

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

For suggested answers, see Appendix A.

# 22 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

## SUMMARY OF KEY CONCEPTS

>To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to [goo.gl/zkjz9t](http://goo.gl/zkjz9t).

### CONCEPT 22.1

#### The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species (pp. 469–471)

- Darwin proposed that life's diversity arose over long periods of time from ancestral species through natural selection, a departure from prevailing views. For example, Cuvier studied **fossils** but denied that **evolution** occurs; he proposed that sudden catastrophic events in the past caused species to disappear from an area. Lamarck hypothesized that species evolve, but the underlying mechanisms he proposed are not supported by evidence.

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

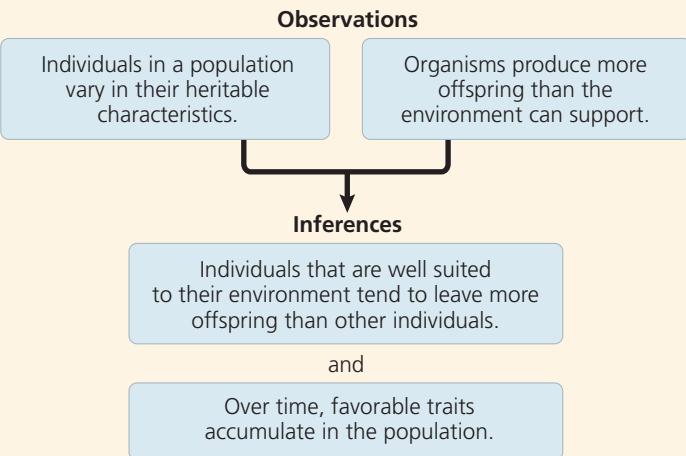
### CONCEPT 22.2

#### Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life (pp. 471–476)

- Darwin's experiences during the voyage of the *Beagle* gave rise to his idea that new species originate from ancestral forms through

the accumulation of **adaptations**. He refined his theory for many years and finally published it in 1859 after learning that Wallace had come to the same idea.

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



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

### CONCEPT 22.3

## Evolution is supported by an overwhelming amount of scientific evidence (pp. 476–484)

- Researchers have directly observed natural selection leading to evolution in many studies in diverse organisms.
- Organisms share characteristics because of common descent (**homology**) or because natural selection affects independently evolving species in similar environments in similar ways (**convergent evolution**).
- Fossils show that past organisms differed from living organisms, that many species have become extinct, and that species have evolved over long periods of time; fossils also document the evolutionary origin of new groups of organisms.
- Evolutionary theory can explain some **biogeographic** patterns.

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

### TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the Mastering Biology eText or Study Area, or go to [goo.gl/GruWRg](http://goo.gl/GruWRg).

#### Levels 1-2: Remembering/Understanding

- Which of the following is an observation or inference on which natural selection is based?
  - Individuals do not vary in their heritable characteristics.
  - Only well-adapted individuals produce offspring.
  - Species produce more offspring than the environment can support.
  - Nearly all of each individual's offspring will survive and reproduce.
- Which of the following observations helped Darwin shape his concept of descent with modification?
  - Species diversity declines farther from the equator.
  - Fewer species live on islands than on the nearest continents.
  - Birds live on islands located farther from the mainland than the birds' maximum nonstop flight distance.
  - South American temperate plants are more similar to South American tropical plants than to European temperate ones.

#### Levels 3-4: Applying/Analyzing

- Within six months of effectively using methicillin to treat *S. aureus* infections in a community, all new *S. aureus* infections were caused by a resistant strain (MRSA). How can this best be explained?
  - A patient must have become infected with MRSA from another community.
  - In response to the drug, *S. aureus* began making drug-resistant versions of the protein targeted by the drug.
  - Some drug-resistant bacteria were present at the start of treatment, and natural selection increased their frequency.
  - S. aureus* evolved to resist vaccines.

- DNA sequences in many human genes are very similar to the sequences of corresponding genes in chimpanzees. The most likely explanation for this result is that
  - humans and chimpanzees share a relatively recent common ancestor.
  - humans evolved from chimpanzees.
  - chimpanzees evolved from humans.
  - convergent evolution led to the DNA similarities.
- The upper forelimbs of humans and bats have fairly similar skeletal structures, whereas the corresponding bones in whales have very different shapes and proportions. However, genetic data suggest that all three kinds of organisms diverged from a common ancestor at about the same time. Which of the following is the most likely explanation for these data?
  - Forelimb evolution was adaptive in people and bats, but not in whales.
  - Natural selection in an aquatic environment resulted in significant changes to whale forelimb anatomy.
  - Genes mutate faster in bats than in humans or whales.
  - Whales are not properly classified as mammals.

#### Levels 5-6: Evaluating/Creating

- EVOLUTION CONNECTION** Explain why anatomical and molecular features often fit a similar nested pattern. In addition, describe a process that can cause this not to be the case.
- SCIENTIFIC INQUIRY • DRAW IT** Mosquitoes resistant to the pesticide DDT first appeared in India in 1959, but now are found throughout the world. (a) Graph the data in the table below.  
(b) After examining the graph, hypothesize why the percentage of mosquitoes resistant to DDT rose rapidly. (c) Suggest an explanation for the global spread of DDT resistance.

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

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

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

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

#### 9. SYNTHESIZE YOUR KNOWLEDGE



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

For selected answers, see Appendix A.

#### Explore Scientific Papers with Science in the Classroom AAAS

How are some coral reefs responding to climate change?

Go to "Take the Heat" at

[www.scienceintheclassroom.org](http://www.scienceintheclassroom.org).

→ **Instructors:** Questions can be assigned in Mastering Biology.

# 23 The Evolution of Populations

## KEY CONCEPTS

- 23.1** Genetic variation makes evolution possible p. 487
- 23.2** The Hardy-Weinberg equation can be used to test whether a population is evolving p. 489
- 23.3** Natural selection, genetic drift, and gene flow can alter allele frequencies in a population p. 493
- 23.4** Natural selection is the only mechanism that consistently causes adaptive evolution p. 497

## Study Tip

**Make a table:** This chapter discusses different types of selection—disruptive, stabilizing, sexual, balancing, frequency-dependent, and heterozygote advantage. These types of selection are not all mutually exclusive, and some evolutionary changes are examples of more than one. To help you study, make a table like the one shown listing each type of selection, its distinguishing features, and example(s) from the chapter.

Type of selection	Distinguishing features	Example
Balancing selection	Maintains two or more phenotypes in a population; includes frequency-dependent selection and heterozygote advantage	Figures 23.17 and 23.18
Directional selection		

## Go to Mastering Biology

### For Students (in eText and Study Area)

- Get Ready for Chapter 23
- Figure 23.8 Walkthrough: Hardy-Weinberg Equilibrium
- BioFlix® Animation: Natural Selection, Genetic Drift, and Gene Flow

### For Instructors to Assign (in Item Library)

- Tutorial: The Hardy-Weinberg Principle

### Ready-to-Go Teaching Module

(in Instructor Resources)

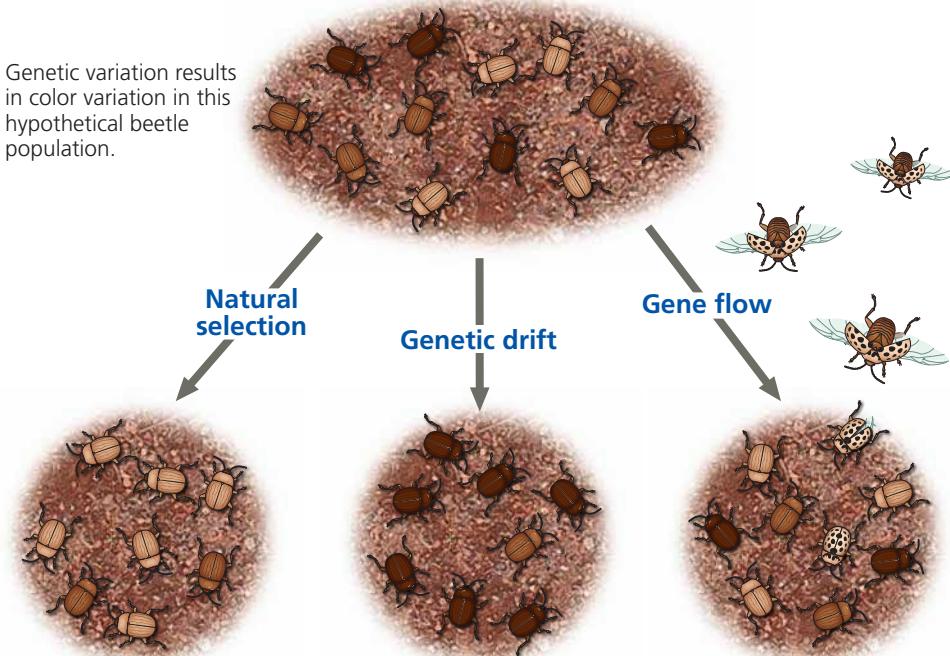
- Mechanisms of Evolution



**Figure 23.1** The medium ground finch (*Geospiza fortis*) is a seed-eating bird that inhabits the Galápagos Islands. In 1977, the *G. fortis* population on the island of Daphne Major was decimated by a long period of drought: Of some 1,200 birds, only 180 survived. The surviving birds had larger, deeper beaks, indicating that this population of finches had evolved.

## What mechanisms can cause the evolution of populations?

Evolution occurs when natural selection, genetic drift, or gene flow alter the allele frequencies of a population over time.



The more visible darker beetles have been preyed on at a higher rate, causing lighter beetles (and the alleles they carry) to become more common over time.

By chance alone, alleles encoding darker color have become more common over several generations.

The arrival of beetles with a spotted color pattern has brought new alleles into the population.

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

To see why, consider the population of medium ground finches decimated by a drought, resulting in only 180 survivors out of some 1,200 birds. Researchers Peter and Rosemary Grant observed that during the drought, small, soft seeds were scarce, while large, hard seeds were more plentiful. Birds with larger, deeper beaks were better able to crack and eat the larger seeds and survived at a higher rate than finches with smaller beaks.

Since beak depth is an inherited trait in these birds, the offspring of surviving birds also tended to have deep beaks. As a result, the average beak depth in the next generation of *G. fortis* was greater than it had been in the pre-drought population (Figure 23.2). The finch population had evolved by natural selection. However, the *individual* finches did not evolve. Each bird had a beak of a particular size, which did not grow larger during the drought. Rather, the proportion of large beaks in the population increased from generation to generation: The population evolved, not its individual members.

Focusing on evolutionary change in populations, we can define evolution on its smallest scale, called **microevolution**, as a change in allele frequencies in a population over generations. In the finch population, for example, birds that had alleles encoding large beaks survived at higher rates than did other birds—causing those alleles to be more common after the drought than they had been before it. There are three main mechanisms that can cause such changes in allele frequencies: natural selection, genetic drift (chance events that alter allele frequencies), and gene flow (the transfer of alleles between populations). Each of these mechanisms affects the genetic composition of populations, but only natural selection consistently improves the degree to which organisms are well suited for life in their environment (adaptation). Before we examine this more closely, let's revisit a prerequisite for these processes: genetic variation.

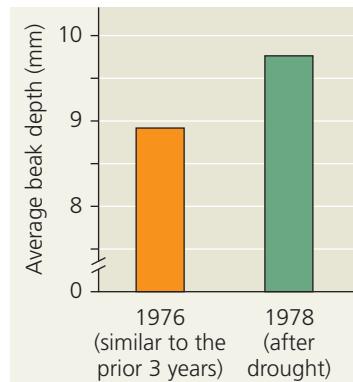
#### Mastering Biology

**Interview with Rosemary and Peter Grant:  
Studying evolution in the Galápagos  
finches**



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

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



**Instructors:** A related Experimental Inquiry Tutorial can be assigned in Mastering Biology.

#### CONCEPT 23.1

## Genetic variation makes evolution possible

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

Just a few years after Darwin published *The Origin of Species*, Gregor Mendel wrote a groundbreaking paper on inheritance in pea plants proposing a model of inheritance in which organisms transmit discrete heritable units (now called genes) to their offspring. Although Darwin did not know about genes, Mendel's paper set the stage for understanding the genetic differences on which evolution is based.

### Genetic Variation

Individuals within all species vary in their phenotypic traits. Humans, for example, vary noticeably in facial features, height, and voice. And though you cannot identify blood group (A, B, AB, or O) from a person's appearance, this and many other molecular traits also vary extensively among individuals.

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

How much do genes and other DNA sequences vary from one individual to another? Genetic variation at the

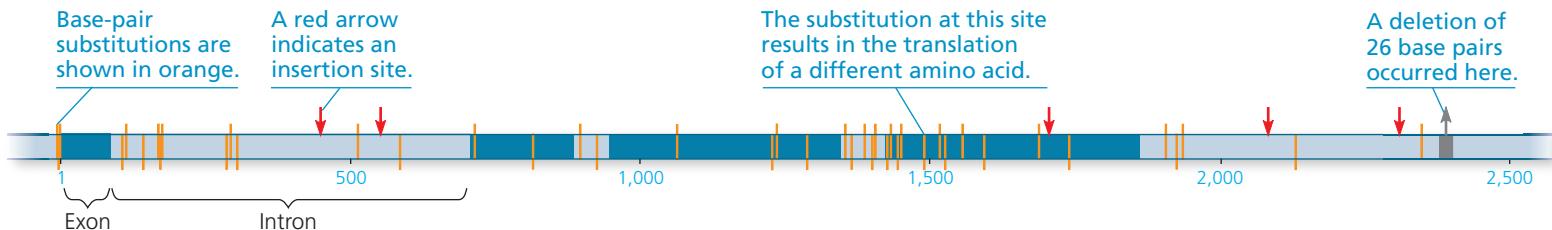
#### ▼ Figure 23.3 Phenotypic variation in horses.



#### ▼ Figure 23.4 Extensive genetic variation at the molecular level.

This diagram summarizes data from a study comparing the DNA sequence of the alcohol dehydrogenase (*Adh*) gene in several fruit flies (*Drosophila melanogaster*).

The *Adh* gene has four exons (dark blue) separated by introns (light blue); the exons include the coding regions that are ultimately translated into the amino acids of the Adh enzyme (see Figure 5.1). Only one substitution has a phenotypic effect, producing a different form of the Adh enzyme.



whole-gene level (*gene variability*) can be quantified as the average percentage of loci that are heterozygous. (Recall that a heterozygous individual has two different alleles for a given locus, whereas a homozygous individual has two identical alleles for that locus.) As an example, on average the fruit fly *Drosophila melanogaster* is heterozygous for about 1,920 of its 13,700 loci (14%) and homozygous for all the rest.

Considerable genetic variation can also be measured at the molecular level of DNA (*nucleotide variability*). But little of this variation results in phenotypic variation. Why? Many nucleotide variations occur within *introns*, noncoding segments of DNA lying between *exons*, the regions retained in mRNA after RNA processing (see Figure 17.12). And of the variations that occur within exons, most do not cause a change in the amino acid sequence of the protein encoded by the gene. For example, in the sequence comparison shown in Figure 23.4, there are 43 nucleotide sites with variable base pairs (where substitutions have occurred), as well as several sites where insertions or deletions have occurred. Although 18 variable sites occur within the four exons of the *Adh* gene, only one of these variations (at site 1,490) results in an amino acid change. Note, however, that this single variable site is enough to cause genetic variation at the level of the gene, and hence two different forms of the Adh enzyme are produced.

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

**MAKE CONNECTIONS** Review Figures 17.6 and 17.11. Explain how a base-pair substitution that alters a coding region of the *Adh* locus could have no effect on amino acid sequence. Then explain how an insertion in an exon could have no effect on the protein produced.

## Sources of Genetic Variation

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

### Formation of New Alleles

New alleles can arise by *mutation*, a change in the nucleotide sequence of an organism's DNA. Mutations can be caused by factors such as errors in DNA replication, exposure to UV light and other high-energy forms of radiation, and exposure to certain chemicals (see Concept 17.5). A change of as little as one base in a gene—a “point mutation”—can have a significant impact on phenotype, as in sickle-cell disease (see Figure 23.18). Furthermore, organisms reflect many generations of past selection, and hence their phenotypes tend to be well suited for life in their environments. As a result, most new mutations that alter a phenotype are at least slightly harmful.

In some cases, natural selection quickly removes such harmful alleles. In diploid organisms, however, harmful alleles that are recessive can be hidden from selection. Indeed, a harmful recessive allele can persist for generations by propagation in heterozygous individuals (where its harmful effects can be masked by the more favorable dominant allele). Such “heterozygote protection” maintains a huge pool of alleles

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



that may be harmful under present conditions, but that could be beneficial if the environment changes.

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

Finally, note that in multicellular organisms, only mutations in cell lines that produce gametes can be passed to offspring. In plants and fungi, this is not as limiting as it may sound, since many different cell lines can produce gametes. But in most animals, the majority of mutations occur in somatic cells and are not passed to offspring.

### Altering Gene Number or Position

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

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

Such increases in gene number appear to have played a major role in evolution. For example, the remote ancestors of mammals had a single gene for detecting odors that has since been duplicated many times. As a result, humans today have about 380 functional olfactory receptor genes, and mice have about 1,200. This dramatic proliferation of olfactory genes probably helped early mammals, enabling them to detect faint odors and to distinguish among many different smells.

### Rapid Reproduction

Mutation rates tend to be low in plants and animals, averaging about one mutation in every 100,000 genes per generation, and are often even lower in prokaryotes. But prokaryotes have many more generations per unit of time, so mutations can quickly generate genetic variation in their populations. The

same is true of viruses. For instance, HIV has a generation time of about two days (that is, it takes two days for a newly formed virus to produce the next generation). HIV also has an RNA genome, which has a much higher mutation rate than a typical DNA genome due to the lack of RNA repair mechanisms in host cells (see Concept 19.2). Thus, single-drug treatments are less effective against HIV: Mutant forms of the virus, resistant to a particular drug, tend to proliferate quickly. The most effective AIDS treatments to date have been drug "cocktails" that combine several medications. This approach has worked well as it is less likely that a set of mutations that together confer resistance to *all* the drugs will occur in a short time period.

### Sexual Reproduction

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

Three mechanisms contribute to this shuffling: crossing over, independent assortment of chromosomes, and fertilization (see Concept 13.4). During meiosis, homologous chromosomes, one inherited from each parent, trade some of their alleles by crossing over. The resulting recombinant chromosomes are then distributed at random into gametes. Then, because myriad possible mating combinations exist in a population, fertilization typically brings together gametes with different genetic backgrounds. Together, these three mechanisms ensure that sexual reproduction rearranges existing alleles into fresh combinations each generation, providing much of the genetic variation that makes evolution possible.

#### Mastering Biology Animation: Origins of Genetic Variation

#### CONCEPT CHECK 23.1

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

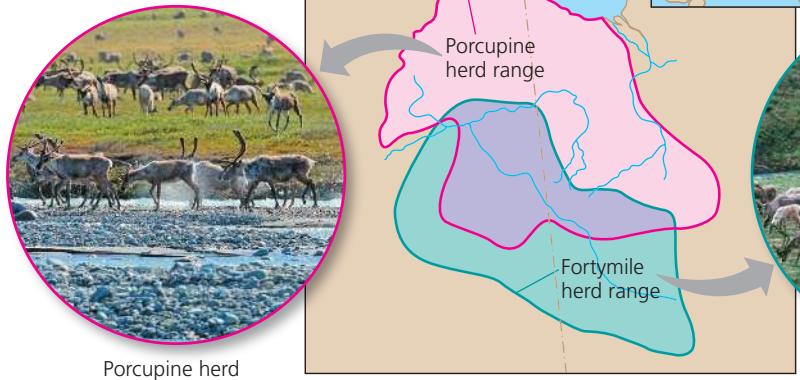
For suggested answers, see Appendix A.

#### CONCEPT 23.2

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

The presence of genetic variation in a population does not guarantee that the population will evolve. For evolution to occur,

▼ **Figure 23.6 One species, two populations.** These two caribou populations in the Yukon are not totally isolated; they sometimes share the same area (shaded purple). Still, members of each population are most likely to breed within their own population.



one or more factors must be at work. In this section, we'll explore one way to test whether evolution is occurring in a population.

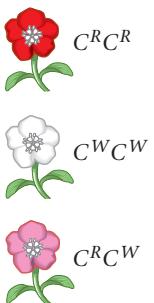
## Gene Pools and Allele Frequencies

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

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

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

Each genotype and each allele has a frequency (proportion) in the population. To see how these frequencies are calculated, suppose our population has 320 plants with red flowers (genotype  $C^R C^R$ ), 160 with pink flowers (genotype  $C^R C^W$ ), and 20 with



white flowers (genotype  $C^W C^W$ ). Since 320 of the 500 plants have red flowers, the frequency of the  $C^R C^R$  genotype is 0.64 (320/500). Likewise, the frequency of the  $C^R C^W$  genotype is 0.32 (160/500) and the frequency of the  $C^W C^W$  genotype is 0.04 (20/500).

With respect to allele frequencies, wildflowers are diploid organisms, so each individual has two alleles for each of its genes. Hence, the 500 individuals in our population have a total of 1,000 copies of the gene for flower color. The  $C^R$  allele accounts for 800 of these copies ( $320 \times 2 = 640$  for  $C^R C^R$  plants, plus  $160 \times 1 = 160$  for  $C^R C^W$  plants). Thus, the frequency of the  $C^R$  allele is  $800/1,000 = 0.8$  (80%).

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

## The Hardy-Weinberg Equation

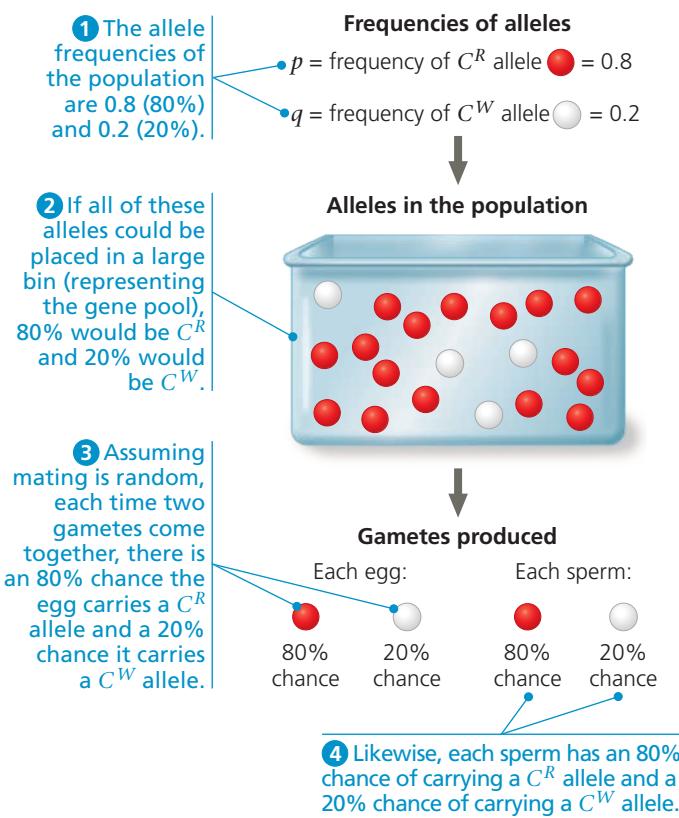
One way to assess whether natural selection or other factors are causing evolution at a particular locus is to determine what the genetic makeup of a population would be if it were *not* evolving at that locus. We can then compare that with the data we actually observed for the population. If there are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

### Hardy-Weinberg Equilibrium

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

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

▼ Figure 23.7 Selecting alleles at random from a gene pool.



**DRAW IT** Draw a bin with six white balls instead of four. For the frequency of  $C^R$  to remain equal to 0.8, how many red balls should the bin contain?

→ Mastering Biology BioFlix® Animation: Allele Frequencies

in a large bin (Figure 23.7). We can think of this bin as holding the population's gene pool for that locus. "Reproduction" occurs by selecting alleles at random from the bin; somewhat similar events occur in nature when fishes release sperm and eggs into the water or when plant sperm (in pollen) is blown about by the wind. By viewing reproduction as a process of randomly selecting and combining alleles from the bin (the gene pool), we are in effect assuming that mating occurs at random: that all male-female matings are equally likely.

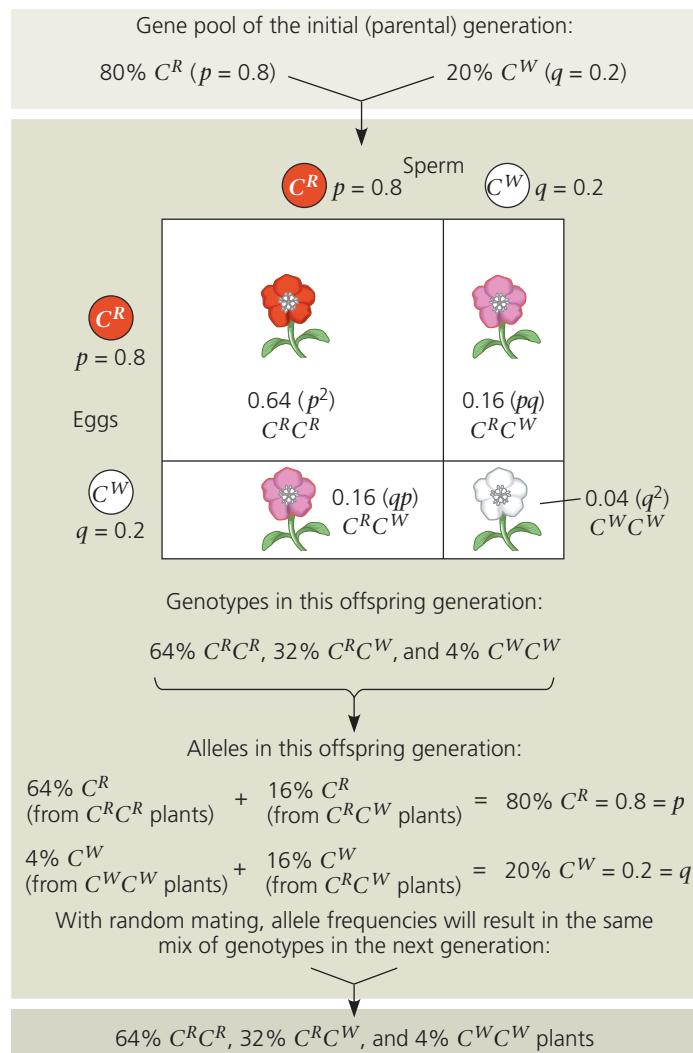
Let's apply the bin analogy to the hypothetical wildflower population discussed earlier. In that population of 500 flowers, the frequency of the allele for red flowers ( $C^R$ ) is  $p = 0.8$ , and the frequency of the allele for white flowers ( $C^W$ ) is  $q = 0.2$ . This implies that a bin holding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

Using the rule of multiplication (see Figure 14.9), we can now calculate the frequencies of the three possible genotypes, assuming random unions of sperm and eggs.

The probability that two  $C^R$  alleles will come together is  $p \times p = p^2 = 0.8 \times 0.8 = 0.64$ . Thus, about 64% of the plants in the next generation will have the genotype  $C^R C^R$ . The frequency of  $C^W C^W$  individuals is expected to be about  $q \times q = q^2 = 0.2 \times 0.2 = 0.04$ , or 4%.  $C^R C^W$  heterozygotes can arise in two different ways. If the sperm provides the  $C^R$  allele and the egg provides the  $C^W$  allele, the resulting heterozygotes will be  $p \times q = 0.8 \times 0.2 = 0.16$ , or 16% of the total. If the sperm provides the  $C^W$  allele and the egg the  $C^R$  allele, the heterozygous offspring will make up  $q \times p = 0.2 \times 0.8 = 0.16$ , or 16%. The frequency of heterozygotes is thus the sum of these possibilities:  $pq + qp = 2pq = 0.16 + 0.16 = 0.32$ , or 32%.

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

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



**WHAT IF?** If the frequency of the  $C^R$  allele were 0.6, predict the frequencies of the  $C^R C^R$ ,  $C^R C^W$ , and  $C^W C^W$  genotypes.

→ Mastering Biology Figure Walkthrough

for Hardy-Weinberg equilibrium states that if a population is not evolving at a locus with two alleles, the three genotypes will appear in the following proportions:

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

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

### Conditions for Hardy-Weinberg Equilibrium

The Hardy-Weinberg approach describes a population that is not evolving. This can occur if a population meets all five of the conditions for Hardy-Weinberg equilibrium listed in **Table 23.1**. But in nature, the allele and genotype frequencies of a population often *do* change over time. Such changes

**Table 23.1** Conditions for Hardy-Weinberg Equilibrium

Condition	Consequence if Condition Does Not Hold
<b>1. No mutations</b>	The gene pool is modified if mutations occur or if entire genes are deleted or duplicated.
<b>2. Random mating</b>	If individuals mate within a subset of the population, such as near neighbors or close relatives (inbreeding), random mixing of gametes does not occur and genotype frequencies change.
<b>3. No natural selection</b>	Allele frequencies change when individuals with different genotypes show consistent differences in their survival or reproductive success.
<b>4. Extremely large population size</b>	In small populations, allele frequencies fluctuate by chance over time (genetic drift).
<b>5. No gene flow</b>	By moving alleles into or out of populations, gene flow can alter allele frequencies.

→ Mastering Biology Animation: Causes of Evolutionary Change

can occur when at least one of the conditions for Hardy-Weinberg equilibrium is not met.

Although departure from the conditions in Table 23.1 is common—resulting in evolutionary change—it is also common for natural populations to be in Hardy-Weinberg equilibrium for specific genes. One way this can happen is if selection alters allele frequencies at some loci but not others. In addition, some populations evolve so slowly that the changes in their allele and genotype frequencies are difficult to distinguish from those predicted for a non-evolving population.

### Applying the Hardy-Weinberg Equation

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

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

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

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

and the frequency of the dominant allele is

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

## Scientific Skills Exercise

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

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

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

#### Data from the Experiment

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

#### INTERPRET THE DATA

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

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

$$2pq = 2 \times 0.99 \times 0.01 = 0.0198 \\ (\text{approximately } 2\% \text{ of the U.S. population})$$

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

#### CONCEPT CHECK 23.2

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

*For suggested answers, see Appendix A.*

2. Next, use the Hardy-Weinberg equation ( $p^2 + 2pq + q^2 = 1$ ) to calculate the day 7 expected frequencies of genotypes  $C^G C^G$ ,  $C^G C^Y$ , and  $C^Y C^Y$  for a population in Hardy-Weinberg equilibrium.

3. (a) Calculate the observed frequencies of genotypes  $C^G C^G$ ,  $C^G C^Y$ , and  $C^Y C^Y$  at day 7. (b) Compare these frequencies to the expected frequencies calculated in question 2. Is the seedling population in Hardy-Weinberg equilibrium at day 7, or is evolution occurring? Explain your reasoning and identify which genotypes, if any, appear to be selected for or against.

4. (a) Calculate the observed frequencies of genotypes  $C^G C^G$ ,  $C^G C^Y$ , and  $C^Y C^Y$  at day 21. (b) Compare these frequencies to the expected frequencies calculated in question 2 and to the observed frequencies at day 7. Is the seedling population in Hardy-Weinberg equilibrium at day 21, or is evolution occurring? Explain your reasoning and identify which genotypes, if any, appear to be selected for or against.

5. Homozygous  $C^Y C^Y$  individuals cannot produce chlorophyll. The ability to photosynthesize becomes more critical as seedlings age and begin to exhaust the supply of food that was stored in the seed from which they emerged. Develop a hypothesis that explains the data for days 7 and 21. Based on this hypothesis, predict how the frequencies of the  $C^G$  and  $C^Y$  alleles will change beyond day 21.

→ **Instructors:** A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.



#### CONCEPT 23.3

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

Note again the five conditions required for a population to be in Hardy-Weinberg equilibrium (see Table 23.1). A deviation from any of these conditions is a potential cause of evolution. New mutations (violation of condition 1) can alter allele frequencies, but because mutations are rare, the change from one generation to the next is likely to be very small. Nonrandom mating (violation of condition 2) can affect the frequencies of homozygous and heterozygous genotypes but by itself has no effect on allele frequencies in the gene pool. (Allele frequencies can change if individuals with certain inherited traits are more likely than other individuals to obtain mates. However, such a situation not only causes a deviation from random mating, but also violates condition 3, no natural selection.)

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

## Natural Selection

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

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

As the *D. melanogaster* example suggests, an allele that confers resistance to an insecticide will increase in frequency in a population exposed to that insecticide. Such changes are not coincidental. By consistently favoring some alleles over others, natural selection can cause **adaptive evolution**, in which traits that enhance survival or reproduction tend to increase in frequency over time. We'll explore this process in Concept 23.4.

## Genetic Drift

If you flip a coin 1,000 times, a result of 700 heads and 300 tails might make you suspicious about that coin. But if you flip a coin only 10 times, an outcome of 7 heads and 3 tails would not be surprising. The smaller the number of coin flips,

the more likely it is that chance alone will cause a deviation from the predicted result. (In this case, the prediction is an equal number of heads and tails.) Chance events can also cause allele frequencies to fluctuate unpredictably from one generation to the next, especially in small populations—a process called **genetic drift**.

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

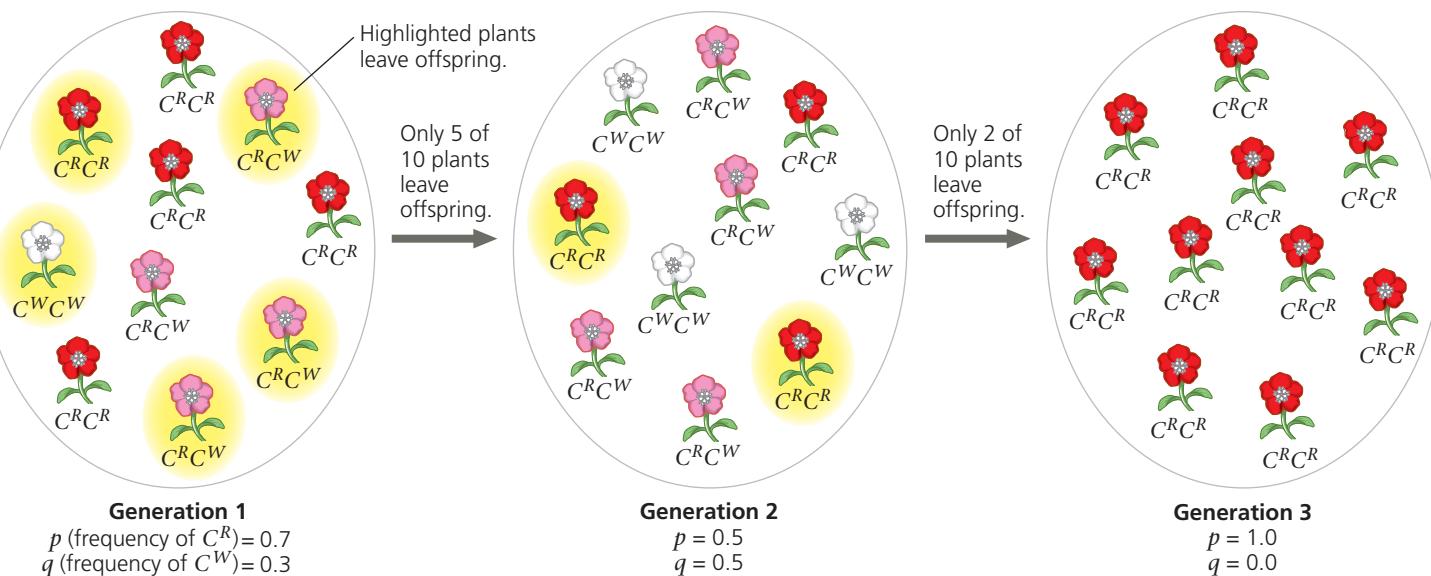
Certain circumstances can result in genetic drift having a significant impact on a population. Two examples are the founder effect and the bottleneck effect.

### The Founder Effect

When a few individuals become isolated from a larger population, this smaller group may establish a new population whose gene pool differs from the source population; this is called the **founder effect**. The founder effect might occur, for example, when a few members of a population are blown by a storm to a new island. Genetic drift, in which chance events alter allele frequencies, can occur in such a case because the

▼ **Figure 23.9** **Genetic drift.** This small wildflower population has a stable size of ten plants. Suppose that by chance only five plants of generation 1 (those highlighted in yellow) produce fertile offspring. Again by chance, only two plants of generation 2 leave fertile offspring.

**VISUAL SKILLS** Based on this diagram, summarize how the frequency of the  $C^W$  allele changes over time.



storm indiscriminately transports some individuals (and their alleles), but not others, from the source population.

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

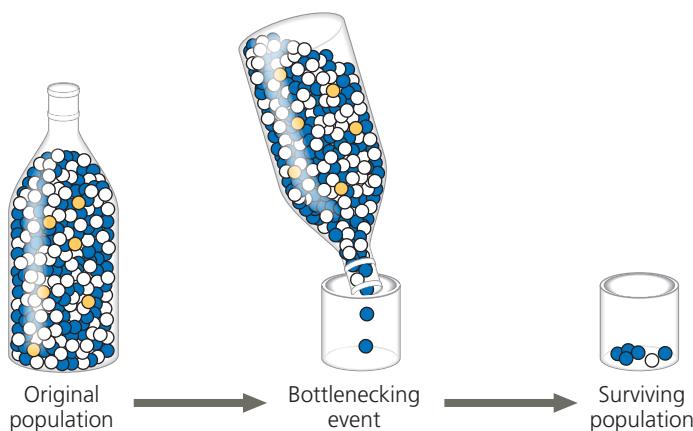
### The Bottleneck Effect

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

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

Human actions sometimes create severe bottlenecks. Millions of greater prairie chickens (*Tympanuchus cupido*) once lived on the prairies of Illinois. As these prairies were converted to farmland during the 1800s and 1900s, the number of greater

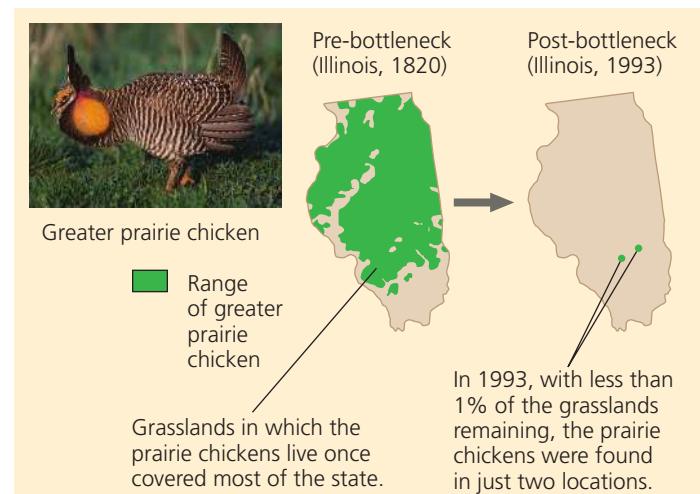
**▼ Figure 23.10 The bottleneck effect.** Shaking a few marbles through the neck of a bottle is analogous to a drastic reduction in the size of a population. By chance, blue marbles are overrepresented in the surviving population and gold marbles are absent.



prairie chickens plummeted (Figure 23.11a). By 1993 fewer than 50 birds remained. These few surviving birds had low levels of genetic variation, and less than 50% of their eggs hatched, compared with much higher hatching rates of the larger populations in Kansas and Nebraska (Figure 23.11b).

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

▼ Figure 23.11 Genetic drift and loss of genetic variation.



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

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

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

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

### Effects of Genetic Drift: A Summary

The examples we've described highlight four key points:

#### 1. Genetic drift is significant in small populations.

Chance events can cause an allele to be disproportionately over- or underrepresented in the next generation. Although chance events occur in populations of all sizes, they tend to alter allele frequencies substantially only in small populations.

#### 2. Genetic drift can cause allele frequencies to change at random.

**Because of genetic drift,** an allele may increase in frequency one year, then decrease the next; the change from year to year is not predictable. Thus, unlike natural selection, which in a given environment consistently favors some alleles over others, genetic drift causes allele frequencies to change at random over time.

#### 3. Genetic drift can lead to a loss of genetic variation within populations.

By causing allele frequencies to fluctuate randomly over time, genetic drift can eliminate alleles from a population. Because evolution depends on genetic variation, such losses can influence how effectively a population can adapt to a change in the environment.

#### 4. Genetic drift can cause harmful alleles to become fixed.

Alleles that are neither harmful nor beneficial can be lost or become fixed (reach a frequency of 100%) by chance through genetic drift. In very small populations, genetic drift can also cause alleles that are slightly harmful to become fixed. When this occurs, the population's survival can be threatened (as in greater prairie chickens).

## Gene Flow

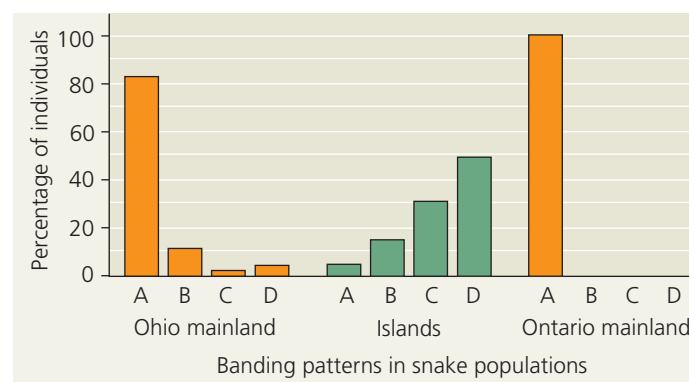
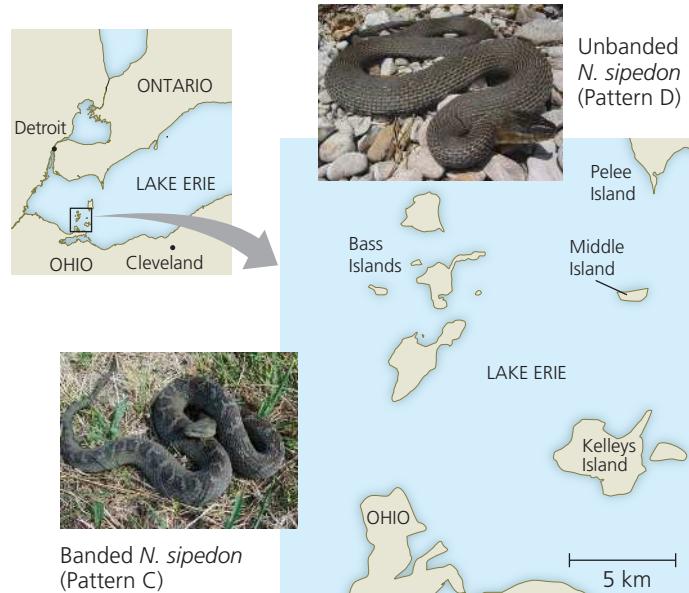
Natural selection and genetic drift are not the only phenomena affecting allele frequencies. Allele frequencies can also change by **gene flow**, the transfer of alleles into or out of a population due to the movement of fertile individuals or their gametes. For example, suppose that near our original hypothetical wildflower population there is another population consisting primarily of white-flowered individuals ( $C^W C^W$ ). Insects carrying pollen from these plants may fly to and pollinate

plants in our original population. The introduced  $C^W$  alleles would modify our original population's allele frequencies in the next generation. Because alleles are transferred between populations, gene flow tends to reduce the genetic differences between populations. In fact, if it is extensive enough, gene flow can result in two populations combining into a single population with a common gene pool.

Alleles transferred by gene flow can also affect how well populations are adapted to local environmental conditions. For instance, mainland and island populations of the Lake Erie water snake (*Nerodia sipedon*) differ in their color patterns (Figure 23.12): Nearly all snakes from the Ohio or Ontario mainlands are strongly banded, whereas the majority of snakes

▼ **Figure 23.12 Gene flow and local adaptation in the Lake**

**Erie water snake (*Nerodia sipedon*).** Researchers assigned letters to variations in coloration in *N. sipedon* populations. Color pattern A is strong banding, patterns B and C are intermediate banding, and pattern D is no banding. Banding is advantageous for camouflage in mainland environments, whereas having no bands is advantageous in island environments. However, gene flow from the mainland causes banding to persist in island populations.



**WHAT IF?** Suppose a severe weather event caused island populations to decrease in size but did not affect the size of mainland populations. Predict how gene flow from the mainland would affect color patterns in island populations in the year immediately after the storm. Explain.

from islands are unbanded or intermediate. Banding coloration is an inherited trait, determined by a few loci (with alleles that encode bands being dominant to alleles that encode the absence of bands). On islands, water snakes live along rocky shorelines, while on the mainland, they live in marshes. Snakes without bands are more well camouflaged in island habitats than are snakes with bands. Hence, on islands, snakes without bands survive at higher rates than do snakes with bands.

These data indicate that snakes without bands are favored by natural selection in island populations. Thus, we might expect that *all* snakes on islands would lack bands. Why is this not the case? The answer lies in gene flow from the mainland. In any given year, three to ten snakes from the mainland swim to the islands and join the populations there. As a result, each year such migrants transfer alleles for banded coloration from the mainland (where nearly all snakes have bands) to the islands. This ongoing gene flow has prevented selection from removing all of the alleles for banded coloration from island populations—thereby preventing island populations from adapting fully to local conditions.

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

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

→ **Mastering Biology BioFlix® Animation: Natural Selection, Genetic Drift, and Gene Flow**

**CONCEPT CHECK 23.3**

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

For suggested answers, see Appendix A.

**CONCEPT 23.4**

## Natural selection is the only mechanism that consistently causes adaptive evolution

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

### Natural Selection: A Closer Look

To see how natural selection can cause adaptive evolution, we’ll begin with the concept of relative fitness and the different ways that selection acts on an organism’s phenotype.

#### Relative Fitness

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

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

#### Directional, Disruptive, and Stabilizing Selection

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

**Directional selection** occurs when conditions favor individuals exhibiting one extreme of a phenotypic

range, thereby shifting a population's frequency curve for the phenotypic character in one direction or the other (**Figure 23.13a**). Directional selection is common when a population's environment changes or when members of a population migrate to a new (and different) habitat. For instance, an increase in the relative abundance of large seeds over small seeds led to an increase in beak depth in a population of Galápagos finches (see Figure 23.2).

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

**Stabilizing selection** (**Figure 23.13c**) acts against both extreme phenotypes and favors intermediate variants. This mode of selection reduces variation and tends to maintain

the status quo for a particular phenotypic character. For example, the birth weights of most human babies lie in the range of 3–4 kg (6.6–8.8 pounds). Babies who are much smaller suffer considerably higher rates of mortality; babies who are much larger show a slight increase in mortality.

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

Mastering Biology HHMI Video: Selection for Tuskless Elephants



## The Key Role of Natural Selection in Adaptive Evolution

The adaptations of organisms include many striking examples. Certain octopuses, for example, have the ability to change color rapidly, enabling them to blend into different backgrounds. Another example is the remarkable jaws of snakes (**Figure 23.14**), which allow them to swallow prey much larger than their own head (a feat analogous to a person swallowing a whole watermelon).

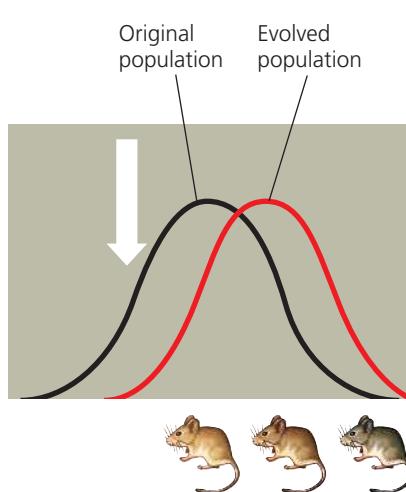
Other adaptations, such as a version of an enzyme that shows improved function in cold environments, may be less visually dramatic but just as important for survival and reproduction.

Such adaptations can arise gradually over time as natural selection increases the frequencies of alleles that enhance survival or reproduction. As the proportion of individuals that have favorable traits increases, the degree to which a

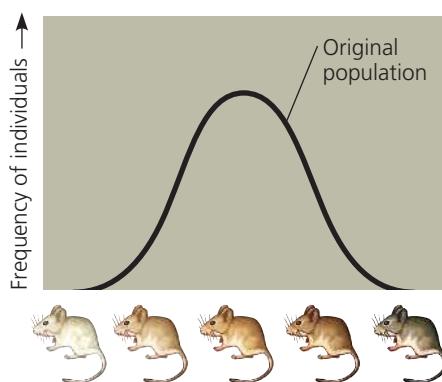
▼ **Figure 23.13 Modes of selection.**

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

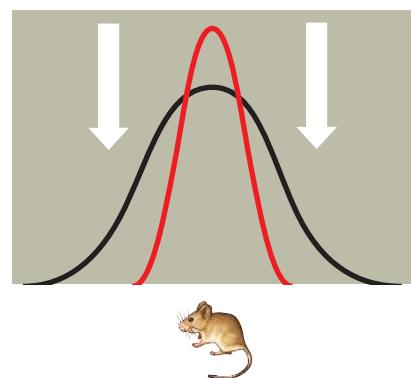
**MAKE CONNECTIONS** Review Figure 22.13. Which mode of selection has occurred in soapberry bug populations that feed on the introduced golden rain tree? Explain.



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



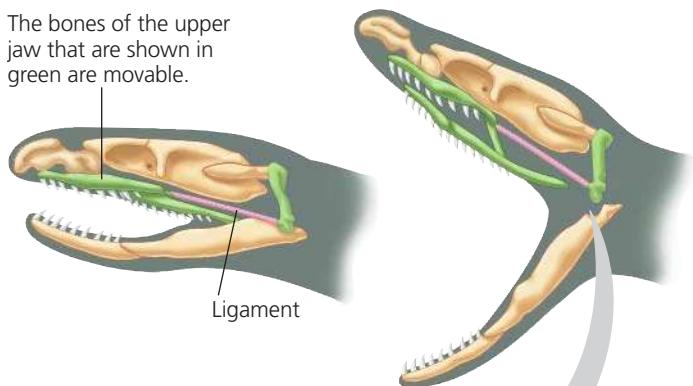
(b) **Disruptive selection** favors variants at both ends of the distribution. These mice have colonized a patchy habitat made up of light and dark rocks, with the result that mice of an intermediate color are selected against.



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

▼ Figure 23.14 Movable jaw bones in snakes.

The bones of the upper jaw that are shown in green are movable.



The skull bones of most terrestrial vertebrates are relatively rigidly attached to one another, limiting jaw movement. In contrast, most snakes have movable bones in their upper jaw, allowing them to swallow food much larger than their head.



species is well suited for life in its environment improves; that is, adaptive evolution occurs. However, the physical and biological components of an organism's environment may change over time. As a result, what constitutes a "good match" between an organism and its environment can be a moving target, making adaptive evolution a continuous, dynamic process. Environmental conditions can also differ from place to place, causing different alleles to be favored in different locations. When this occurs, natural selection can cause the populations of a species to differ genetically from one another.

And what about genetic drift and gene flow? Both can, in fact, increase the frequencies of alleles that enhance survival or reproduction, but neither does so consistently. Genetic drift can cause the frequency of a slightly beneficial allele to increase, or, alternately, to decrease. Similarly, gene flow may introduce alleles that are advantageous or ones that are disadvantageous. Natural selection is the only evolutionary mechanism that consistently leads to adaptive evolution.

→ Mastering Biology HHMI Video: Got Lactase?  
The Co-Evolution of Genes and Culture



## Sexual Selection

Charles Darwin was the first to explore the implications of **sexual selection**, a process in which individuals with certain inherited characteristics are more likely than other individuals of the same sex to obtain mates. Sexual selection can result in **sexual dimorphism**, a difference in secondary



▲ Figure 23.15 Sexual dimorphism and sexual selection.

A peacock (left) and a peahen (right) show extreme sexual dimorphism. There is intrasexual selection between competing males, followed by intersexual selection when the females choose among the showiest males.

sexual characteristics between males and females of the same species (Figure 23.15). These distinctions include differences in size, color, ornamentation, and behavior.

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

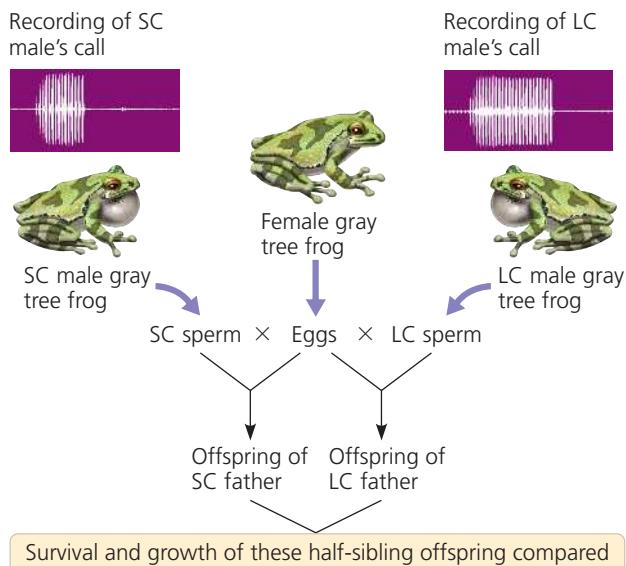
In **intersexual selection**, also called *mate choice*, individuals of one sex (usually the females) are choosy in selecting their mates from the other sex. In many cases, the female's choice depends on the showiness of the male's appearance or behavior (see Figure 23.15). What intrigued Darwin about mate choice is that male showiness may not seem adaptive in any other way and may in fact pose some risk. For example, bright plumage may make male birds more visible to predators. But if such characteristics help a male gain a mate, and if this benefit outweighs the risk from predation, then both the bright plumage and the female preference for it will be reinforced because they enhance overall reproductive success.

How do female preferences for certain male characteristics evolve in the first place? One hypothesis is that females prefer male traits that are correlated with "good genes." If the trait preferred by females is indicative of a male's overall genetic quality, both the male trait and female preference

▼ Figure 23.16 Inquiry

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

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



### Results

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

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

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

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

**INQUIRY IN ACTION** Read and analyze the original paper in *Inquiry in Action: Interpreting Scientific Papers*.

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

for it should increase in frequency. **Figure 23.16** describes one experiment testing this hypothesis in gray tree frogs.

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

## Balancing Selection

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

### Frequency-Dependent Selection

In **frequency-dependent selection**, the fitness of a phenotype depends on how common it is in the population. Consider the scale-eating fish (*Perissodus microlepis*) of Lake Tanganyika, in Africa. These fish attack other fish from behind, darting in to remove a few scales from the flank of their prey. Of interest here is a peculiar feature of the scale-eating fish: Some are “left-mouthed” and some are “right-mouthed.”

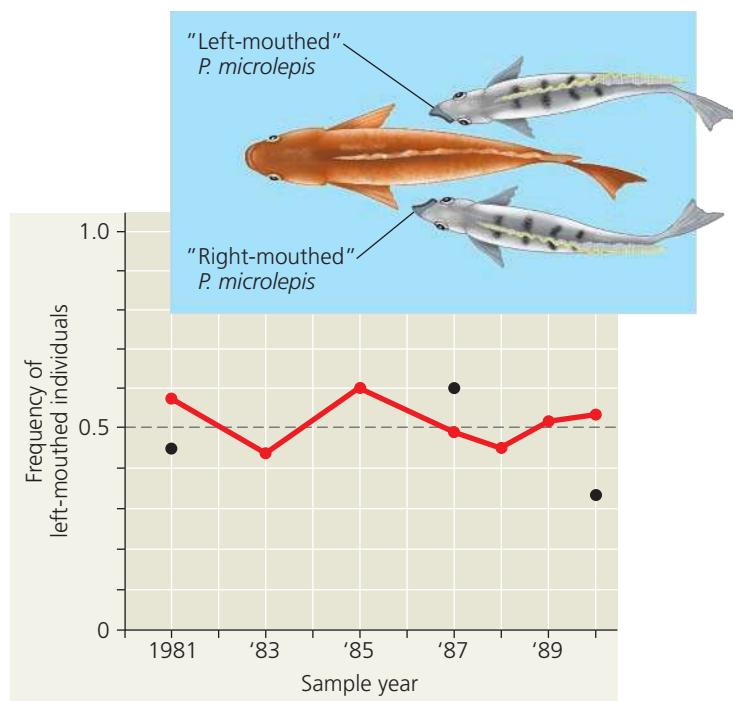
Because their mouth twists to the left, left-mouthed fish typically attack their prey’s right flank (**Figure 23.17**). (To see why, twist your lower jaw and lips to the left and imagine trying to take a bite from the left side of a fish, approaching it from behind.) Similarly, right-mouthed fish attack from the left. Prey species guard against attack from whatever phenotype of scale-eating fish is most common. Thus, from year to year, selection favors whichever mouth phenotype is least common. As a result, the frequency of left- and right-mouthed fish oscillates over time, and this balancing selection keeps the frequency of each phenotype close to 50%.

### Heterozygote Advantage

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

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

**▼ Figure 23.17 Frequency-dependent selection.** In a population of the scale-eating fish *Perissodus microlepis*, the frequency of left-mouthed individuals (red data points) rises and falls in a regular manner. The black data points indicate the frequency of left-mouthed individuals among adults that reproduced in three sample years.



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

heterozygotes, not enough become sickled to cause sickle-cell disease.

As described in **Figure 23.18**, heterozygotes for the sickle-cell allele are protected against the most severe effects of malaria, a disease caused by a parasite that infects red blood cells. One reason for this partial protection is that the body destroys sickled red blood cells rapidly, killing the parasites they harbor. Malaria is a major killer in some tropical regions. In such regions, selection favors heterozygotes over homozygous dominant individuals, who are more vulnerable to the effects of malaria, and also over homozygous recessive individuals, who develop sickle-cell disease. These selective pressures have caused the frequency of the sickle-cell allele to reach relatively high levels in areas where the malaria parasite, which is carried by mosquitoes, is common.

## Why Natural Selection Cannot Fashion Perfect Organisms

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

### 1. Selection can act only on existing variations.

Natural selection favors only the fittest phenotypes

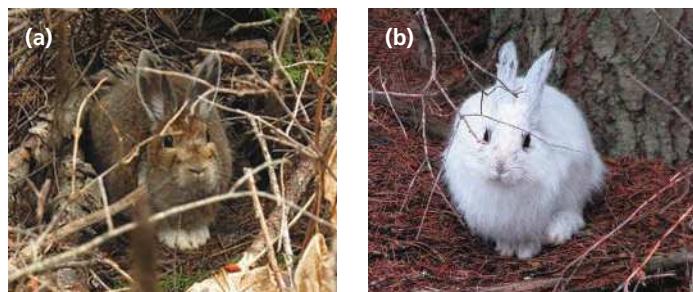
among those currently in the population, which may not be the ideal traits. New advantageous alleles do not arise on demand. For example, historically, snowshoe hares (*Lepus americanus*) have molted, changing their coats from brown to white, at a time of year that matched the onset of snowfall, providing camouflage all winter. But due to climate change, the first snowfall now occurs later in the year. In some populations, the date at which the hares change their coat color has remained the same, causing the hares to be poorly camouflaged early in winter and thus easier for predators to spot and kill (**Figure 23.19**). Because their gene pools lack alleles that could delay when molting occurs, these populations have been unable to adapt to changing conditions.

### 2. Evolution is limited by historical constraints.

Each species has a legacy of descent with modification from ancestral forms. Evolution does not scrap the ancestral anatomy and build each new complex structure from scratch; rather, evolution co-opts existing structures and adapts them to new situations. We could imagine that if a terrestrial animal were to adapt to an environment in which flight would be advantageous, it might be best just to grow an extra pair of limbs that would serve as wings. However, evolution does not work this way; instead, it operates on the traits an organism already has. Thus, in birds and bats, an existing pair of limbs took on new functions for flight as these organisms evolved from nonflying ancestors.

**3. Adaptations are often compromises.** Each organism must do many different things. A seal spends part of its time on rocks; it could probably walk better if it had legs instead of flippers, but then it would not swim nearly as well. We humans owe much of our versatility and athleticism to our prehensile hands and flexible limbs, but these also make us prone to sprains, torn ligaments, and dislocations. Structural reinforcement has been compromised for agility. Organisms face many such *trade-offs* in which the ability to perform one function may reduce the ability to perform another—and as with seals and humans, those trade-offs can restrict adaptive evolution.

**▼ Figure 23.19 Lack of variation in a population can limit adaptation.** For the snowshoe hare, changing its coat color from brown (a) to white (b) too early is disadvantageous, but the population lacks alleles that would encode a delay in molting.



▼ Figure 23.18

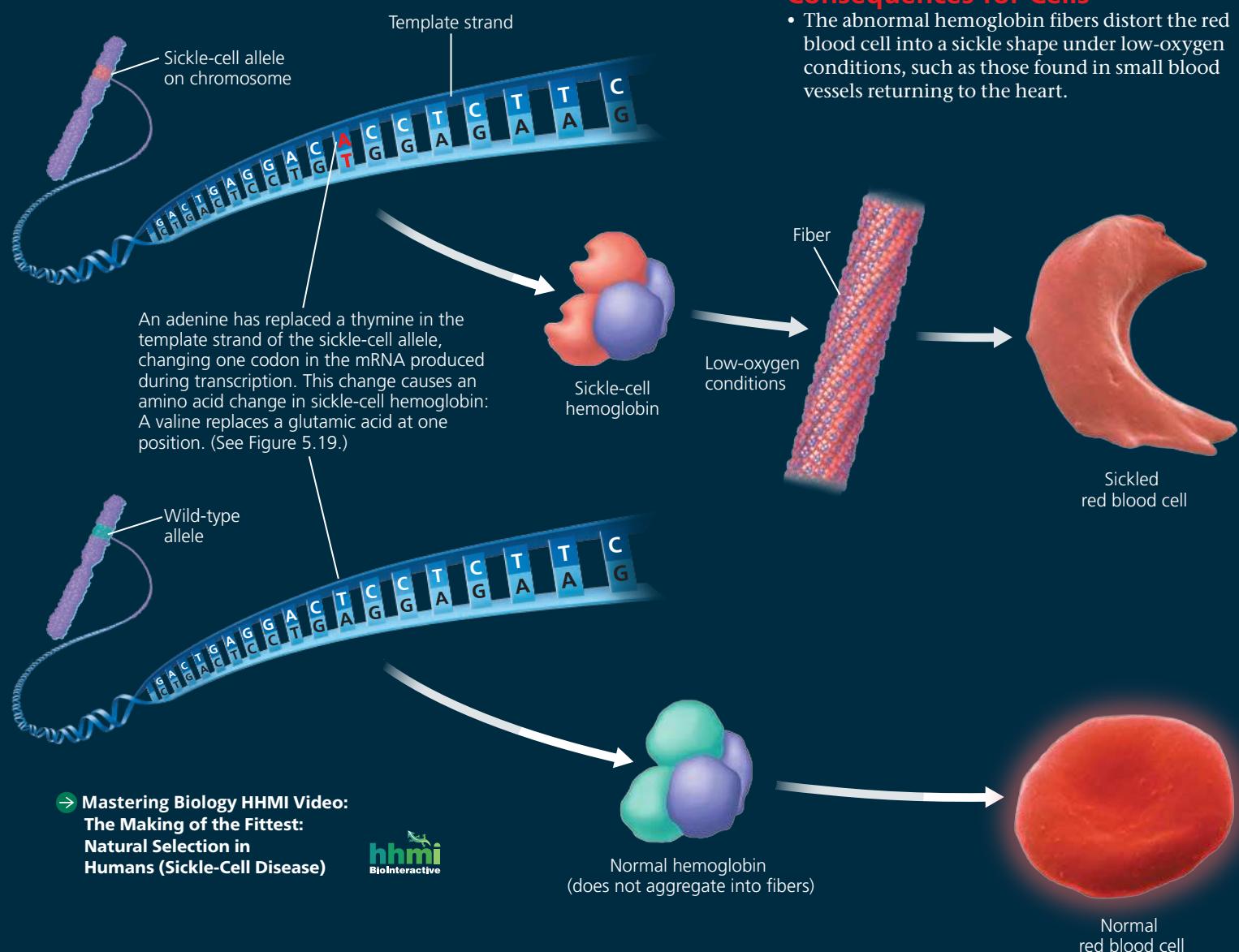
## MAKE CONNECTIONS

### The Sickle-Cell Allele

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

#### Events at the Molecular Level

- Due to a point mutation, the sickle-cell allele differs from the wild-type allele by a single nucleotide. (See Figure 17.26.)
- The resulting change in one amino acid leads to hydrophobic interactions between the sickle-cell hemoglobin proteins under low-oxygen conditions.
- As a result, the sickle-cell proteins bind to each other in chains that together form a fiber.

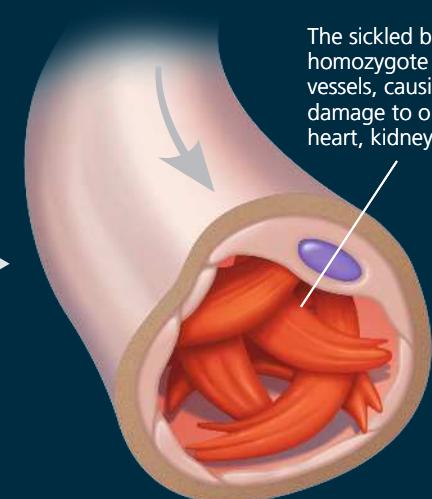




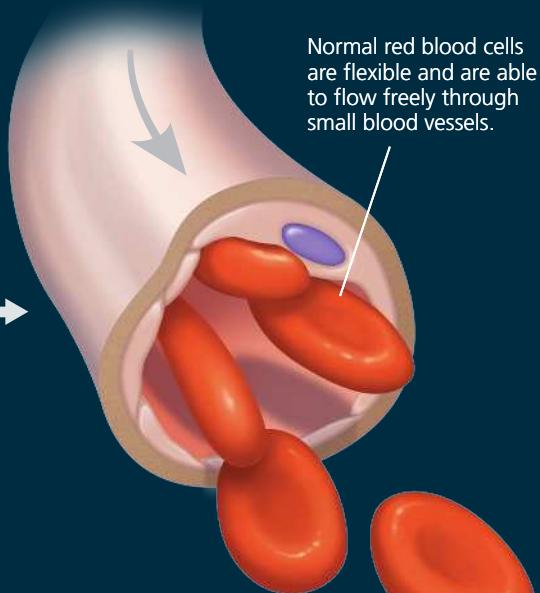
Infected mosquitoes spread malaria when they bite people. (See Figure 28.16.)

## Effects on Individual Organisms

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



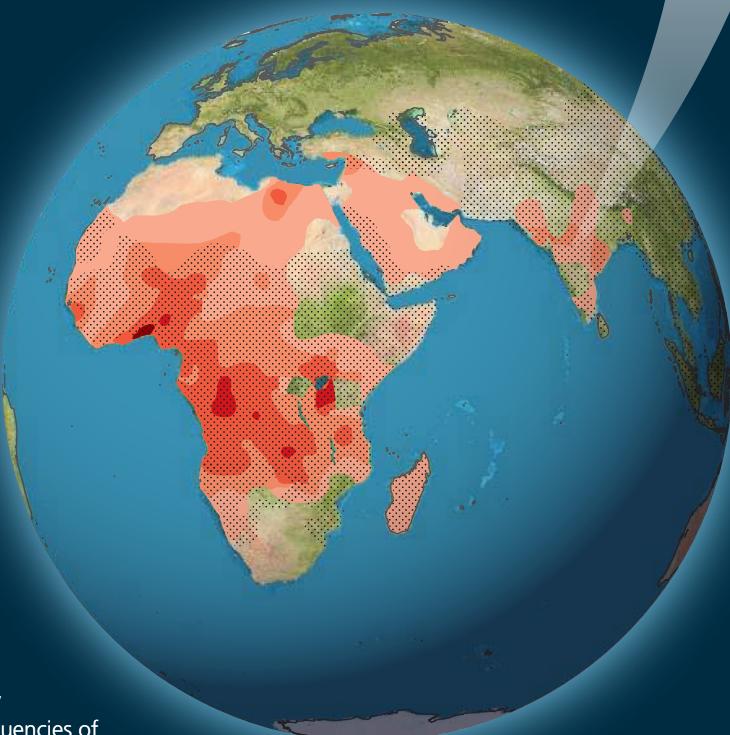
The sickled blood cells of a homozygote block small blood vessels, causing great pain and damage to organs such as the heart, kidney, and brain.



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

## Evolution in Populations

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



### Key

Frequencies of the sickle-cell allele

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

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

### MAKE CONNECTIONS

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

#### 4. Chance, natural selection, and the environment interact.

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

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

#### CONCEPT CHECK 23.4

- What is the relative fitness of a sterile mule? Explain.
- Explain why natural selection is the only mechanism that consistently leads to adaptive evolution in a population.
- VISUAL SKILLS** Consider a population in which heterozygotes at a certain locus have an extreme phenotype (such as being larger than homozygotes) that confers a selective advantage. Compare this description to the three types of selection shown in Figure 23.13. Does this situation represent directional, disruptive, or stabilizing selection? Explain.

For suggested answers, see Appendix A.

# 23 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

## SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to [goo.gl/zkjz9t](http://goo.gl/zkjz9t).

### CONCEPT 23.1

#### Genetic variation makes evolution possible (pp. 487–489)

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

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

### CONCEPT 23.2

#### The Hardy-Weinberg equation can be used to test whether a population is evolving (pp. 489–493)

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

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

### CONCEPT 23.3

#### Natural selection, genetic drift, and gene flow can alter allele frequencies in a population (pp. 493–497)

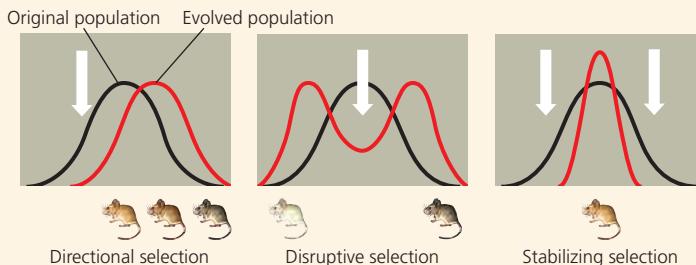
- In natural selection, individuals that have certain inherited traits tend to survive and reproduce at higher rates than other individuals *because of* those traits.
- In **genetic drift**, chance fluctuations in allele frequencies over generations tend to reduce genetic variation.
- Gene flow**, the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

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

### CONCEPT 23.4

#### Natural selection is the only mechanism that consistently causes adaptive evolution (pp. 497–504)

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



- Unlike genetic drift and gene flow, natural selection consistently increases the frequencies of alleles that enhance survival and reproduction, thus improving the degree to which organisms are well-suited for life in their environment.
- Sexual selection** can result in secondary sex characteristics that can give individuals advantages in mating.
- Balancing selection** occurs when natural selection maintains two or more forms in a population.

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

Q How might secondary sex characteristics in males differ from those in females in a species in which females compete for mates?

## TEST YOUR UNDERSTANDING

→ For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to [goo.gl/GruWRg](http://goo.gl/GruWRg).

### Levels 1-2: Remembering/Understanding

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

### Levels 3-4: Applying/Analyzing

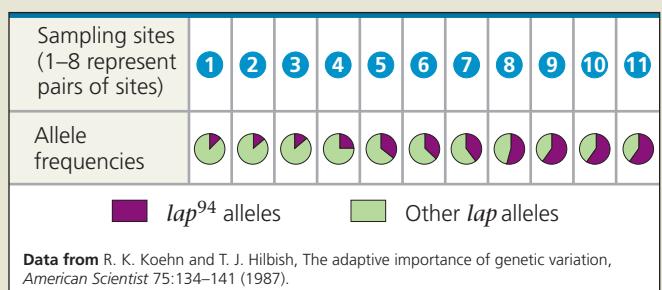
- If the nucleotide variability of a locus equals 0%, what is the gene variability and number of alleles at that locus?
  - (A) gene variability = 0%; number of alleles = 0
  - (B) gene variability = 0%; number of alleles = 1
  - (C) gene variability = 0%; number of alleles = 2
  - (D) gene variability > 0%; number of alleles = 2
- One population of a species has 25 individuals, all with genotype *AA*; a second population of this species has 40 individuals, all with genotype *aa*. Assume that these populations live far apart but in similar environmental conditions. Based on this information, the observed genetic variation most likely resulted from
  - (A) genetic drift.
  - (B) gene flow.
  - (C) nonrandom mating.
  - (D) directional selection.
- A fruit fly population has a gene with two alleles, *A*<sub>1</sub> and *A*<sub>2</sub>. Tests show that 70% of the gametes produced in the population contain the *A*<sub>1</sub> allele. If the population is in Hardy-Weinberg equilibrium, what proportion of the flies carry both *A*<sub>1</sub> and *A*<sub>2</sub>?
  - (A) 0.7
  - (B) 0.49
  - (C) 0.42
  - (D) 0.21

### Levels 5-6: Evaluating/Creating

- EVOLUTION CONNECTION** Using at least two examples, explain how the process of evolution is revealed by the imperfections of living organisms.
- SCIENTIFIC INQUIRY • INTERPRET THE DATA** For populations of the marine mussel *Mytilus edulis* around Long Island, New York, researchers measured the frequency of a particular allele (*lap*<sup>94</sup>) for an enzyme involved in regulating the mussel's saltwater balance. They presented their data as a series of pie charts linked to sampling sites within Long Island Sound, where the salinity is highly variable, and along the coast of the open ocean, where salinity is constant. (a) Create a data table for the 11 sampling sites by estimating the frequency of *lap*<sup>94</sup> from the pie charts. (b) Graph the frequencies for sites 1–8 to show how the frequency of this allele changes with increasing salinity in Long Island Sound (from southwest to northeast). Evaluate how the data from sites 9–11 compare with the data from the sites within the Sound. (c) Considering the various mechanisms that can alter allele frequency, construct a hypothesis that explains the patterns

in the data and that accounts for the following observations:

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



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

### 9. SYNTHESIZE YOUR KNOWLEDGE



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

For selected answers, see Appendix A.

#### Explore Scientific Papers with Science in the Classroom AAAS

How does a native species evolve in response to an introduced species? Go to "There's a New Kid in Town" at [www.scienceintheclassroom.org](http://www.scienceintheclassroom.org).

→ **Instructors:** Questions can be assigned in **Mastering Biology**.

# 24 The Origin of Species

## KEY CONCEPTS

- 24.1** The biological species concept emphasizes reproductive isolation p. 507
- 24.2** Speciation can take place with or without geographic separation p. 511
- 24.3** Hybrid zones reveal factors that cause reproductive isolation p. 516
- 24.4** Speciation can occur rapidly or slowly and can result from changes in few or many genes p. 520

## Study Tip

**Make a table:** Some processes that can lead to speciation only occur in allopatric (geographically separated) populations, while others also occur in sympatric (geographically overlapping) populations. To help you keep track of these processes and the geographic conditions under which they can occur, fill in the table as you read the chapter.

Process (include page # or figure #)	Can occur in allopatric populations (yes/no)?	Can occur in sympatric populations (yes/no)?
Sexual selection (Figure 24.12)	Yes	Yes

## → Go to Mastering Biology

### For Students (in eText and Study Area)

- Get Ready for Chapter 24
- Figure 24.10 Walkthrough: One Mechanism for Allopolyploid Speciation in Plants

### For Instructors to Assign (in Item Library)

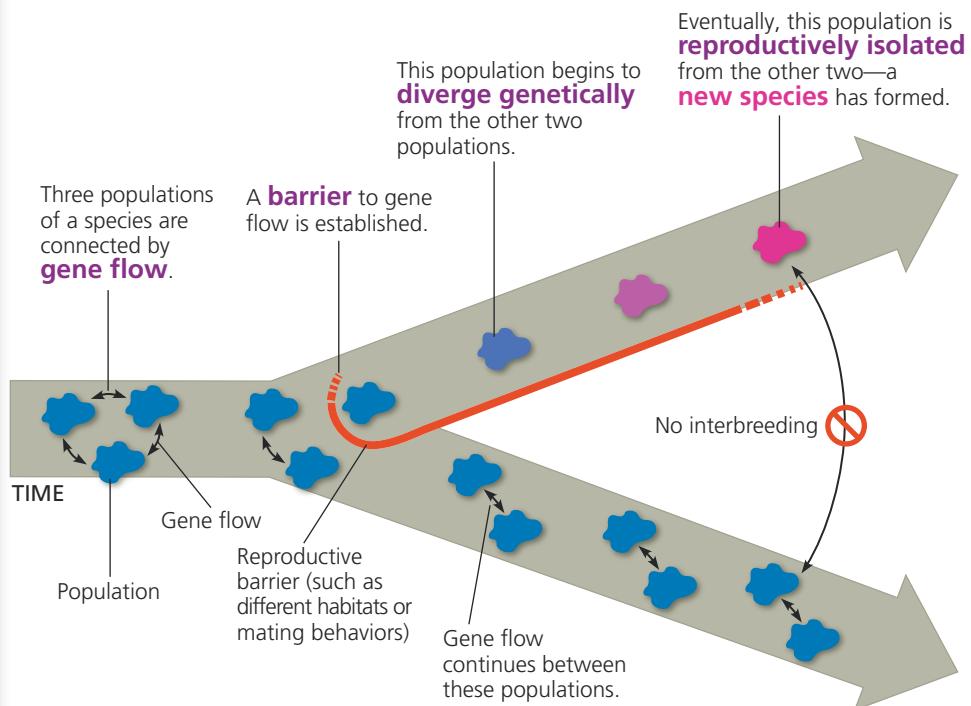
- Interpreting Data: Evolution of Reproductive Barriers in Lab Populations of Fruit Flies
- Problem-Solving Exercise: Is Hybridization Promoting Insecticide Resistance?



**Figure 24.1** This flightless cormorant is one of many species in the Galápagos Islands that are found nowhere else in the world. How did a bird that cannot fly come to live in this isolated place? When Darwin visited the Galápagos, he also was intrigued by its unique species, and later concluded that they must have originated in the islands from ancestors that had traveled from South America.

## How do new species originate from existing species?

Over time, populations of a single species connected by gene flow can diverge genetically, giving rise to a new species:



When Darwin came to the Galápagos Islands, he noted that they were teeming with unique species, like the flightless bird in Figure 24.1. Later, he realized that these species had formed relatively recently, writing in his diary, “Both in space and time, we seem to be brought somewhat near to that great fact—that mystery of mysteries—the first appearance of new beings on this Earth.”

The “mystery of mysteries” that captivated Darwin is **speciation**, the process by which one species splits into two species. Speciation fascinated Darwin (and many biologists since) because it has produced the tremendous diversity of life, repeatedly yielding new species that differ from existing ones. Speciation also helps to explain the many features that organisms share (the unity of life): When one species splits into two, the species that result share many characteristics because they are descended from this common ancestor. For example, at the DNA sequence level, such similarities indicate that the flightless cormorant in Figure 24.1 is closely related to flying cormorants found in the Americas. This suggests that the flightless cormorant originated from an ancestral cormorant species that flew from the mainland to the Galápagos.

Speciation forms a conceptual bridge between **microevolution**, changes over time in allele frequencies in a population, and **macroevolution**, the broad pattern of evolution above the species level. An example of macroevolutionary change is the origin of new groups of organisms, such as mammals or flowering plants, through a series of speciation events. We examined microevolutionary mechanisms in Chapter 23, and we’ll turn to macroevolution in Chapter 25. In this chapter, we’ll explore the mechanisms by which new species originate from existing ones. First, let’s establish what we actually mean by a “species.”

## CONCEPT 24.1

### The biological species concept emphasizes reproductive isolation

The word *species* is Latin for “kind” or “appearance.” In daily life, we commonly distinguish between various “kinds” of organisms—dogs and cats, for instance—based on differences in their appearance. But are organisms truly divided into the discrete units we call species? To answer this question, biologists compare not only the morphology (body form) of different groups of organisms but also their physiology, biochemistry, and DNA sequences. The results generally confirm that morphologically distinct species are indeed discrete groups, differing in many ways besides their body forms.

#### The Biological Species Concept

The primary definition of species used in this textbook is the **biological species concept**. According to this concept, a

▼ **Figure 24.2** The biological species concept is based on the potential to interbreed, not on physical similarity.



(a) **Similarity between different species.** The eastern meadowlark (*Sturnella magna*, left) and the western meadowlark (*Sturnella neglecta*, right) have similar body shapes and colorations. Nevertheless, they are distinct biological species because their songs and other behaviors are different enough to prevent interbreeding should they meet in the wild.



(b) **Diversity within a species.** As diverse as we may be in appearance, all humans belong to a single biological species (*Homo sapiens*), defined by our capacity to interbreed successfully.

**species** is a group of populations whose members have the potential to interbreed in nature and produce viable, fertile offspring—but do not produce viable, fertile offspring with members of other such groups (**Figure 24.2**). Thus, the members of a biological species are united by being reproductively compatible, at least potentially. All human beings, for example, belong to the same species. A businesswoman in Manhattan may be unlikely to meet a dairy farmer in Mongolia, but if the two should happen to meet and mate, they could have viable babies who develop into fertile adults. In contrast, humans and chimpanzees remain distinct biological species, even where they live in the same region, because many factors keep them from interbreeding and producing fertile offspring.

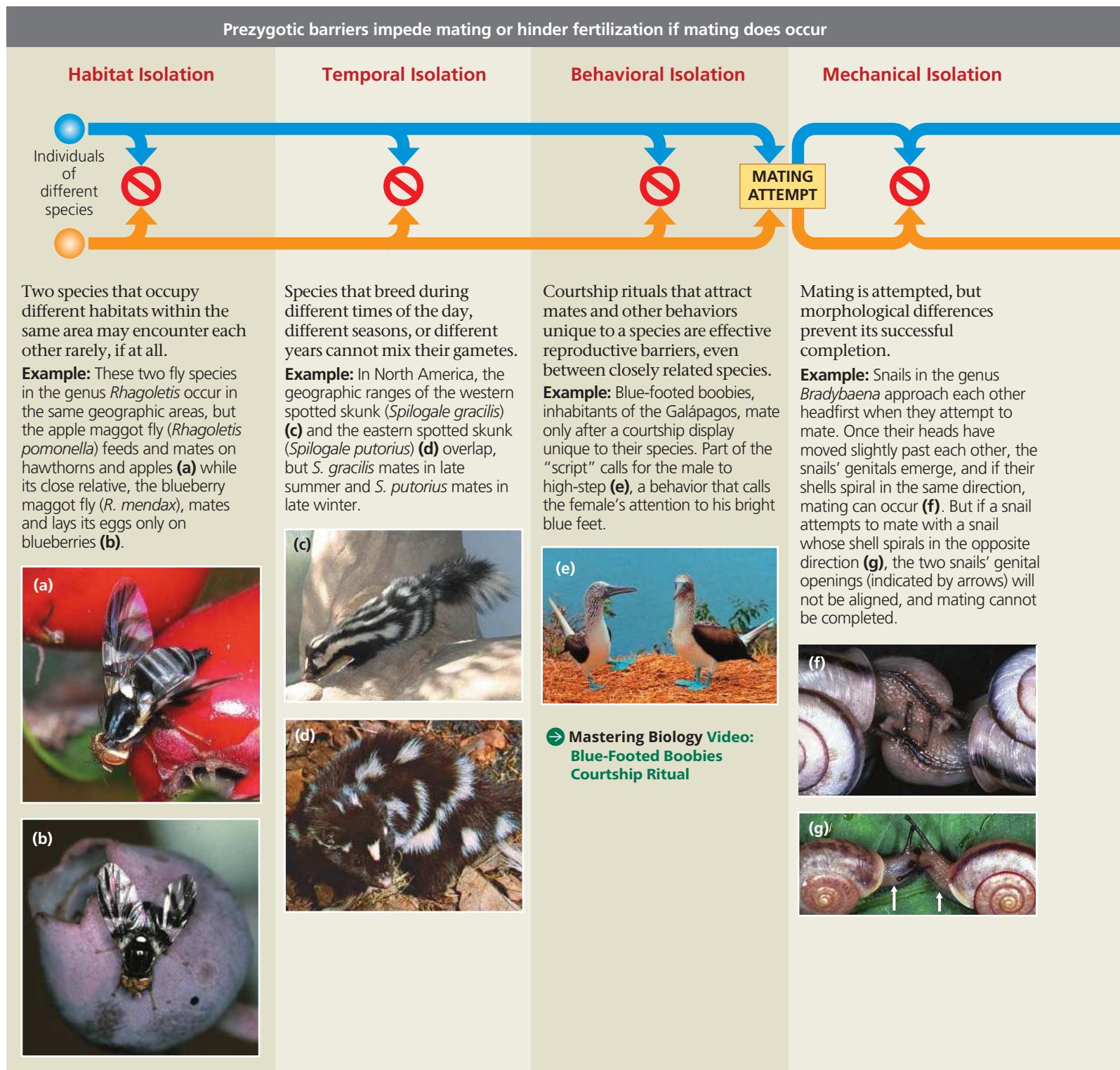
What holds the gene pool of a species together, causing its members to resemble each other more than they resemble members of other species? Recall the evolutionary mechanism of *gene flow*, the transfer of alleles between populations

(see Concept 23.3). Typically, gene flow occurs between the different populations of a species. This ongoing exchange of alleles tends to hold the populations together genetically. But as we'll explore in this chapter, a reduction or lack of gene flow can play a key role in the formation of new species.

### Reproductive Isolation

Because biological species are defined in terms of reproductive compatibility, the formation of a new species hinges on **reproductive isolation**—the existence of biological

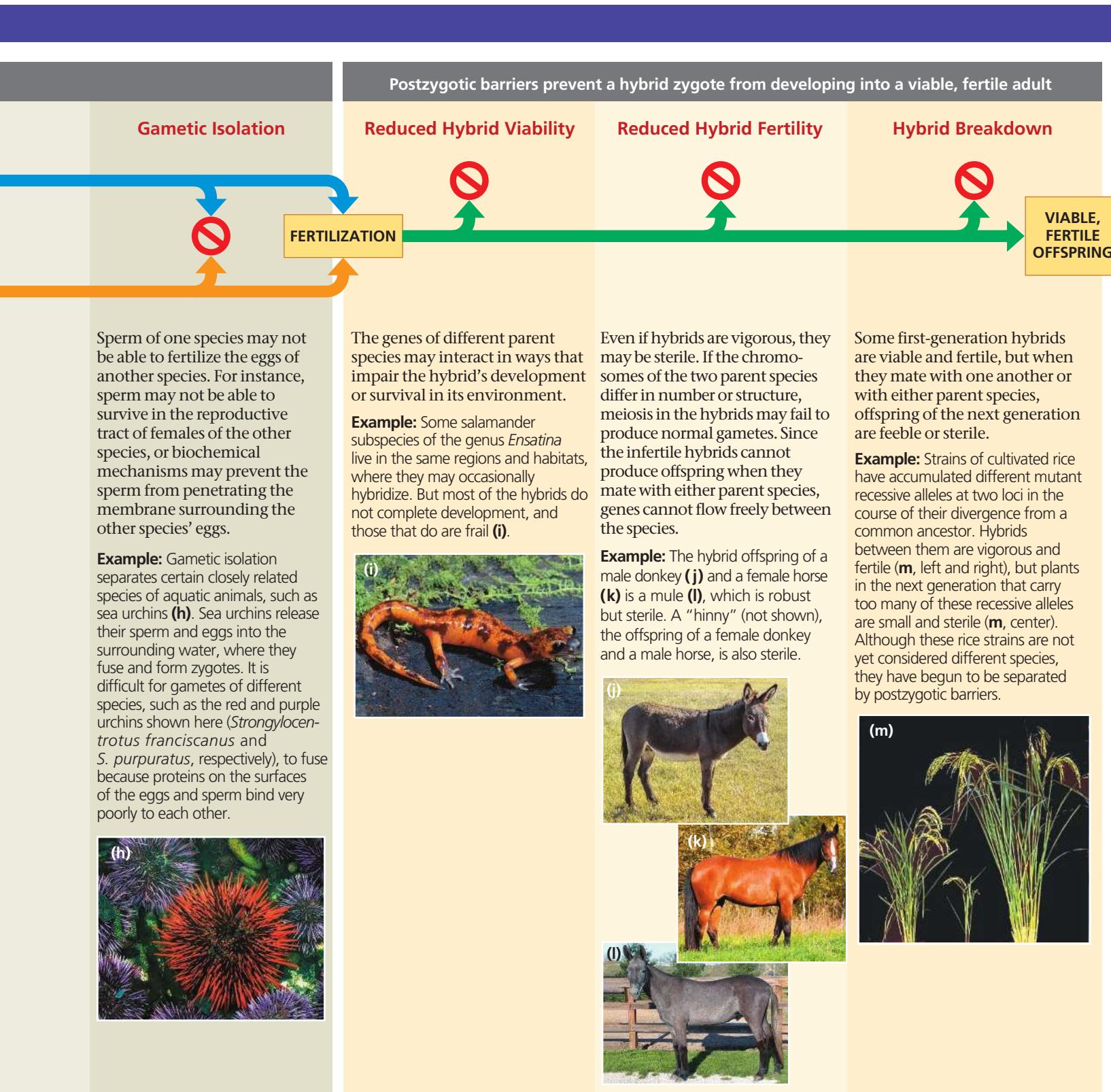
▼ Figure 24.3 Exploring Reproductive Barriers



factors (barriers) that impede members of two species from interbreeding and producing viable, fertile offspring (**Figure 24.3**). Such barriers block gene flow between the species and limit the formation of **hybrids**, offspring that result from an interspecific mating. Although a single

barrier may not prevent all gene flow, a combination of several barriers can effectively isolate a species' gene pool.

Clearly, a fly cannot mate with a frog or a fern, but the reproductive barriers between more closely related species are not so obvious. As described in Figure 24.3, these barriers can be



classified according to whether they contribute to reproductive isolation before or after fertilization. **Prezygotic barriers** (“before the zygote”) block fertilization from occurring. Such barriers typically act in one of three ways: by impeding members of different species from attempting to mate, by preventing an attempted mating from being completed successfully, or by hindering fertilization if mating is completed successfully. If a sperm cell from one species overcomes prezygotic barriers and fertilizes an ovum from another species, a variety of **postzygotic barriers** (“after the zygote”) may contribute to reproductive isolation after the hybrid zygote is formed. Developmental errors may reduce survival among hybrid embryos. Or problems after birth may cause hybrids to be infertile or decrease their chance of surviving long enough to reproduce.

 [Mastering Biology Video: Prezygotic Barriers to Mating in Galápagos Finches by Peter and Rosemary Grant](#)

### Limitations of the Biological Species Concept

One strength of the biological species concept is that it directs our attention to a way by which speciation can occur: by the evolution of reproductive isolation. However, the number of species to which this concept can be usefully applied is limited. There is, for example, no way to evaluate the reproductive isolation of fossils. The biological species concept also does not apply to organisms that reproduce asexually all or most of the time, such as prokaryotes. (Many prokaryotes do transfer genes among themselves, as we will discuss in Concept 27.2, but this is not part of their reproductive process.) Furthermore, in the biological species concept, species are designated by the *absence* of gene flow. But there are many pairs of species that are morphologically and ecologically distinct, and yet gene flow occurs between them. An example is the grizzly bear (*Ursus arctos*) and polar bear (*Ursus maritimus*), whose hybrid offspring have been dubbed “grolar bears” (Figure 24.4). As we’ll discuss, natural selection can cause such species to remain distinct even though some gene flow occurs between them. Because of the limitations to the biological species concept, alternative species concepts are useful in certain situations.

### Other Definitions of Species

While the biological species concept emphasizes the *separateness* of different species due to reproductive barriers, several other definitions emphasize the *unity within* a species. For example, the **morphological species concept** distinguishes a species by body shape and other structural features. The morphological species concept can be applied to asexual and sexual organisms, and it can be useful even without information on the extent of gene flow. In practice, scientists often distinguish species using morphological criteria. A disadvantage of this approach, however, is that it relies on subjective criteria; researchers may disagree on which structural features distinguish a species.



 **▲ Figure 24.4** Hybridization between two species of bears in the genus *Ursus*.

The **ecological species concept** defines a species in terms of its ecological niche, the sum of how members of the species interact with the nonliving and living parts of their environment (see Concept 54.1). For example, two species of oak trees might differ in their size or in their ability to tolerate dry conditions, yet still occasionally interbreed. Because they occupy different ecological niches, these oaks would be considered separate species even though they are connected by some gene flow. Unlike the biological species concept, the ecological species concept can accommodate asexual as well as sexual species. It also emphasizes the role of disruptive natural selection as organisms adapt to different environments.

In addition to those discussed here, more than 20 other species definitions have been proposed. The usefulness of each definition depends on the situation and the research questions being asked. For our purposes of studying how species originate, the biological species concept, with its focus on reproductive barriers, is particularly helpful.

 [Mastering Biology HHMI Video: The Origin of Species: The Beak of the Finch](#)



#### CONCEPT CHECK 24.1

1. (a) Which species concept(s) could you apply to both asexual and sexual species? (b) Which would be most useful for identifying species in the field? Explain.
2. **WHAT IF?** Suppose two bird species live in a forest and are not known to interbreed. One species feeds and mates in the treetops and the other on the ground. But in captivity, the birds can interbreed and produce viable, fertile offspring. What type of reproductive barrier most likely keeps these species separate in nature? Explain.

*For suggested answers, see Appendix A.*

## Speciation can take place with or without geographic separation

Having discussed what constitutes a unique species, let's return to the process by which such species arise from existing species. We'll describe this process by focusing on the geographic setting in which gene flow is interrupted between populations of the existing species—in allopatric speciation the populations are geographically isolated, while in sympatric speciation they are not (Figure 24.5).

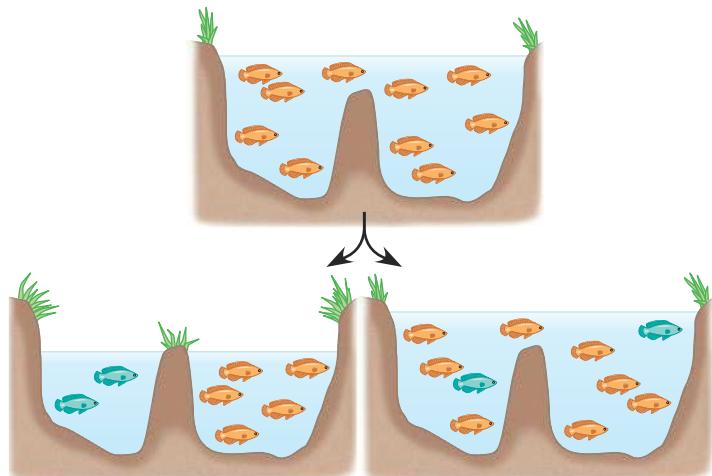
### Allopatric ("Other Country") Speciation

In **allopatric speciation** (from the Greek *allos*, other, and *patra*, homeland), gene flow is interrupted when a population is divided into geographically isolated subpopulations. For example, the water level in a lake may subside, resulting in two or more smaller lakes that are now home to separated populations (see Figure 24.5a). Or a river may change course and divide a population of animals that cannot cross it. Allopatric speciation can also occur without geologic change, such as when individuals colonize a remote area and their descendants become geographically isolated from the parent population. The flightless cormorant shown in Figure 24.1 probably originated in this way from an ancestral flying species that reached the Galápagos Islands.

### The Process of Allopatric Speciation

How formidable must a geographic barrier be to promote allopatric speciation? The answer depends on the ability of the organisms to move about. Birds, mountain lions, and coyotes can cross rivers and canyons—as can windblown pollen

▼ Figure 24.5 The geography of speciation.



**(a) Allopatric speciation.** A population forms a new species while geographically isolated from its parent population.

**(b) Sympatric speciation.** A subset of a population forms a new species without geographic separation.

and the seeds of some flowering plants. In contrast, small rodents may find a river or canyon a formidable barrier.

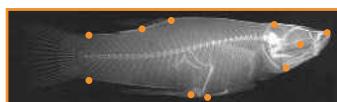
Once geographic isolation has occurred, the separated gene pools may diverge. Different mutations arise, and natural selection and genetic drift may alter allele frequencies in different ways in the separated populations. Reproductive isolation may then evolve as a by-product of the genetic divergence that results from selection or drift.

**Figure 24.6** describes an example. On Andros Island, in the Bahamas, populations of the mosquitofish *Gambusia hubbsi* colonized a series of ponds that later became isolated from one another. Genetic analyses indicate that little or no gene flow currently occurs between the ponds. The environments of these ponds are very similar except that some contain predatory fishes, while others do not. In ponds with predatory fishes, selection has favored the evolution of a mosquitofish body shape that enables rapid bursts of speed (see Figure 24.6a). In ponds without predatory fishes, selection has favored a different body shape, one that improves the ability to swim for long periods of time (see Figure 24.6b).

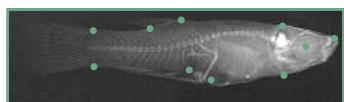
How have these different selective pressures affected the evolution of reproductive barriers? Researchers studied this question by bringing together mosquitofish from the two types of ponds. They found that female mosquitofish prefer to mate with males whose body shape is similar to their own. This preference establishes a behavioral barrier

### ▼ Figure 24.6 Evolution in mosquitofish populations.

Different body shapes have evolved in mosquitofish populations from ponds with and without predators. These differences affect how quickly the fishes can accelerate to escape and their survival rate when exposed to predators.

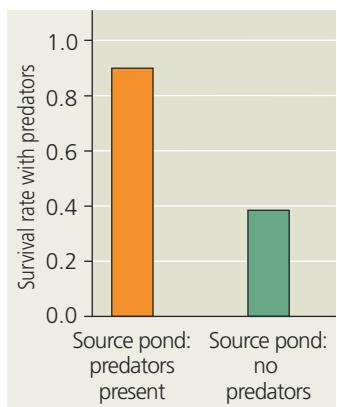
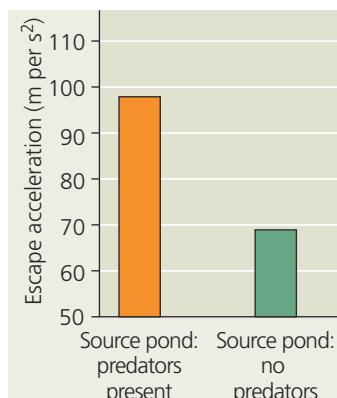


In ponds with predatory fishes, the mosquitofish's head is streamlined and the tail is powerful, enabling rapid bursts of speed.



In ponds without predatory fishes, mosquitofish have a different body shape that favors long, steady swimming.

#### (a) Differences in body shape



#### (b) Differences in escape acceleration and survival

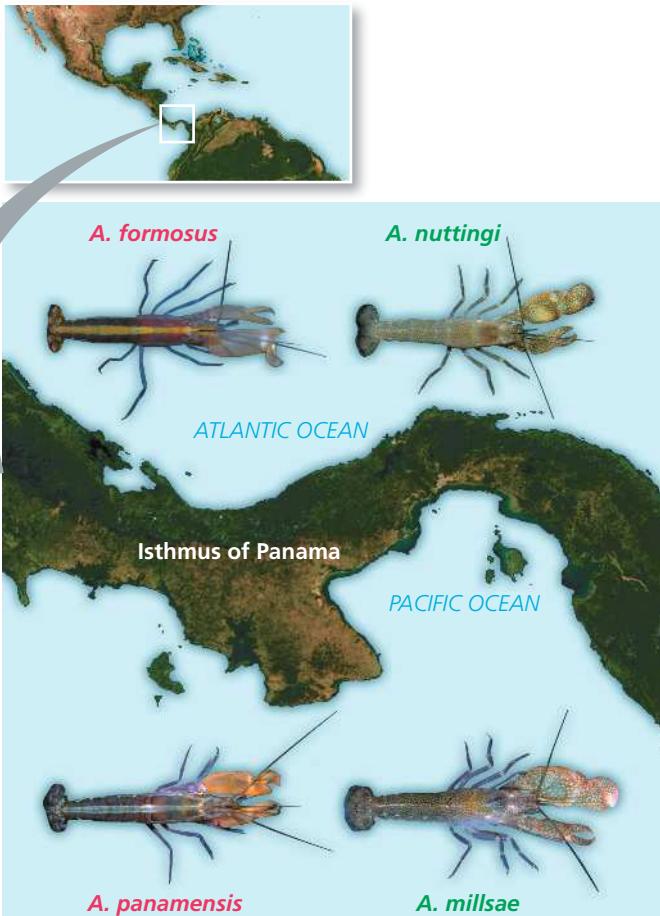
to reproduction between mosquitofish from ponds with predators and those from ponds without predators. Thus, as a by-product of selection for avoiding predators, reproductive barriers have formed in these allopatric populations.

### Evidence of Allopatric Speciation

Many studies provide evidence that speciation can occur in allopatric populations. For example, laboratory studies show that reproductive barriers can develop when populations are isolated experimentally and subjected to different environmental conditions (**Figure 24.7**).

Field studies indicate that allopatric speciation also can occur in nature. Consider the 30 species of snapping shrimp in the genus *Alpheus* that live off the Isthmus of Panama, the land bridge that connects South and North America (**Figure 24.8**). Fifteen of these species live on the Atlantic side of the isthmus, while the other 15 live on the Pacific side. Before the isthmus formed, gene flow could occur between the Atlantic and Pacific populations of snapping shrimp. Did the species on different sides of the isthmus originate by allopatric speciation? Morphological and genetic data group these shrimp into 15 pairs of *sister species*, pairs whose member species are each other's closest relative. In each of these

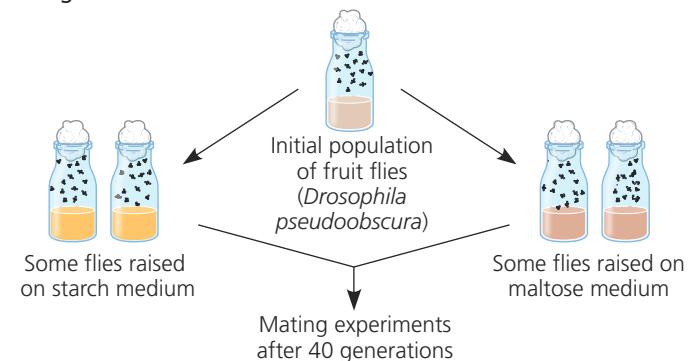
**▼ Figure 24.8 Allopatric speciation in snapping shrimp (*Alpheus*)**. The shrimp pictured are just 2 of the 15 pairs of sister species that arose as populations were divided by the formation of the Isthmus of Panama. The color-coded type indicates the sister species.



### ▼ Figure 24.7 Inquiry

#### Can divergence of allopatric populations lead to reproductive isolation?

**Experiment** A researcher divided a laboratory population of the fruit fly *Drosophila pseudoobscura*, raising some flies on a starch medium and others on a maltose medium. After one year (about 40 generations), natural selection resulted in divergent evolution: Populations raised on starch digested starch more efficiently, while those raised on maltose digested maltose more efficiently. The researcher then put flies from the same or different populations in mating cages and measured mating frequencies. All flies used in the mating preference tests were reared for one generation on a standard cornmeal medium.



**Results** Mating patterns among populations of flies raised on different media are shown below. When flies from "starch populations" were mixed with flies from "maltose populations," the flies tended to mate with like partners (see the lefthand table). But in a control group consisting of flies from two different populations adapted to starch, the flies were about as likely to mate with flies of the other population as with flies of their own population (see the righthand table); similar results were obtained for control groups adapted to maltose.

		Female		Female	
		Starch	Maltose	Starch population 1	Starch population 2
Male		Starch	22	9	18
		Maltose	8	20	15
Number of matings in experimental group					
Number of matings in control group					

**Conclusion** In the experimental group, the strong preference of "starch flies" and "maltose flies" to mate with like-adapted flies indicates that a reproductive barrier was forming between these fly populations. Although this barrier was not absolute (some mating between starch flies and maltose flies did occur), after 40 generations reproductive isolation appeared to be increasing. This barrier may have been caused by differences in courtship behavior that arose as an incidental by-product of differing selective pressures as these allopatric populations adapted to different sources of food.

**Data from** D. M. B. Dodd, Reproductive isolation as a consequence of adaptive divergence in *Drosophila pseudoobscura*, *Evolution* 43:1308–1311 (1989).

**WHAT IF?** Why were all flies used in the mating preference tests reared on a standard medium (rather than on starch or maltose)?

15 pairs, one of the sister species lives on the Atlantic side of the isthmus, while the other lives on the Pacific side. This fact strongly suggests that the two species arose as a consequence of geographic separation. Furthermore, genetic analyses indicate that the *Alpheus* species originated from 9 to 3 million years ago, with the sister species that live in the deepest water diverging first. These divergence times are consistent with geologic evidence that the isthmus formed gradually, starting 10 million years ago, and closing completely about 3 million years ago.

The importance of allopatric speciation is also suggested by the fact that regions that are isolated or highly subdivided by barriers typically have more species than do otherwise similar regions that lack such features. For example, many unique plants and animals are found on the geographically isolated Hawaiian Islands (we'll return to the origin of Hawaiian species in Concept 25.4). Field studies also show that reproductive isolation between two populations generally increases as the geographic distance between them increases, a finding consistent with allopatric speciation. In the **Scientific Skills Exercise**, you can analyze data from one such study that examined reproductive isolation in geographically separated salamander populations.

## Scientific Skills Exercise

### Identifying Independent and Dependent Variables, Making a Scatter Plot, and Interpreting Data

**Does Distance Between Salamander Populations Increase Their Reproductive Isolation?** Allopatric speciation begins when populations become geographically isolated, reducing mating between individuals in different populations and thus reducing gene flow. It is logical that as distance between populations increases, so will their degree of reproductive isolation. To test this hypothesis, researchers studied populations of the dusky salamander (*Desmognathus ochrophaeus*) living on different mountain ranges in the southern Appalachians.

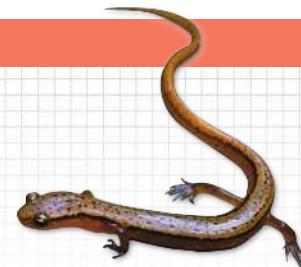
**How the Experiment Was Done** The researchers tested the reproductive isolation of pairs of salamander populations by leaving one male and one female together and later checking the females for the presence of sperm. Four mating combinations were tested for each pair of populations (A and B)—two *within* the same population (female A with male A and female B with male B) and two *between* populations (female A with male B and female B with male A).

**Data from the Experiment** The researchers used an index of reproductive isolation that ranged from a value of 0 (no isolation) to a value of 2 (full isolation). The proportion of successful matings for each mating combination was measured, with 100% success = 1 and no success = 0. The reproductive isolation value for two populations is the sum of the proportion of successful matings of each type within populations (AA + BB) minus the sum of the proportion

Note that while geographic isolation prevents interbreeding between members of allopatric populations, physical separation is not a biological barrier to reproduction. Biological reproductive barriers such as those described in Figure 24.3 are intrinsic to the organisms themselves. Hence, it is biological barriers that can prevent interbreeding when members of different populations come into contact with one another.

### Sympatric ("Same Country") Speciation

In **sympatric speciation** (from the Greek *syn*, together), speciation occurs in populations that live in the same geographic area (see Figure 24.5b). How can reproductive barriers form between sympatric populations while their members remain in contact with each other? Although such contact (and the ongoing gene flow that results) makes sympatric speciation less common than allopatric speciation, sympatric speciation can occur if gene flow is reduced by such factors as polyploidy, sexual selection, and habitat differentiation. (Note that sexual selection and habitat differentiation also can promote allopatric speciation.)



of successful matings of each type between populations (AB + BA). The table provides distance and reproductive isolation data for 27 pairs of dusky salamander populations.

#### INTERPRET THE DATA

- State the researchers' hypothesis, and identify the independent and dependent variables in this study. Explain why the researchers used four mating combinations for each pair of populations.
- Calculate the value of the reproductive isolation index (a) if all of the matings within a population were successful, but none of the matings between populations were successful; (b) if salamanders are equally successful in mating with members of their own population and members of another population.
- Make a scatter plot to help you visualize any patterns that might indicate a relationship between the variables. Plot the independent variable on the x-axis and the dependent variable on the y-axis. (For additional information about graphs, see the Scientific Skills Review in Appendix D.)
- Interpret your graph by (a) explaining in words any pattern indicating a possible relationship between the variables and (b) hypothesizing the possible cause of such a relationship.

→ **Instructors:** A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

**Data from** S. G. Tilley, A. Verrell, and S. J. Arnold, Correspondence between sexual isolation and allozyme differentiation: a test in the salamander *Desmognathus ochrophaeus*, *Proceedings of the National Academy of Sciences USA* 87:2715–2719 (1990).

Geographic Distance (km)	15	32	40	47	42	62	63	81	86	107	107	115	137	147
Reproductive Isolation Value	0.32	0.54	0.50	0.50	0.82	0.37	0.67	0.53	1.15	0.73	0.82	0.81	0.87	0.87
Distance (continued)	137	150	165	189	219	239	247	53	55	62	105	179	169	
Isolation (continued)	0.50	0.57	0.91	0.93	1.5	1.22	0.82	0.99	0.21	0.56	0.41	0.72	1.15	

## Polyplody

A species may originate from an accident during cell division that results in extra sets of chromosomes, a condition called **polyplody**. Polyploid speciation occasionally occurs in animals; for example, the gray tree frog *Hyla versicolor* (see Figure 23.16) is thought to have originated in this way. However, polyplody is far more common in plants. In fact, botanists estimate that more than 80% of the plant species alive today are descended from ancestors that formed by polyploid speciation.

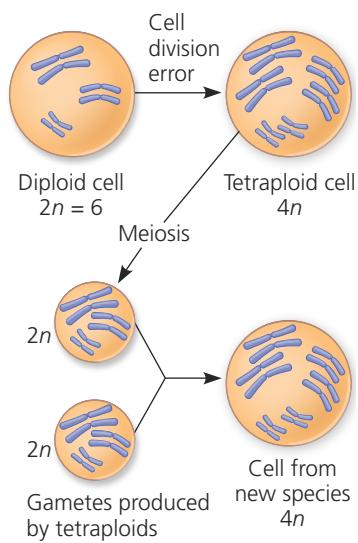
Two distinct forms of polyplody have been observed in plant (and a few animal) populations. An **autopolyploid** (from the Greek *autos*, self) is an individual that has more than two chromosome sets that are all derived from a single species. In plants, for example, a failure of cell division could double a cell's chromosome number from the original number ( $2n$ ) to a tetraploid number ( $4n$ ) (Figure 24.9).

A tetraploid can produce fertile tetraploid offspring by self-pollinating or by mating with other tetraploids. In addition, the tetraploids are reproductively isolated from  $2n$  plants of the original population because the triploid ( $3n$ ) offspring of such unions have reduced fertility. Thus, in just one generation, autopolyploidy can generate reproductive isolation without any geographic separation.

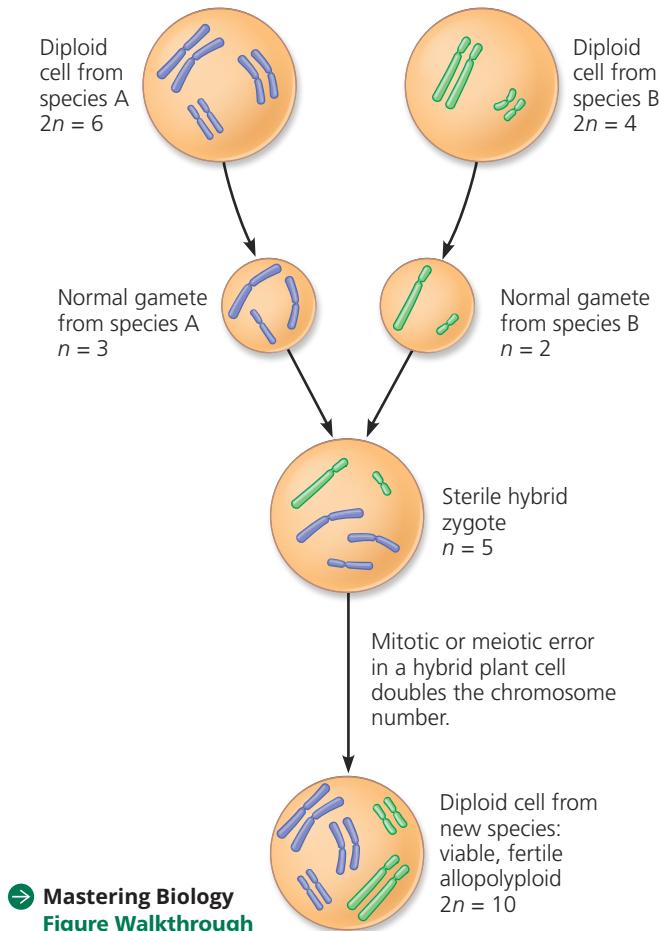
A second form of polyplody can occur when two different species interbreed and produce hybrid offspring. Most such hybrids are sterile because the set of chromosomes from one species cannot pair during meiosis with the set of chromosomes from the other species. However, an infertile hybrid may be able to propagate itself asexually (as many plants can do). In subsequent generations, various mechanisms can change a sterile hybrid into a fertile polyploid called an **allopolyploid** (Figure 24.10). The allopolyploids are fertile when mating with each other but cannot interbreed with either parent species; thus, they represent a new biological species. The new species has a diploid chromosome number equal to the sum of the diploid chromosome numbers of the two parent species.

Although it can be challenging to study speciation in the field, scientists have documented at least five new plant species that have originated by polyploid speciation since 1850. One of these examples involves the origin of a new species of goatsbeard plant (genus *Tragopogon*) in the Pacific Northwest. *Tragopogon* first arrived in the region when humans introduced

▼ Figure 24.9 Sympatric speciation by autopolyploidy.



▼ Figure 24.10 One mechanism for allopolyploid speciation in plants. Most hybrids are sterile because their chromosomes are not homologous and cannot pair during meiosis. However, such a hybrid may be able to reproduce asexually. This diagram traces one mechanism by which sterile hybrids can give rise to fertile allopolyploids that are members of a new species.

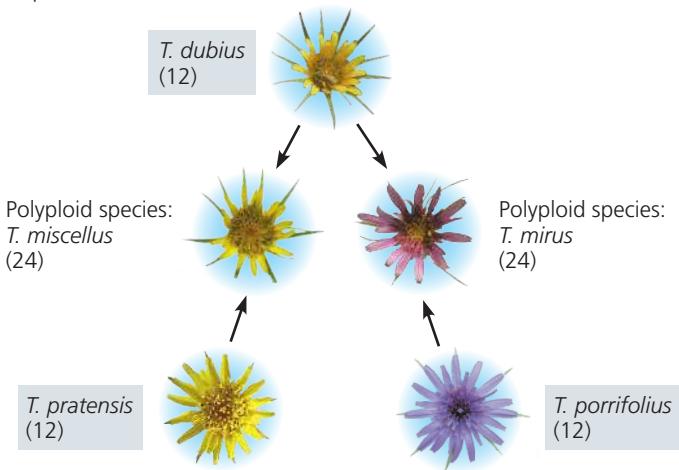


Mastering Biology  
Figure Walkthrough

three European species in the early 1900s: *T. pratensis*, *T. dubius*, and *T. porrifolius*. These three species are now common in the Pacific Northwest and many other parts of North America. In 1950, a new *Tragopogon* species was discovered near the Idaho-Washington border, a region where all three European species also were found. Genetic analyses revealed that this new species, *Tragopogon miscellus*, is an allopolyploid that originated from a hybrid of two of the European species (Figure 24.11). Although the *T. miscellus* population grows mainly by reproduction of its own members, hybridization between the parent species (followed by a mitotic or meiotic error that doubles the chromosome number) continues to add new members to the *T. miscellus* population. Later, scientists discovered another new *Tragopogon* species, *T. mirus*, which also arose by polyploid speciation.

Many important agricultural crops—such as oats, cotton, potatoes, tobacco, and wheat—are polyploids. For example, the wheat used for bread, *Triticum aestivum*, is an allohexaploid (six sets of chromosomes, two sets from each of three different species). The events that eventually led to modern wheat probably began about 8,000 years ago in the Middle

▼ **Figure 24.11 Allopolyploid speciation in *Tragopogon*.** The gray boxes indicate the parent species of the two new polyploid species. The diploid chromosome number of each species is shown in parentheses.



**VISUAL SKILLS** Based on this diagram, identify the two parent species of each polyploid species.

East when an early cultivated wheat species hybridized with a wild grass. Today, plant geneticists generate new polyploids in the laboratory by using chemicals that induce meiotic and mitotic errors. By harnessing the evolutionary process, researchers can produce new polyploid species with desired qualities, such as a polyploid that combines the high yield of wheat with the hardiness of rye.

#### Mastering Biology Animation: Speciation by Changes in Ploidy

### Sexual Selection

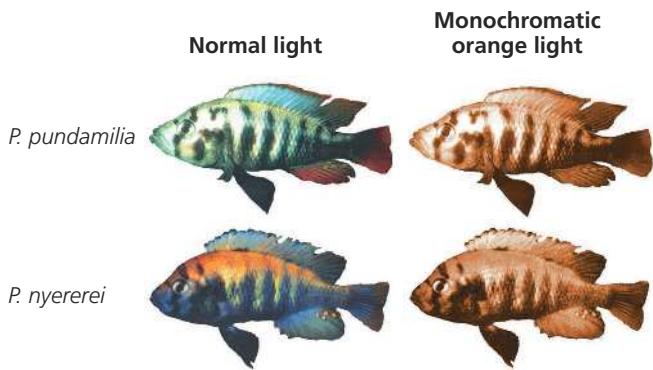
There is evidence that sympatric speciation can also be driven by sexual selection. Clues to how this can occur have been found in cichlid fish from one of Earth's hot spots of animal speciation, East Africa's Lake Victoria. This lake was once home to as many as 600 species of cichlids. Genetic data indicate that these species originated within the last 100,000 years from a small number of colonizing species that arrived from other lakes and rivers. How did so many species—more than double the number of freshwater fish species known in all of Europe—originate within a single lake?

One hypothesis is that subgroups of the original cichlid populations adapted to different food sources and the resulting genetic divergence contributed to speciation in Lake Victoria. But sexual selection, in which (typically) females select males based on their appearance (see Concept 23.4), may also have been a factor. Researchers have studied two closely related sympatric species of cichlids that differ mainly in the coloration of breeding males: Breeding *Pundamilia pundamilia* males have a blue-tinged back, whereas breeding *Pundamilia nyererei* males have a red-tinged back (**Figure 24.12**). Their results suggest that mate choice based on male breeding coloration can act as a reproductive barrier that keeps the gene pools of these two species separate.

#### ▼ Figure 24.12 Inquiry

### Does sexual selection in cichlids result in reproductive isolation?

**Experiment** Researchers placed males and females of *Pundamilia pundamilia* and *P. nyererei* together in two aquarium tanks, one with natural light and one with a monochromatic orange lamp. Under normal light, the two species are noticeably different in male breeding coloration; under monochromatic orange light, the two species are very similar in color. The researchers then observed the mate choices of the females in each tank.



**Results** Under normal light, females of each species strongly preferred males of their own species. But under orange light, females of each species responded indiscriminately to males of both species. The resulting hybrids were viable and fertile.

**Conclusion** The researchers concluded that mate choice by females based on male breeding coloration can act as a reproductive barrier that keeps the gene pools of these two species separate. Since the species can still interbreed when this prezygotic barrier is breached in the laboratory, the genetic divergence between the species is likely to be small. This suggests that speciation in nature has occurred relatively recently.

**Data from** O. Seehausen and J. J. M. van Alphen, The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex), *Behavioral Ecology and Sociobiology* 42:1–8 (1998).

**WHAT IF?** Suppose that female cichlids living in the murky waters of a polluted lake could not distinguish colors well. In such waters, how might the gene pools of these species change over time?

### Habitat Differentiation

Sympatric speciation can also occur when a subpopulation exploits a habitat or resource not used by the parent population. Consider the North American apple maggot fly (*Rhagoletis pomonella*), a pest of apples. The fly's original habitat was the native hawthorn tree (see Figure 24.3a), but about 200 years ago, some populations colonized apple trees that had been introduced by European settlers. Apple maggot flies usually mate on or near their host plant. This results in a prezygotic barrier (habitat isolation) between populations that feed on apples and populations that feed on hawthorns. Furthermore, because apples mature more quickly than hawthorn fruit, natural selection has favored apple-feeding flies with rapid development. These apple-feeding populations now show temporal isolation from the hawthorn-feeding

*R. pomonella*, providing a second prezygotic barrier to gene flow between the two populations. Researchers also have identified alleles that benefit the flies that use one host plant but harm the flies that use the other host plant. Natural selection operating on these alleles has provided a postzygotic barrier to reproduction, further limiting gene flow. Altogether, although the two populations are still classified as subspecies rather than separate species, sympatric speciation appears to be well under way.

## Allopatric and Sympatric Speciation: A Review

Now let's recap the processes by which new species form. In allopatric speciation, a new species forms in geographic isolation from its parent population. Geographic isolation severely restricts gene flow. Intrinsic barriers to reproduction with members of the parent population may then arise as a by-product of genetic changes that occur within the isolated population. Many different processes can produce such genetic changes, including natural selection under different environmental conditions, genetic drift, and sexual selection. Once formed, reproductive barriers that arise in allopatric populations can prevent interbreeding with the parent population even if the populations come back into contact.

Sympatric speciation, in contrast, requires the emergence of a reproductive barrier that isolates a subset of a population from the remainder of the population in the same area. Though rarer than allopatric speciation, sympatric speciation can occur when gene flow to and from the isolated subpopulation is blocked. This can occur as a result of polyploidy, a condition in which an organism has extra sets of chromosomes. Sympatric speciation also can result from sexual selection. Finally, sympatric speciation can occur when a subset of a population becomes reproductively isolated because of natural selection that results from a switch to a habitat or food source not used by the parent population.

Having reviewed the geographic context in which species originate, we'll next explore in more detail what can happen when new or partially formed species come into contact.

→ Mastering Biology HHMI Video: Anole Lizards: An Example of Speciation 

### CONCEPT CHECK 24.2

1. Summarize key differences between allopatric and sympatric speciation. Which type of speciation is more common, and why?
2. Describe two mechanisms that can decrease gene flow in sympatric populations, thereby making sympatric speciation more likely to occur.
3. **WHAT IF?** Is allopatric speciation more likely to occur on an island close to a mainland or on a more isolated island of the same size? Explain your prediction.
4. **MAKE CONNECTIONS** Review the process of meiosis in Figure 13.8. Describe how an error during meiosis could lead to polyploidy.

For suggested answers, see Appendix A.

### CONCEPT 24.3

## Hybrid zones reveal factors that cause reproductive isolation

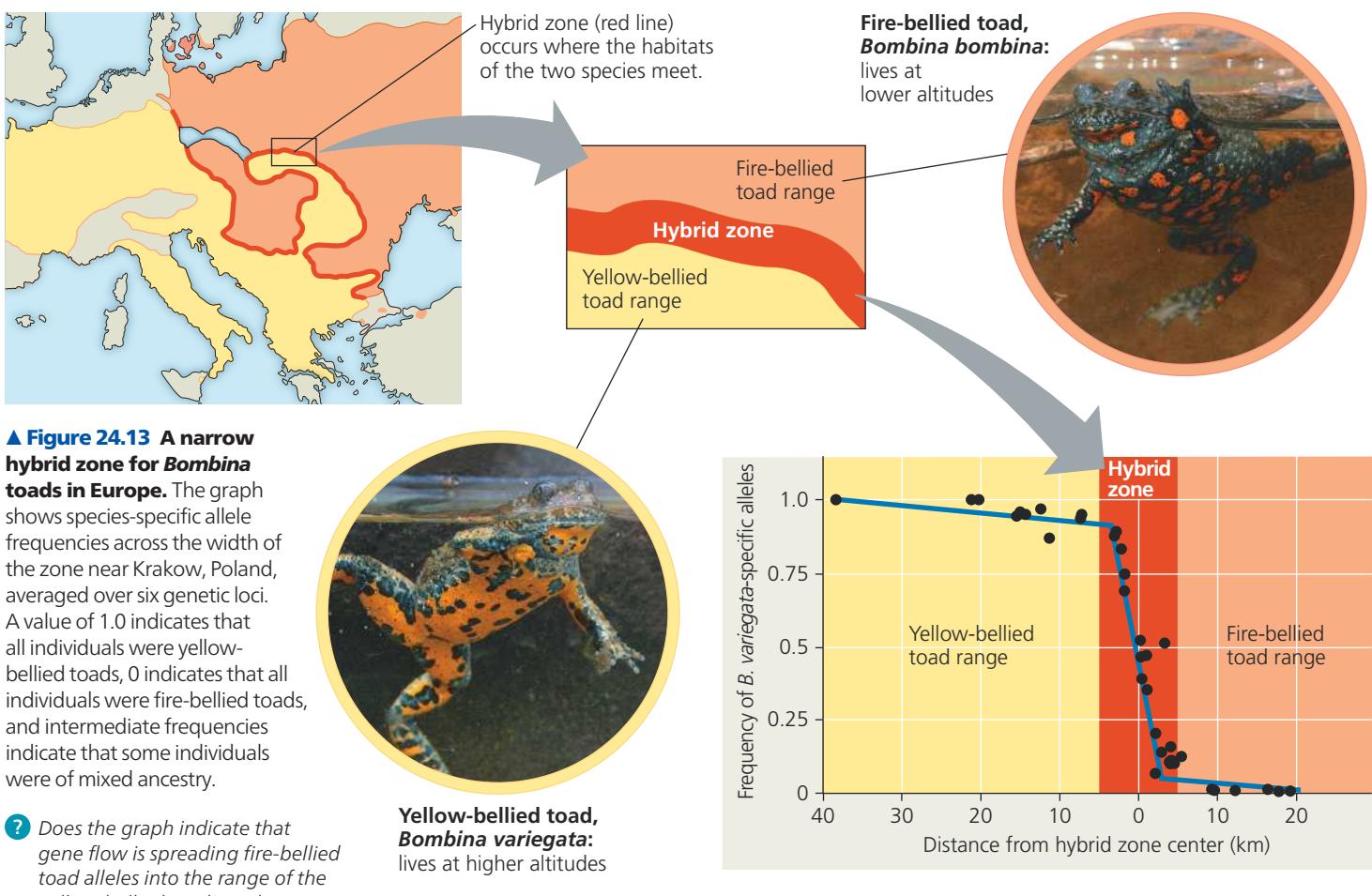
What happens if species with incomplete reproductive barriers come into contact with one another? One possible outcome is the formation of a **hybrid zone**, a region in which members of different species meet and mate, producing at least some offspring of mixed ancestry. In this section, we'll explore hybrid zones and what they reveal about factors that cause the evolution of reproductive isolation.

### Patterns Within Hybrid Zones

Some hybrid zones form as narrow bands, such as the one depicted in **Figure 24.13** for the yellow-bellied toad (*Bombina variegata*) and its close relative, the fire-bellied toad (*B. bombina*). This hybrid zone, represented by the red line on the map, extends for 4,000 km but is less than 10 km wide in most places. The hybrid zone occurs where the higher-altitude habitat of the yellow-bellied toad meets the lowland habitat of the fire-bellied toad. Across a given “slice” of the zone, the frequency of alleles specific to yellow-bellied toads typically decreases from close to 100% at the edge where only yellow-bellied toads are found to around 50% in the central portion of the zone and to close to 0% at the edge where only fire-bellied toads are found.

What causes such a pattern of allele frequencies across a hybrid zone? We can infer that there is an obstacle to gene flow—otherwise, alleles from one parent species would also be common in the gene pool of the other parent species. Are geographic barriers reducing gene flow? Not in this case, since the toads can move throughout the hybrid zone. A more important factor is that hybrid toads have increased rates of embryonic mortality and a variety of morphological abnormalities, including ribs that are fused to the spine and malformed tadpole mouthparts. Because the hybrids have poor survival and reproduction, they produce few viable offspring with members of the parent species. As a result, hybrid individuals rarely serve as a stepping-stone from which alleles are passed from one species to the other. Outside the hybrid zone, additional obstacles to gene flow may be provided by natural selection in the different environments in which the parent species live.

Hybrid zones typically are located wherever the habitats of the interbreeding species meet. Those regions often resemble a group of isolated patches scattered across the landscape—more like the pattern of spots on a Dalmatian than the continuous band shown in Figure 24.13. But regardless of whether they have complex or simple spatial patterns, hybrid zones form when two species lacking complete barriers to reproduction come into contact. What happens when the habitats of the interbreeding species change over time?



**▲ Figure 24.13 A narrow hybrid zone for *Bombina* toads in Europe.** The graph shows species-specific allele frequencies across the width of the zone near Krakow, Poland, averaged over six genetic loci. A value of 1.0 indicates that all individuals were yellow-bellied toads, 0 indicates that all individuals were fire-bellied toads, and intermediate frequencies indicate that some individuals were of mixed ancestry.

?

Does the graph indicate that gene flow is spreading fire-bellied toad alleles into the range of the yellow-bellied toad? Explain.

## Hybrid Zones and Environmental Change

A change in environmental conditions can alter where the habitats of interbreeding species meet. When this happens, an existing hybrid zone can move to a new location, or a novel hybrid zone may form.

For example, black-capped chickadees (*Poecile atricapillus*) and Carolina chickadees (*P. carolinensis*) interbreed in a narrow hybrid zone that runs from New Jersey to Kansas. Recent studies have shown that the location of this hybrid zone has shifted northward as the climate has warmed (Figure 24.14). In another example, a series of warm winters prior to 2003 enabled the southern flying squirrel (*Glaucomys volans*) to expand northward into the range of the northern flying squirrel, *G. sabrinus*. Previously, the ranges of these two species had not overlapped. Genetic analyses showed that these flying squirrels began to hybridize where their ranges came into contact, thereby forming a novel hybrid zone induced by climate change.

Finally, note that a hybrid zone can be a source of novel genetic variation that improves the ability of one or both parent species to cope with changing environmental conditions. This can occur when an allele found only in one parent species is transferred first to hybrid individuals and then to the other parent species when hybrids breed with the second parent species. Recent

genetic analyses have shown that hybridization has been a source for such novel genetic variation in some insect, mammal, bird, and plant species. In the **Problem-Solving Exercise**, you can examine one such example: a case in which hybridization may have led to the transfer of insecticide-resistance alleles between species of mosquitoes that transmit malaria.

**▼ Figure 24.14 A shift in a hybrid zone resulting from climate change.** Black-capped (a) and Carolina chickadees (b) interbreed in a hybrid zone that runs from Kansas to New Jersey. In Pennsylvania, the center of this hybrid zone moved 12 km to the north from 2002 to 2012. This shift is consistent with predictions based on the warmer winter temperatures that have resulted from climate change.



(a) Black-capped chickadee (*Poecile atricapillus*)



(b) Carolina chickadee (*Poecile carolinensis*)

## PROBLEM-SOLVING EXERCISE

### Is hybridization promoting insecticide resistance in mosquitoes that transmit malaria?

Malaria is a leading cause of human illness and mortality worldwide, with 200 million people infected and 600,000 deaths each year. In the 1960s, the incidence of malaria was reduced, owing to the use of insecticides that killed mosquitoes in the genus *Anopheles*, which transmit the disease from person to person. But today, mosquitoes are becoming resistant to insecticides—causing a resurgence in malaria.



Insecticide-treated bed nets have helped reduce cases of malaria in many countries, but resistance to insecticides is rising in mosquito populations.

→ **Instructors:** A version of this Problem-Solving Exercise can be assigned in **Mastering Biology**.

In this exercise, you will investigate whether alleles encoding resistance to insecticides have been transferred between closely related species of *Anopheles*.

**Your Approach** The principle guiding your investigation is that DNA analyses can detect the transfer of resistance alleles between closely related mosquito species. To find out whether such transfers have occurred, you will analyze DNA results from two species of mosquitoes that transmit malaria (*Anopheles gambiae* and *A. coluzzii*) and from *A. gambiae* × *A. coluzzii* hybrids.

**Your Data** Resistance to DDT and other insecticides in *Anopheles* is affected by a sodium channel gene, *kdr*. The *r* allele of this gene confers resistance, while the wild-type (+/+) genotype is not resistant. Researchers sequenced the *kdr* gene from mosquitoes collected in Mali during three time periods: pre-2006 (2002 and 2004), 2006, and post-2006 (2009–2012). *A. gambiae* and *A. coluzzii* were collected during all three time periods, but their hybrids only occurred in 2006, the first year that insecticide-treated bed nets were used to reduce the spread of malaria. A likely explanation is that the introduction of the treated bed nets may have briefly favored hybrid individuals, which are usually at a selective disadvantage.

Observed numbers of mosquitoes by <i>kdr</i> genotype			
	+/+	+/ <i>r</i>	<i>r/r</i>
<b><i>A. gambiae</i>:</b>			
Pre-2006	3	5	2
2006	8	8	7
Post-2006	3	3	57
<b>Hybrids: 2006</b>	10	7	0
<b><i>A. coluzzii</i>:</b>			
Pre-2006	226	0	0
2006	70	7	0
Post-2006	79	127	94

### Your Analysis

1. (a) Calculate the *kdr* genotype frequencies in *A. gambiae* for each time period. To do this, divide the number of individuals that have a given genotype by the total number of individuals observed for that time period. (b) How did the *kdr* genotype frequencies change over time? Describe a hypothesis that accounts for these observations.
2. How did the frequencies of *kdr* genotypes change over time in *A. coluzzii*? Describe a hypothesis that accounts for these observations.
3. Do these results indicate that hybridization can lead to the transfer of adaptive alleles? Explain.
4. Predict how the transfer of the *r* allele to *A. coluzzii* populations could affect the number of malaria cases in the years immediately following the transfer.

## Hybrid Zones over Time

Studying a hybrid zone is like observing a naturally occurring experiment on speciation. Will the hybrids become reproductively isolated from their parents and form a new species? This has occurred by polyploid speciation in some cases, as we saw for the formation of two new species of goatsbeard plants (see Figure 24.11). Hybridization also has led to what may turn out to be a new species of finch in the Galápagos archipelago: A 2018 study found that descendants of hybrids between the large cactus finch (*Geospiza conirostris*) and the medium ground finch (*G. fortis*) are becoming reproductively isolated from both parent species. As of 2019, this emerging species is known informally as “Big Bird.”

In other cases, however, interspecific hybrids do not become reproductively isolated from their parent species.

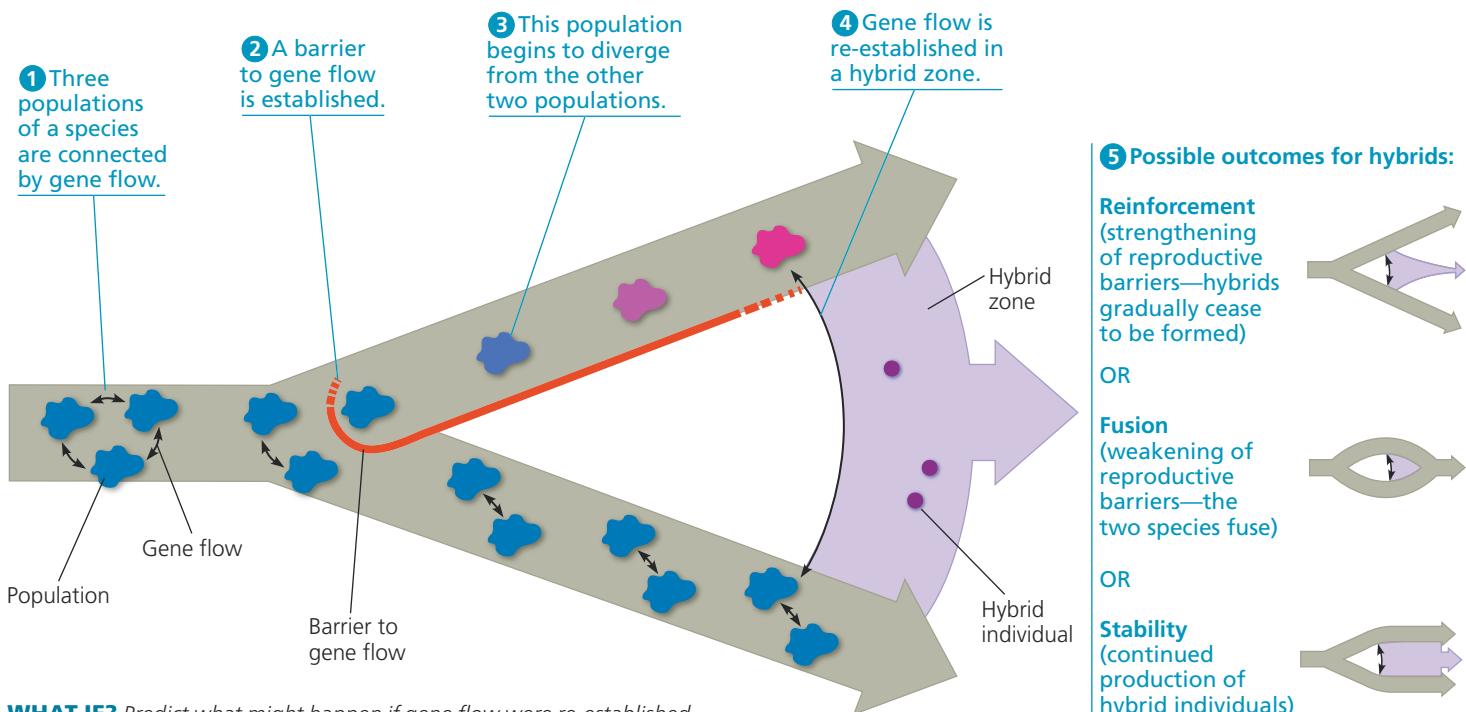
In such situations, there are three common outcomes for a hybrid zone over time: reinforcement of barriers, fusion of species, or stability (Figure 24.15). Let’s examine what studies suggest about these possibilities.

### Reinforcement: Strengthening Reproductive Barriers

Hybrids often are less fit than members of their parent species. In such cases, natural selection should strengthen prezygotic barriers to reproduction, reducing the formation of unfit hybrids. Because this process involves *reinforcing* reproductive barriers, it is called **reinforcement**. If reinforcement is occurring, a logical prediction is that barriers to reproduction between species should be stronger for sympatric populations than for allopatric populations.

▼ **Figure 24.15 Formation of a hybrid zone and common outcomes for hybrids over time.**

The thick gray and purple arrows represent the passage of time.



As an example, let's consider two species of European flycatcher, the pied flycatcher (*Ficedula hypoleuca*) and the collared flycatcher (*Ficedula albicollis*). In allopatric populations of these birds, males of the two species closely resemble one another, while in sympatric populations, the males look very different. Female flycatchers do not select males of the other species when given a choice between males from sympatric populations, but they frequently do make mistakes when selecting between males from allopatric populations. Thus, barriers to reproduction are stronger in birds from sympatric populations than in birds from allopatric populations, as you would predict if reinforcement were occurring. Similar results have been observed in a number of organisms, including some fishes, insects, plants, and other birds.

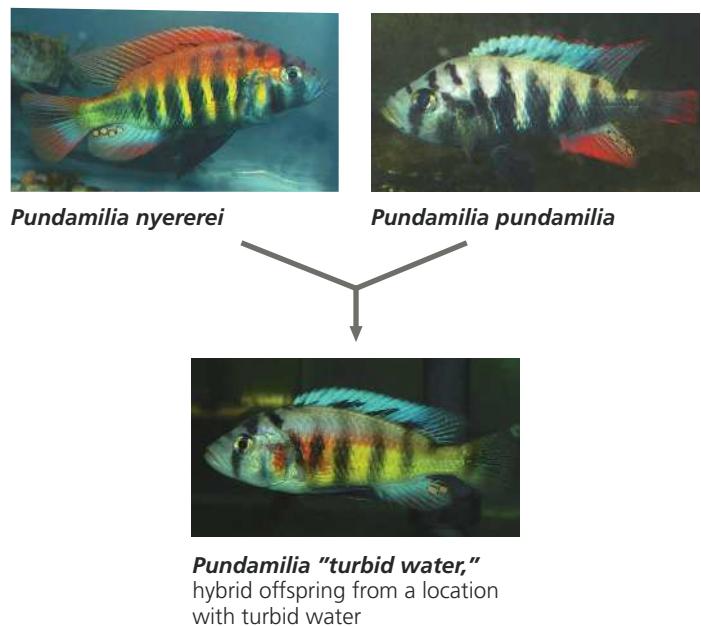
### Fusion: Weakening Reproductive Barriers

Barriers to reproduction may be weak when two species meet in a hybrid zone. Indeed, so much gene flow may occur that reproductive barriers weaken further and the gene pools of the two species become increasingly alike. In effect, the speciation process reverses, eventually causing the two hybridizing species to fuse into a single species.

For example, genetic and morphological evidence indicates that the recent loss of the large tree finch from the Galápagos island of Floreana resulted from extensive hybridization with another finch species on that island. Such a situation also may be occurring among Lake Victoria cichlids (Figure 24.16). Many pairs of ecologically similar cichlid

▼ **Figure 24.16 Fusion: the breakdown of reproductive barriers.**

Increasingly cloudy water in Lake Victoria over the past several decades may have weakened reproductive barriers between *P. nyererei* and *P. pundamilia*. In areas of cloudy water, the two species have hybridized extensively, causing their gene pools to fuse.



species are reproductively isolated because the females of one species prefer to mate with males of one color, while females of the other species prefer to mate with males of a different color (see Figure 24.12). Results from field and laboratory studies indicate that murky waters caused by

pollution have reduced the ability of females to use color to distinguish males of their own species from males of closely related species. In some polluted waters, many hybrids have been produced, leading to fusion of the parent species' gene pools and a loss of species.

### Stability: Continued Formation of Hybrid Individuals

Many hybrid zones are stable in the sense that hybrids continue to be produced. In some cases, this occurs because the hybrids survive or reproduce better than members of either parent species, at least in certain habitats or years. But stable hybrid zones have also been observed in cases where the hybrids are selected *against*—an unexpected result.

For example, hybrids continue to form in the *Bombina* hybrid zone even though they are strongly selected against. One explanation relates to the narrowness of the *Bombina* hybrid zone (see Figure 24.13). Evidence suggests that members of both parent species migrate into the zone from the parent populations located outside the zone, thus leading to the continued production of hybrids. If the hybrid zone were wider, this would be less likely to occur, since the center of the zone would receive little gene flow from distant parent populations located outside the hybrid zone.

Sometimes the outcomes in hybrid zones match our predictions (European flycatchers and cichlid fishes), and sometimes they don't (*Bombina*). But whether our predictions are upheld or not, events in hybrid zones can shed light on how barriers to reproduction between closely related species change over time. In the next section, we'll examine how interactions between hybridizing species can also provide a glimpse into the speed and genetic control of speciation.

#### CONCEPT CHECK 24.3

1. What are hybrid zones, and why can they be viewed as “natural laboratories” in which to study speciation?
2. **WHAT IF?** Consider two species that diverged while geographically separated but resumed contact before reproductive isolation was complete. Predict the outcome over time if the two species mated indiscriminately and (a) hybrid offspring survived and reproduced more poorly than offspring from intraspecific matings or (b) hybrid offspring survived and reproduced as well as offspring from intraspecific matings.

For suggested answers, see Appendix A.

#### CONCEPT 24.4

### Speciation can occur rapidly or slowly and can result from changes in few or many genes

Darwin faced many questions when he began to ponder that “mystery of mysteries”—speciation. He found answers to some of those questions when he realized that evolution by natural selection helps explain both the diversity of life and

the adaptations of organisms (see Concept 22.2). But biologists since Darwin have continued to ask fundamental questions about speciation. How long does it take for new species to form? And how many genes change when one species splits into two? Answers to these questions are also emerging.

### The Time Course of Speciation

We can gather information about how long it takes new species to form from broad patterns in the fossil record and from studies that use morphological data (including fossils) or molecular data to assess the time interval between speciation events in particular groups of organisms.

#### Patterns in the Fossil Record

The fossil record includes many episodes in which new species appear suddenly in a geologic stratum, persist essentially unchanged through several strata, and then disappear. For example, there are dozens of species of marine invertebrates that make their debut in the fossil record with novel morphologies, but then change little for millions of years before becoming extinct. The term **punctuated equilibria** is used to describe these periods of apparent stasis punctuated by sudden change (Figure 24.17a). Other species do not show a punctuated pattern; instead, they appear to have changed more gradually over long periods of time (Figure 24.17b).

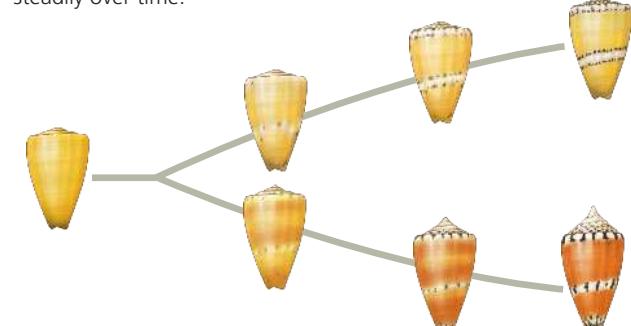
What might punctuated and gradual patterns tell us about how long it takes new species to form? Suppose that a species survived for 5 million years, but most of the morphological changes that caused it to be designated a new species occurred during its first 50,000 years—just 1% of the total existence of

▼ Figure 24.17 Two models for the tempo of speciation.

- (a) **Punctuated model.** New species change most as they branch from a parent species and then change little for the rest of their existence.



- (b) **Gradual model.** Species diverge from one another more slowly and steadily over time.



the species. Time periods this short (in geologic terms) often cannot be distinguished in fossil strata, in part because the rate of sediment accumulation may be too slow to separate layers this close in time. Thus, based on its fossils, the species would seem to have appeared suddenly and then lingered with little or no change before becoming extinct. Even though such a species may have originated more slowly than its fossils suggest (in this case taking up to 50,000 years), a punctuated pattern indicates that speciation occurred relatively rapidly. For species whose fossils changed much more gradually, we also cannot tell exactly when a new biological species formed, since information about reproductive isolation does not fossilize. However, it is likely that speciation in such groups occurred relatively slowly, perhaps taking millions of years.

#### Mastering Biology

**Interview with Stephen Jay Gould: An “architect” of the concept of punctuated equilibria**



### Speciation Rates

The existence of fossils that display a punctuated pattern suggests that once the process of speciation begins, it can be completed relatively rapidly—a suggestion supported by many studies. For example, rapid speciation appears to have produced the wild sunflower *Helianthus anomalus*. Genetic evidence indicates that this species originated by the hybridization of two other sunflower species, *H. annuus* and *H. petiolaris*. The hybrid species *H. anomalus* is ecologically distinct and reproductively isolated from both parent species (Figure 24.18). Unlike the outcome of allopolyploid speciation, in which there is a change in chromosome number after hybridization, in these sunflowers the two parent species and the hybrid all have the same number of chromosomes ( $2n = 34$ ). How, then, did speciation occur? To study this question, researchers performed an experiment designed to mimic events in nature (Figure 24.19). Their results indicated that natural selection could produce extensive genetic changes in hybrid populations over short periods of time. These changes appear to have caused the hybrids to diverge reproductively from their parents and form a new species, *H. anomalus*.

#### ▼ Figure 24.18 A hybrid sunflower species and its dry sand dune habitat

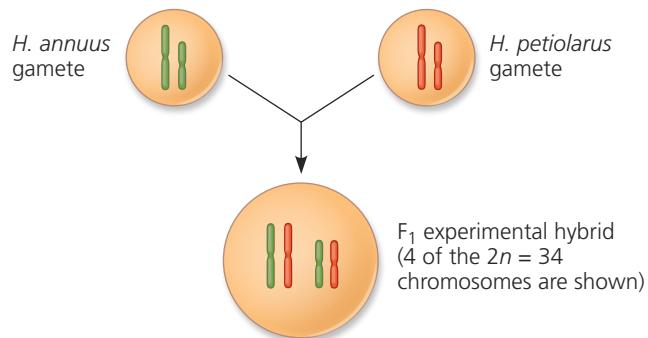
**dry sand dune habitat.** The wild sunflower *Helianthus anomalus* shown here originated via the hybridization of two other sunflowers, *H. annuus* and *H. petiolaris*, which live in nearby but moister environments.



▼ Figure 24.19 Inquiry

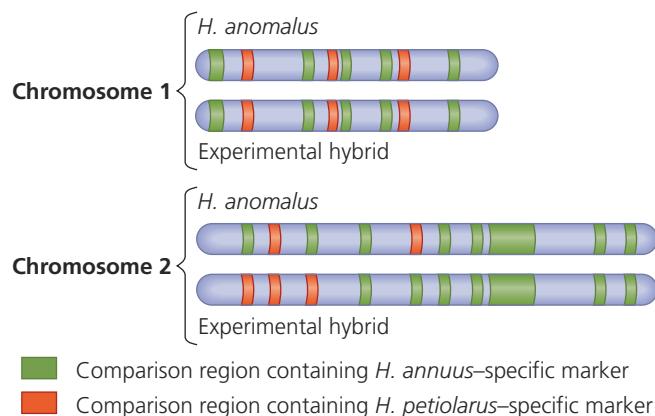
### How does hybridization lead to speciation in sunflowers?

**Experiment** Loren Rieseberg and his colleagues crossed the two parent sunflower species, *H. annuus* and *H. petiolaris*, to produce experimental hybrids in the laboratory (for each gamete, only two of the  $n = 17$  chromosomes are shown).



Note that in the first (F<sub>1</sub>) generation, each chromosome of the experimental hybrids consisted entirely of DNA from one or the other parent species. The researchers then tested whether the F<sub>1</sub> and subsequent generations of experimental hybrids were fertile. They also used species-specific genetic markers to compare the chromosomes in the experimental hybrids with the chromosomes in the naturally occurring hybrid *H. anomalus*.

**Results** Although only 5% of the F<sub>1</sub> experimental hybrids were fertile, after just four more generations the hybrid fertility rose to more than 90%. The chromosomes of individuals from this fifth hybrid generation differed from those in the F<sub>1</sub> generation (see above) but were similar to those in *H. anomalus* individuals from natural populations:



**Conclusion** Over time, the chromosomes in the population of experimental hybrids became similar to the chromosomes of *H. anomalus* individuals from natural populations. This suggests that the observed rise in the fertility of the experimental hybrids may have occurred as selection eliminated regions of DNA from the parent species that were not compatible with one another. Overall, it appeared that the initial steps of the speciation process occurred rapidly and could be mimicked in a laboratory experiment.

**Data from** L. H. Rieseberg et al., Role of gene interactions in hybrid speciation: evidence from ancient and experimental hybrids, *Science* 272:741–745 (1996).

**WHAT IF?** The increased fertility of the experimental hybrids could have resulted from natural selection for thriving under laboratory conditions. Evaluate this alternative explanation for the result.

The sunflower example, along with the apple maggot fly, Lake Victoria cichlid, and fruit fly examples discussed earlier, suggests that new species can arise rapidly *once divergence begins*. But what is the total length of time between speciation events? This interval consists of the time that elapses before populations of a newly formed species start to diverge from one another plus the time it takes for speciation to be complete once divergence begins. It turns out that the total time between speciation events varies considerably. In a survey of data from 84 groups of plants and animals, speciation intervals ranged from 4,000 years (in cichlids of Lake Nabugabo, Uganda) to 40 million years (in some beetles). Overall, the time between speciation events averaged 6.5 million years and was rarely less than 500,000 years.

These data suggest that on average, millions of years may pass before a newly formed plant or animal species will itself give rise to another new species. As you'll read in Concept 25.4, this finding has implications for how long it takes life on Earth to recover from mass extinction events. Moreover, the extreme variability in the time it takes new species to form indicates that organisms do not have an internal "speciation clock" that causes them to produce new species at regular intervals. Instead, speciation begins only after gene flow between populations is interrupted, perhaps by changing environmental conditions or by unpredictable events, such as a storm that transports a few individuals to a new area. Furthermore, once gene flow is interrupted, the populations must diverge genetically to such an extent that they become reproductively isolated—all before other events cause gene flow to resume, possibly reversing the speciation process (see Figure 24.16).

## Studying the Genetics of Speciation

Studies of ongoing speciation (as in hybrid zones) can reveal traits that cause reproductive isolation. By identifying the genes that control those traits, scientists can explore a fundamental question of evolutionary biology: How many genes influence the formation of new species?

In some cases, the evolution of reproductive isolation results from the effects of a single gene. For example, in Japanese snails of the genus *Euhadra*, a change in a single gene results in a mechanical barrier to reproduction. This gene controls the direction in which the shells spiral. When their shells spiral in different directions, the snails' genitalia are oriented in a manner that prevents mating (Figure 24.3f and g show a similar example). Recent genetic analyses have uncovered other single genes that cause reproductive isolation in fruit flies or mice.

A major barrier to reproduction between two closely related species of monkey flower, *Mimulus cardinalis* and *M. lewisii*, also appears to be influenced by a relatively small number of genes. These two species are isolated by several prezygotic and postzygotic barriers. Of these, one prezygotic barrier, pollinator choice, accounts for most of the isolation: In a hybrid zone between *M. cardinalis* and *M. lewisii*, nearly 98% of pollinator visits were restricted to one species or the other.

### ▼ Figure 24.20 A locus that influences pollinator choice.

Pollinator preferences provide a strong barrier to reproduction between *Mimulus lewisii* and *M. cardinalis*. After transferring the *M. lewisii* allele for a flower-color locus into *M. cardinalis* and vice versa, researchers observed a shift in some pollinators' preferences.



(a) Typical *Mimulus lewisii*



(b) *M. lewisii* with an *M. cardinalis* flower-color allele



(c) Typical *Mimulus cardinalis*



(d) *M. cardinalis* with an *M. lewisii* flower-color allele

**WHAT IF?** If *M. cardinalis* individuals that had the *M. lewisii* *yup* allele were planted in an area that housed both monkey flower species, how might the production of hybrid offspring be affected?

The two monkey flower species are visited by different pollinators: Hummingbirds prefer the red-flowered *M. cardinalis*, and bumblebees prefer the pink-flowered *M. lewisii*. Pollinator choice is affected by at least two loci in the monkey flowers, one of which, the "yellow upper," or *yup*, locus, influences flower color (**Figure 24.20**). By crossing the two parent species to produce F<sub>1</sub> hybrids and then performing repeated backcrosses of these F<sub>1</sub> hybrids to each parent species, researchers succeeded in transferring the *M. cardinalis* allele at this locus into *M. lewisii*, and vice versa. In a field experiment, *M. lewisii* plants with the *M. cardinalis* *yup* allele received 68-fold more visits from hummingbirds than did wild-type *M. lewisii*. Similarly, *M. cardinalis* plants with the *M. lewisii* *yup* allele received 74-fold more visits from bumblebees than did wild-type *M. cardinalis*. Thus, a mutation at a single locus can influence pollinator preference and hence contribute to reproductive isolation in monkey flowers.

In other organisms, the speciation process is influenced by larger numbers of genes and gene interactions. For example, hybrid sterility between two subspecies of the fruit fly *Drosophila pseudoobscura* results from gene interactions among at least four loci, and postzygotic isolation in the sunflower hybrid zone

discussed earlier is influenced by at least 26 chromosome segments (and an unknown number of genes). Overall, studies suggest that few or many genes can influence the evolution of reproductive isolation and hence the emergence of a new species.

## From Speciation to Macroevolution

As you've seen, speciation may begin with differences as small as the color on a cichlid's back. However, as speciation occurs again and again, such differences can accumulate and become more pronounced, eventually leading to the formation of new groups of organisms that differ greatly from their ancestors (as in the origin of whales from terrestrial mammals; see Figure 22.20). Moreover, as one group of organisms increases in size by producing many new species, another group of organisms may shrink, losing species to extinction. The cumulative effects of

many such speciation and extinction events have helped shape the sweeping evolutionary changes that are documented in the fossil record. In the next chapter, we turn to such large-scale evolutionary changes as we begin our study of macroevolution.

### CONCEPT CHECK 24.4

1. Speciation can occur rapidly between diverging populations, yet the time between speciation events is often more than a million years. Explain this apparent contradiction.
2. Summarize evidence that the *yup* locus acts as a prezygotic barrier to reproduction in two species of monkey flowers. Do these results show that the *yup* locus alone controls barriers to reproduction between these species? Explain.
3. **MAKE CONNECTIONS** Compare Figures 13.12 and 24.19. What cellular process could cause the hybrid chromosomes in Figure 24.19 to have DNA from both parent species? Explain.

For suggested answers, see Appendix A.

# 24 Chapter Review



→ Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

## SUMMARY OF KEY CONCEPTS

- To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to [goo.gl/zkjz9t](http://goo.gl/zkjz9t).

### CONCEPT 24.1

#### The biological species concept emphasizes reproductive isolation (pp. 507–510)

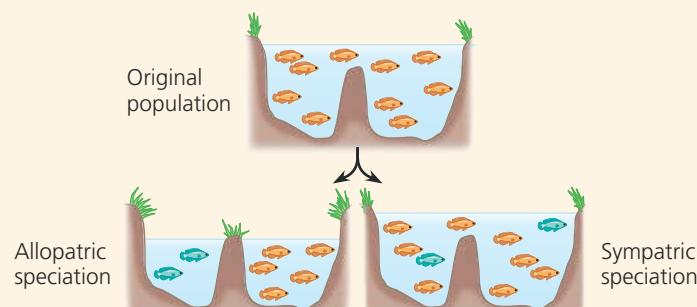
- A biological **species** is a group of populations whose individuals may interbreed and produce viable, fertile offspring with each other but not with members of other species.
- New species form when **reproductive isolation** between populations develops through the establishment of **prezygotic** or **postzygotic barriers** that separate gene pools.

- ?
- Explain the role of gene flow in the biological species concept.

### CONCEPT 24.2

#### Speciation can take place with or without geographic separation (pp. 511–516)

- In **allopatric speciation**, gene flow is reduced when two populations of one species become geographically separated from each other. One or both populations may undergo evolutionary change during the period of separation, resulting in the establishment of barriers to reproduction.



- In **sympatric speciation**, a new species originates while remaining in the same geographic area as the parent species. Plant species (and, more rarely, animal species) have evolved sympatrically through **polyploidy**. Sympatric speciation can also result from sexual selection and habitat shifts.

- ?
- Can factors that cause sympatric speciation also cause allopatric speciation? Explain.

### CONCEPT 24.3

#### Hybrid zones reveal factors that cause reproductive isolation (pp. 516–520)

- Many groups of organisms form **hybrid zones** in which members of different species meet and mate, producing at least some offspring of mixed ancestry.
- Many hybrid zones are **stable**, in that hybrid offspring continue to be produced over time. In others, **reinforcement** strengthens prezygotic barriers to reproduction, thus decreasing the formation of unfit hybrids. In still other hybrid zones, barriers to reproduction may weaken over time, resulting in the **fusion** of the species' gene pools (reversing the speciation process).

- ?
- What factors can support the long-term stability of a hybrid zone if the parent species live in different environments?

### CONCEPT 24.4

#### Speciation can occur rapidly or slowly and can result from changes in few or many genes (pp. 520–523)

- New species can form rapidly once divergence begins, but it can take millions of years for that to happen. The time interval between speciation events varies considerably, from a few thousand years to tens of millions of years.
- Researchers have identified particular genes involved in some cases of speciation. Speciation can be driven by a few or many genes.

- ?
- Is speciation something that happened only in the distant past, or are new species continuing to arise today? Explain.

## TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

### Levels 1-2: Remembering/Understanding

- The *largest* unit within which gene flow can readily occur is a
  - population.
  - species.
  - genus.
  - hybrid.
- Males of different species of the fruit fly *Drosophila* that live in the same parts of the Hawaiian Islands have different elaborate courtship rituals. These rituals involve fighting other males and making stylized movements that attract females. What type of reproductive isolation does this represent?
  - habitat isolation
  - temporal isolation
  - behavioral isolation
  - gametic isolation
- According to the punctuated equilibria model,
  - given enough time, most existing species will branch gradually into new species.
  - most new species accumulate their unique features relatively rapidly as they come into existence, then change little for the rest of their duration as a species.
  - most evolution occurs in sympatric populations.
  - speciation is usually due to a single mutation.

### Levels 3-4: Applying/Analyzing

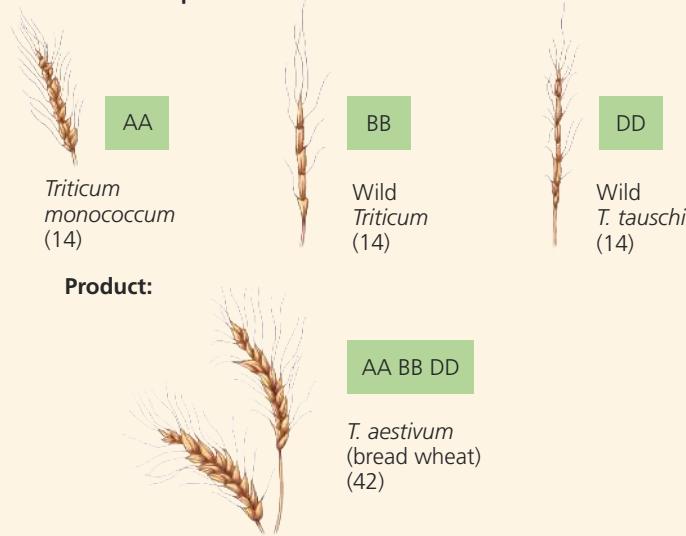
- Bird guides once listed the myrtle warbler and Audubon's warbler as distinct species. Recently, these birds have been classified as eastern and western forms of a single species, the yellow-rumped warbler. Which of the following pieces of evidence, if true, would be cause for this reclassification?
  - The two forms interbreed often in nature, and their offspring survive and reproduce well.
  - The two forms live in similar habitats and have similar food requirements.
  - The two forms have many genes in common.
  - The two forms are very similar in appearance.
- Which of the following factors would be the most likely to contribute to allopatric speciation?
  - The separated population is large, and genetic drift occurs.
  - Selection pressures in the isolated population are similar to those in the ancestral population.
  - Gene flow between the two populations is extensive.
  - Different mutations begin to distinguish the gene pools of the separated populations.
- Plant species A has a diploid chromosome number of 12. Plant species B has a diploid number of 16. A new species, C, arises as an allopolyploid from A and B. The diploid number for species C would probably be
  - 14.
  - 16.
  - 28.
  - 56.

### Levels 5-6: Evaluating/Creating

- EVOLUTION CONNECTION** Explain the biological basis for assigning all human populations to a single species. Can you think of a scenario by which a second human species could originate in the future?
- SCIENTIFIC INQUIRY • DRAW IT** In this chapter, you read that bread wheat (*Triticum aestivum*) is an allohexaploid, containing two sets of chromosomes from each of three different parent species. Genetic analysis suggests that each of the three species pictured following this question

contributed chromosome sets to *T. aestivum*. (The capital letters represent sets of chromosomes, each of which can be traced to a particular species, *not* individual genes. The numbers in parentheses are the species' chromosome numbers.) Evidence also indicates that the first polyploidy event began with the spontaneous hybridization of the early cultivated wheat species *T. monococcum* and a wild *Triticum* grass species. Draw a diagram of one possible chain of events that could have produced the allohexaploid *T. aestivum*.

#### Ancestral species:



- WRITE ABOUT A THEME: INFORMATION** In sexually reproducing species, each individual inherits DNA from both parent organisms. In a short essay (100–150 words), apply this idea to what occurs when organisms of two species that have homologous chromosomes mate and produce ( $F_1$ ) hybrid offspring. What percentage of the DNA in the  $F_1$  hybrids' chromosomes comes from each parent species? As the hybrids mate and produce  $F_2$  and later-generation hybrid offspring, describe how recombination and natural selection may affect whether the DNA in hybrid chromosomes is derived from one parent species or the other.

#### 10. SYNTHESIZE YOUR KNOWLEDGE



Suppose that females of one population of strawberry poison dart frogs (*Dendrobates pumilio*) prefer to mate with males that are orange-red in color. In a different population, females prefer males with yellow skin. Explain how such differences could arise and how they could affect the evolution of reproductive isolation in allopatric versus sympatric populations.

For selected answers, see Appendix A.