

The Origin of Species



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

EVOLUTION

KEY CONCEPTS

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

OVERVIEW

That “Mystery of Mysteries”

Darwin came to the Galápagos Islands eager to explore landforms newly emerged from the sea. He noted that these volcanic islands, despite their geologic youth, were teeming with plants and animals found nowhere else in the world

(**Figure 24.1**). Later he realized that these species, like the islands, were relatively new. He wrote in his diary: “Both in space and time, we seem to be brought somewhat near to that great fact—that mystery of mysteries—the first appearance of new beings on this Earth.”

The “mystery of mysteries” that captivated Darwin is **speciation**, the process by which one species splits into two or more species. Speciation fascinated Darwin (and many biologists since) because it is responsible for the tremendous diversity of life, repeatedly yielding new species that differ from existing ones. Speciation explains not only differences between species, but also similarities between them (the unity of life). When one species splits into two, the species that result share many characteristics because they are descended from this common ancestral species. For example, DNA similarities indicate that the flightless cormorant (*Phalacrocorax harrisi*) in Figure 24.1 is closely related to flying cormorants found in the Americas. This suggests that the flightless cormorant may have originated from an ancestral cormorant species that migrated from the mainland to the Galápagos.

Speciation also 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 (mutation, natural selection, genetic drift, and gene flow) in Chapter 23, and we’ll turn to macroevolution in Chapter 25. In this chapter, we will explore the “bridge”—the mechanisms by which new species originate from existing ones. First, however, we need to establish what we actually mean when we talk about “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—from differences in their appearance. But are organisms truly divided into the discrete units we call species, or is this classification an arbitrary attempt to impose order on the natural world? To answer this question, biologists compare not only the morphology (body form) of different groups of organisms but also less obvious differences in 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 **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 repro-



(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.

▲ **Figure 24.2** The biological species concept is based on the potential to interbreed rather than on physical similarity.

ductively 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 that develop into fertile adults. In contrast, humans and chimpanzees remain distinct biological species even where they share territory, 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 other species? To answer this question, we need to return to the evolutionary mechanism called *gene flow*, the transfer of alleles between populations (see Chapter 23). Typically, gene flow occurs between the different populations of a species. This ongoing exchange of alleles tends to hold the populations together genetically. As we'll explore in the following sections, the absence of gene flow plays a key role in the formation of new species, as well as in keeping them apart once their potential to interbreed has been reduced.

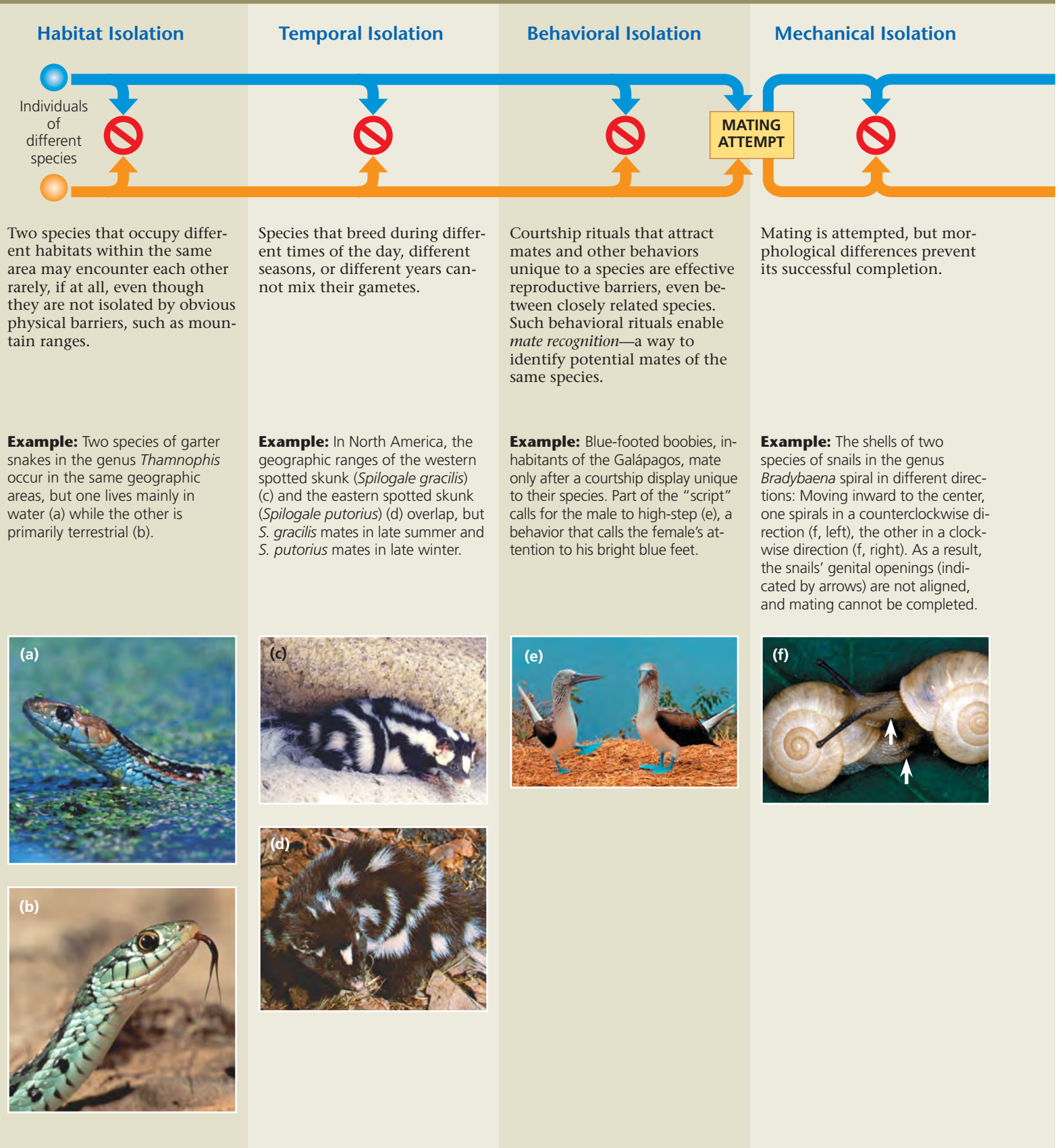
Reproductive Isolation

Because biological species are defined in terms of reproductive compatibility, the formation of a new species hinges on **reproductive isolation**—the existence of biological factors (barriers) that impede members of two species from interbreeding and producing viable, fertile offspring. Such barriers block gene flow between the species and limit the formation of **hybrids**, offspring that result from an inter-specific 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. 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. For example, developmental errors may reduce survival among hybrid embryos. Or problems after birth may cause hybrids to be infertile or may decrease their chance of surviving long enough to reproduce. Figure 24.3, on the next two pages, describes prezygotic and postzygotic barriers in more detail.

Exploring Reproductive Barriers

Prezygotic barriers impede mating or hinder fertilization if mating does occur



Postzygotic barriers prevent a hybrid zygote from developing into a viable, fertile adult

Gametic Isolation

Reduced Hybrid Viability

Reduced Hybrid Fertility

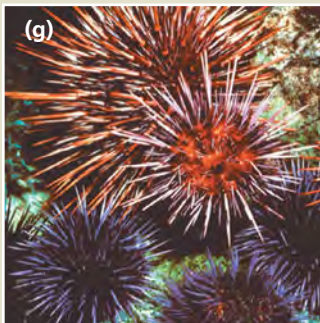
Hybrid Breakdown

FERTILIZATION

VIABLE, FERTILE OFFSPRING

Sperm of one species may not be able to fertilize the eggs of another species. For instance, sperm may not be able to survive in the reproductive tract of females of the other species, or biochemical mechanisms may prevent the sperm from penetrating the membrane surrounding the other species' eggs.

Example: Gametic isolation separates certain closely related species of aquatic animals, such as sea urchins (g). Sea urchins release their sperm and eggs into the surrounding water, where they fuse and form zygotes. It is difficult for gametes of different species, such as the red and purple urchins shown here, to fuse because proteins on the surfaces of the eggs and sperm bind very poorly to each other.



The genes of different parent species may interact in ways that impair the hybrid's development or survival in its environment.

Example: Some salamander subspecies of the genus *Ensatina* live in the same regions and habitats, where they may occasionally hybridize. But most of the hybrids do not complete development, and those that do are frail (h).



Even if hybrids are vigorous, they may be sterile. If the chromosomes of the two parent species differ in number or structure, meiosis in the hybrids may fail to produce normal gametes. Since the infertile hybrids cannot produce offspring when they mate with either parent species, genes cannot flow freely between the species.

Example: The hybrid offspring of a male donkey (i) and a female horse (j) is a mule (k), which is robust but sterile. A "hinny" (not shown), the offspring of a female donkey and a male horse, is also sterile.



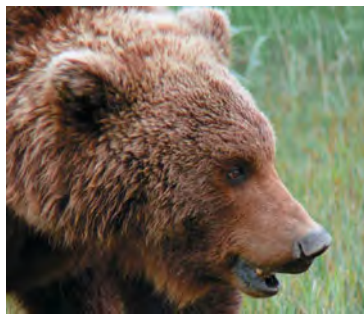
Some first-generation hybrids are viable and fertile, but when they mate with one another or with either parent species, offspring of the next generation are feeble or sterile.

Example: Strains of cultivated rice have accumulated different mutant recessive alleles at two loci in the course of their divergence from a common ancestor. Hybrids between them are vigorous and fertile (l, left and right), but plants in the next generation that carry too many of these recessive alleles are small and sterile (l, center). Although these rice strains are not yet considered different species, they have begun to be separated by postzygotic barriers.



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 Chapter 27, 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. This observation has led some researchers to argue that the biological species concept overemphasizes gene flow and downplays the role of natural selection. Because of the limitations to the biological species concept, alternative species concepts are useful in certain situations.



◀ Grizzly bear (*U. arctos*)



▼ Polar bear (*U. maritimus*)



▲ Hybrid “grolar bear”

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

Other Definitions of Species

While the biological species concept emphasizes the *separateness* of species from one another due to reproductive barriers, several other definitions emphasize the *unity within* a species. For example, the **morphological species concept** characterizes 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, this is how scientists distinguish most species. One disadvantage, however, is that this definition relies on subjective criteria; researchers may disagree on which structural features distinguish a species.

The **ecological species concept** views 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 Chapter 54). For example, two species of salamanders might be similar in appearance but differ in the foods they eat or in their ability to tolerate dry conditions. 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 environmental conditions.

The **phylogenetic species concept** defines a species as the smallest group of individuals that share a common ancestor, forming one branch on the tree of life. Biologists trace the phylogenetic history of a species by comparing its characteristics, such as morphology or molecular sequences, with those of other organisms. Such analyses can distinguish groups of individuals that are sufficiently different to be considered separate species. Of course, the difficulty with this species concept is determining the degree of difference required to indicate separate species.

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.

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 you are studying two bird species that 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.

CONCEPT 24.2

Speciation can take place with or without geographic separation

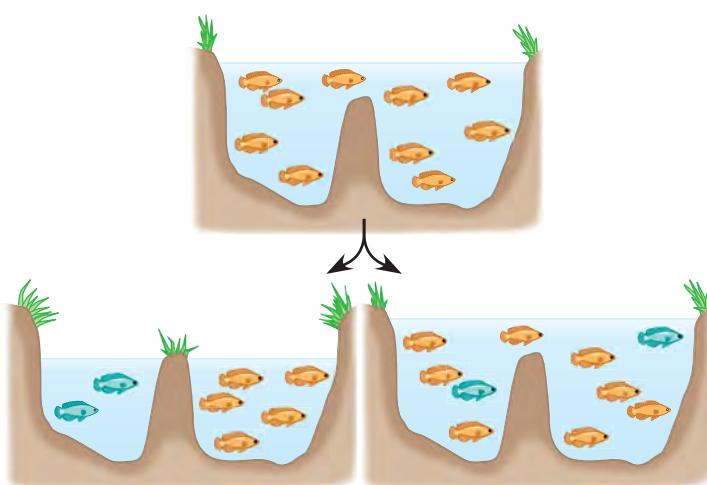
Now that we have a clearer sense of what constitutes a unique species, let's return to our discussion of the process by which such species arise from existing species. Speciation can occur in two main ways, depending on how gene flow is interrupted between populations of the existing species (Figure 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 remodeling, 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 most likely 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 the windblown pollen of pine trees and the seeds of many flowering plants. In con-



- (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.

▲ **Figure 24.5** Two main modes of speciation.

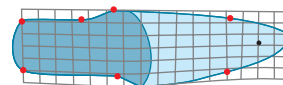


▲ **Figure 24.6** Allopatric speciation of antelope squirrels on opposite rims of the Grand Canyon. Harris's antelope squirrel (*Ammospermophilus harrisi*) inhabits the canyon's south rim (left). Just a few kilometers away on the north rim (right) lives the closely related white-tailed antelope squirrel (*Ammospermophilus leucurus*). Birds and other organisms that can disperse easily across the canyon have not diverged into different species on the two rims.

trast, small rodents may find a wide river or deep canyon a formidable barrier (Figure 24.6).

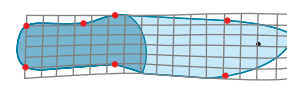
Once geographic separation has occurred, the separated gene pools may diverge. Different mutations arise, and natural selection and genetic drift may alter allele frequencies in different ways in the separated populations. Reproductive isolation may then arise as a by-product of selection or drift having caused the populations to diverge genetically. For 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 many predatory fishes, while others do not. In the "high-predation" ponds, selection has favored the evolution of a mosquitofish body shape that enables rapid bursts of speed (Figure 24.7). In ponds lacking

(a) Under high predation



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

(b) Under low predation



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

▲ **Figure 24.7** Reproductive isolation as a by-product of selection. After bringing together mosquitofish from different ponds, researchers concluded that selection for traits that enable mosquitofish in high-predation ponds to avoid predators has isolated them reproductively from mosquitofish in low-predation ponds.

predatory fishes, selection has favored a different body shape, one that improves the ability to swim for long periods of time. How have these different selective pressures affected the evolution of reproductive barriers? Researchers answered 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 barrier 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 started to form in these allopatric populations.

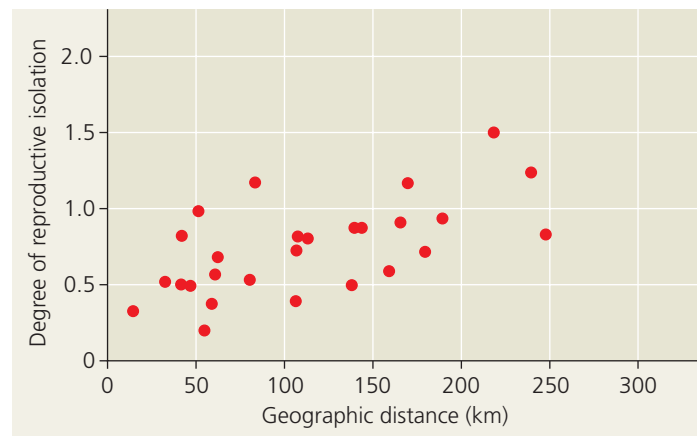
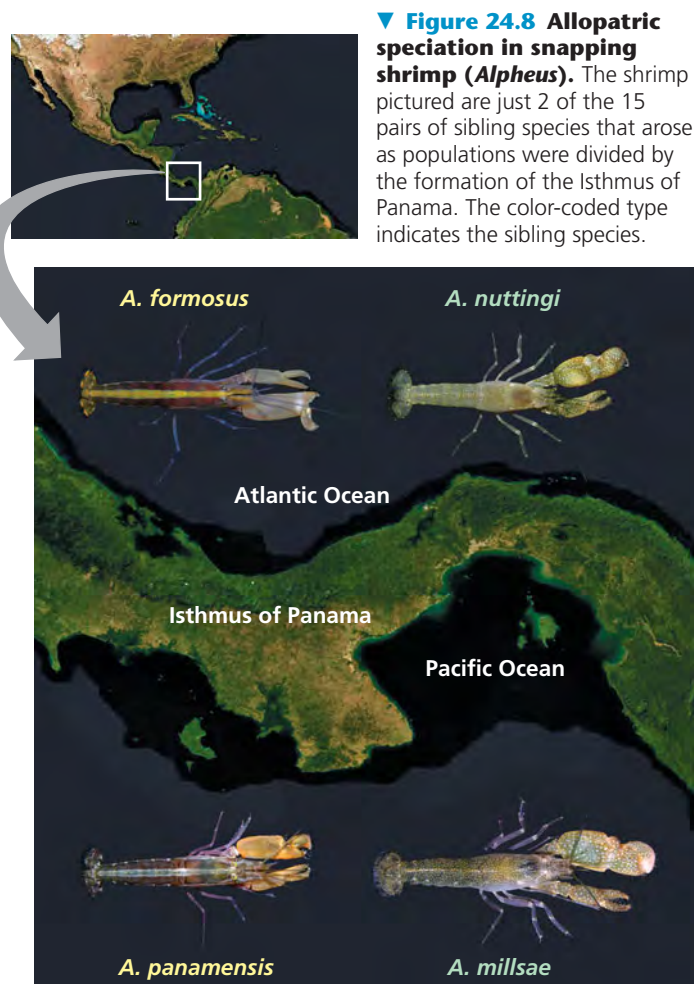
Evidence of Allopatric Speciation

Many studies provide evidence that speciation can occur in allopatric populations. 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 orig-

inate by allopatric speciation? Morphological and genetic data group these shrimp into 15 pairs of *sibling species*, pairs whose member species are each other's closest relative. In each of these 15 pairs, one of the sibling species lives on the Atlantic side of the isthmus, while the other lives on the Pacific side, strongly suggesting 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 sibling 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 Chapter 25). Similarly, unusually high numbers of butterfly species are found in South American regions that are subdivided by many rivers.

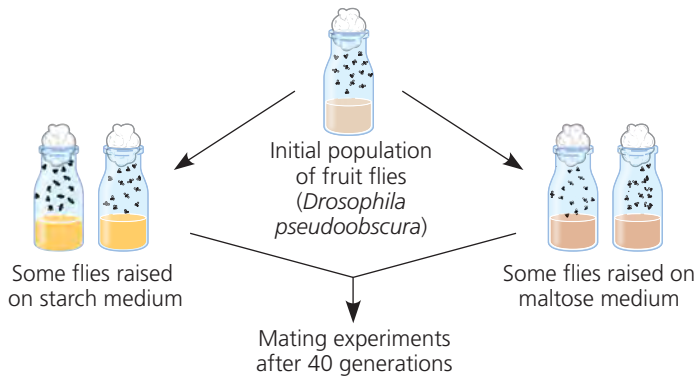
Laboratory and field tests also provide evidence that reproductive isolation between two populations generally increases as the distance between them increases. In a study of dusky salamanders (*Desmognathus ochrophaeus*), biologists brought individuals from different populations into the laboratory and tested their ability to produce viable, fertile offspring (Figure 24.9). The researchers observed little reproductive isolation in salamanders from neighboring populations. In contrast, salamanders from widely separated populations often failed to reproduce, a result consistent with allopatric speciation. In other studies, researchers have tested whether intrinsic reproductive barriers develop when populations are isolated



▲ **Figure 24.9 Reproductive isolation increases with distance in populations of dusky salamanders.** The degree of reproductive isolation is represented here by an index ranging from 0 (no isolation) to 2 (complete isolation).

Can divergence of allopatric populations lead to reproductive isolation?

EXPERIMENT Diane Dodd, then at Yale University, 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. Dodd 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. But in the control group (shown on the right), flies from different populations adapted to starch were about as likely to mate with each other as with flies from their own population; similar results were obtained for control groups adapted to maltose.

| | | Female | |
|------|---------|--------|---------|
| | | Starch | Maltose |
| Male | Starch | 22 | 9 |
| | Maltose | 8 | 20 |

Number of matings in experimental group

| | | Female | |
|------|---------------------|---------------------|---------------------|
| | | Starch population 1 | Starch population 2 |
| Male | Starch population 1 | 18 | 15 |
| | Starch population 2 | 12 | 15 |

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 reproductive barrier was not absolute (some mating between starch flies and maltose flies did occur), after 40 generations it appeared to be under way. 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.

SOURCE 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 a starch or maltose medium)?

experimentally and subjected to different environmental conditions. In such cases, too, the results provide strong support for allopatric speciation (Figure 24.10).

We need to emphasize here that although geographic isolation prevents interbreeding between 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.

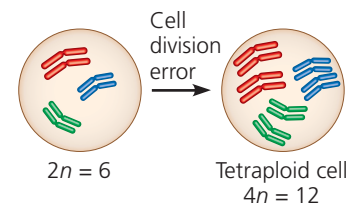
Sympatric (“Same Country”) Speciation

In **sympatric speciation** (from the Greek *syn*, together), speciation occurs in populations that live in the same geographic area. 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, habitat differentiation, and sexual selection. (Note that these factors can also promote allopatric speciation.)

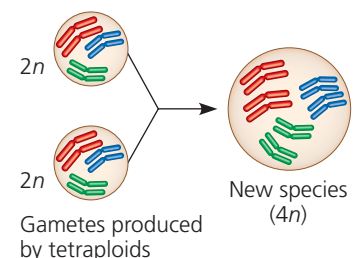
Polyploidy

A species may originate from an accident during cell division that results in extra sets of chromosomes, a condition called **polyploidy**. 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, polyploidy is far more common in plants. 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 polyploidy 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 diploid number ($2n$) to a tetraploid number ($4n$).



A tetraploid can produce fertile tetraploid offspring by self-pollinating or by mating with other tetraploids. In addition, the tetraploids are reproductively isolated from diploid 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.

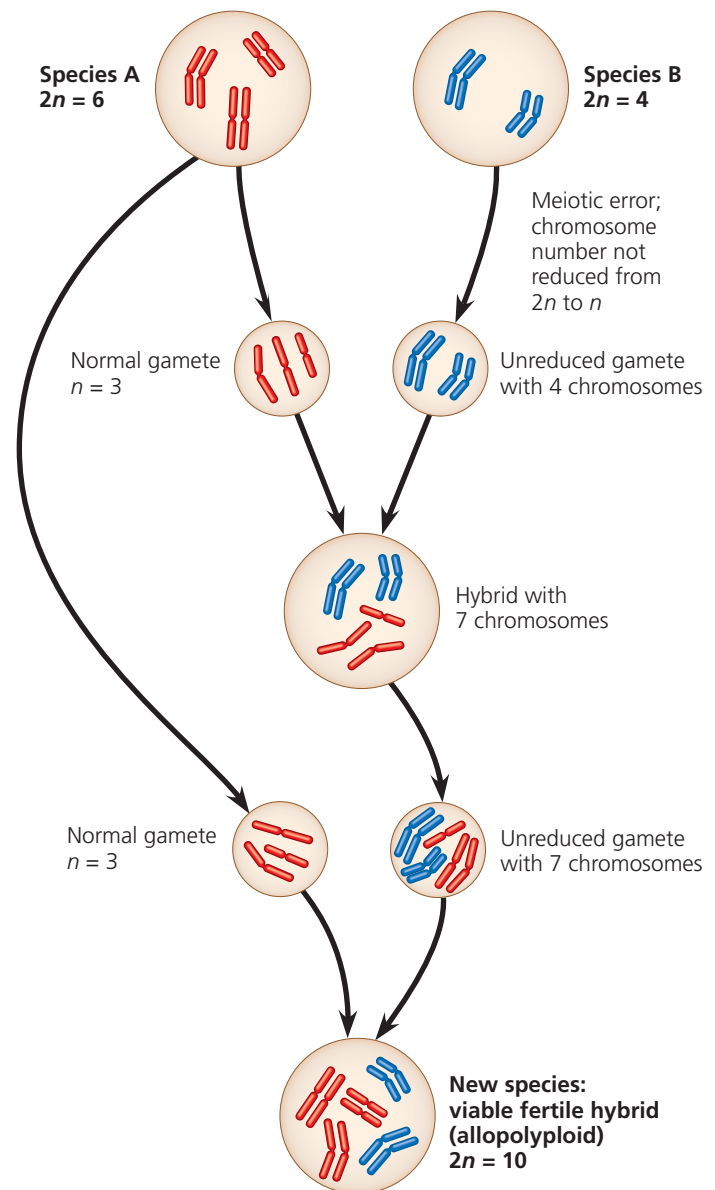
A second form of polyploidy can occur when two different species interbreed and produce hybrid offspring. Most such hybrids are sterile because the set of chromosomes from one species cannot pair during meiosis with the set of chromosomes from the other species. However, an infertile hybrid may be able 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 24.11). The allopolyploids are fertile when mating with each other but cannot interbreed with either parent species; thus, they represent a new biological species.

Although polyploid speciation is relatively rare, even in plants, scientists have documented that at least five new plant species have originated in this way 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 three European species in the early 1900s. These three species are now common weeds in abandoned parking lots and other urban sites. 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 a tetraploid hybrid of two of the European species. Although the *T. miscellus* population grows mainly by reproduction of its own members, additional episodes of hybridization between the parent species continue to add new members to the *T. miscellus* population—just one of many examples in which scientists have observed speciation in progress.

Many important agricultural crops—such as oats, cotton, potatoes, tobacco, and wheat—are polyploids. The wheat used for bread, *Triticum aestivum*, is an allohexaploid (six sets of chromosomes, two sets from each of three different species). The first of the polyploidy events that eventually led to modern wheat probably occurred about 8,000 years ago in the Middle East as a spontaneous hybrid of an early cultivated wheat species and 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 hybrid species with desired qualities, such as a hybrid that combines the high yield of wheat with the hardiness of rye.

Habitat Differentiation

Sympatric speciation can also occur when genetic factors enable a subpopulation to exploit a habitat or resource not used by the parent population. Such is the case with the North American apple maggot fly (*Rhagoletis pomonella*), a



▲ **Figure 24.11 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 that can produce fertile hybrids (allopolyploids) as new species. The new species has a diploid chromosome number equal to the sum of the diploid chromosome numbers of the two parent species.

pest of apples. The fly's original habitat was the native hawthorn tree, but about 200 years ago, some populations colonized apple trees that had been introduced by European settlers. As 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 prezygotic restriction 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. As a result, natural selection operating on these alleles provides 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.

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 rivers and lakes located elsewhere. 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 that the resulting genetic divergence contributed to speciation in Lake Victoria. But sexual selection, in which (typically) females select males based on their appearance (see Chapter 23), 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 is the main reproductive barrier that normally keeps the gene pools of these two species separate.

Allopatric and Sympatric Speciation: A Review

Now let's recap the two main modes 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. As a result, other reproductive barriers from the ancestral species may 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, intrinsic reproductive barriers that arise in allopatric populations can prevent interbreeding with the parent population even if the populations come back into contact.

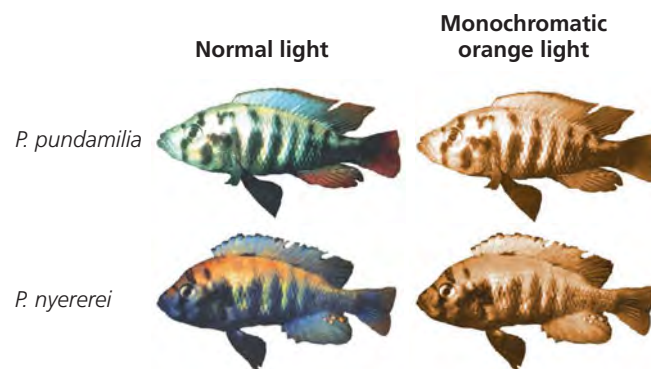
Sympatric speciation, in contrast, requires the emergence of a reproductive barrier that isolates a subset of a population

▼ Figure 24.12

INQUIRY

Does sexual selection in cichlids result in reproductive isolation?

EXPERIMENT Ole Seehausen and Jacques van Alphen, then at the University of Leiden, 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 Seehausen and van Alphen concluded that mate choice by females based on male breeding coloration is the main reproductive barrier that normally keeps the gene pools of these two species separate. Since the species can still interbreed when this prezygotic behavioral 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.

SOURCE 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? If changing the light to orange had not affected the mating behavior of the cichlids, how might the researchers' conclusion have been different?

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 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. Finally, sympatric speciation can result from sexual selection.

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.

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** After reviewing the process of meiosis in Figure 13.8 (p. 254), describe how an error during meiosis could lead to polyploidy.

For suggested answers, see Appendix A.

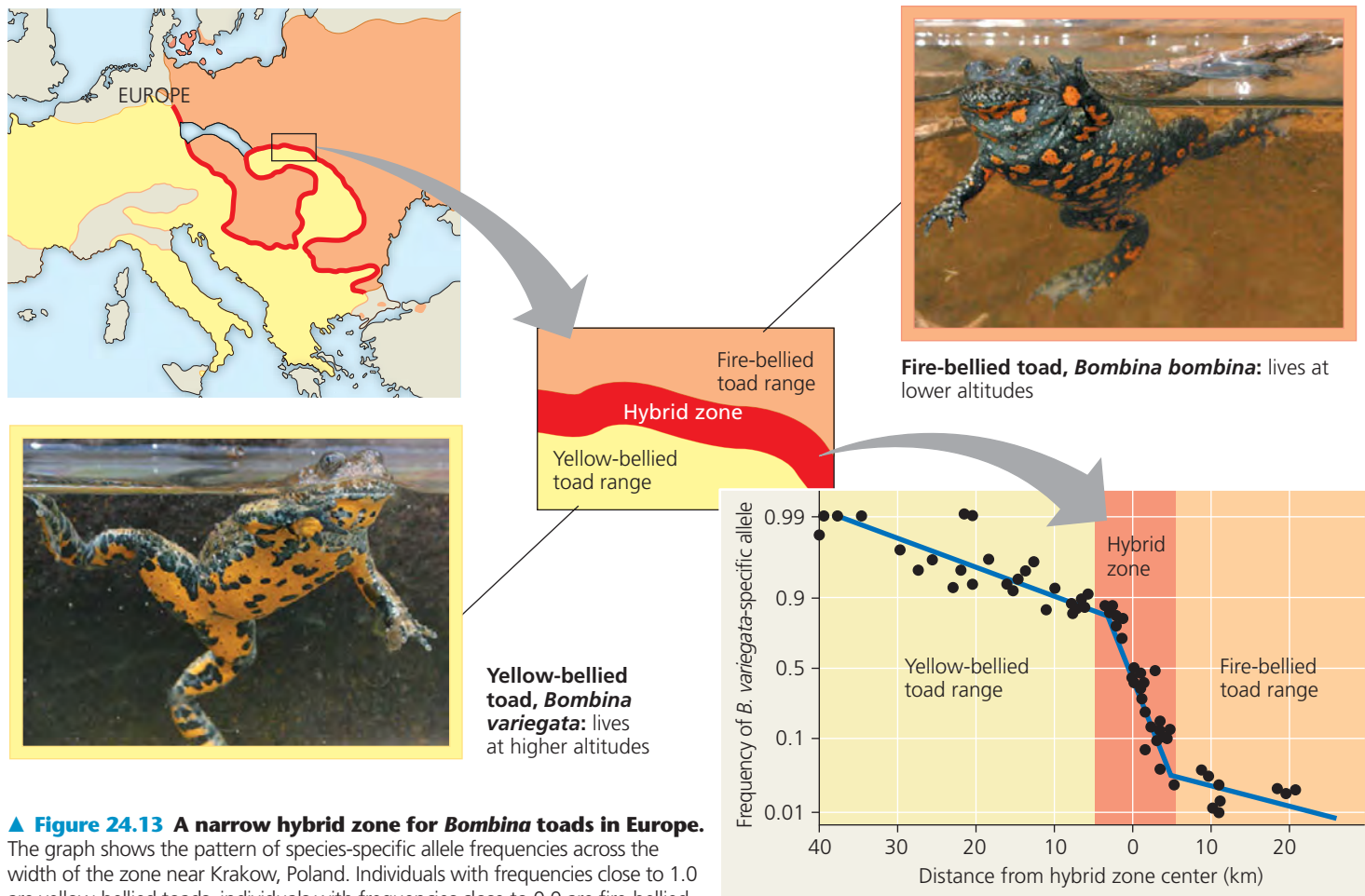
CONCEPT 24.3

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 two species of toads in the genus *Bombina*, the yellow-bellied toad (*B. variegata*) and 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



▲ Figure 24.13 A narrow hybrid zone for *Bombina* toads in Europe.

The graph shows the pattern of species-specific allele frequencies across the width of the zone near Krakow, Poland. Individuals with frequencies close to 1.0 are yellow-bellied toads, individuals with frequencies close to 0.0 are fire-bellied toads, and individuals with intermediate frequencies are considered hybrids.

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

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 50% in the central portion of the zone, 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.

Other hybrid zones have more complicated spatial patterns. For example, many plant species only occur in locations that have a very particular set of environmental conditions. Favorable “patches” that have such conditions are often scattered irregularly across the landscape and are

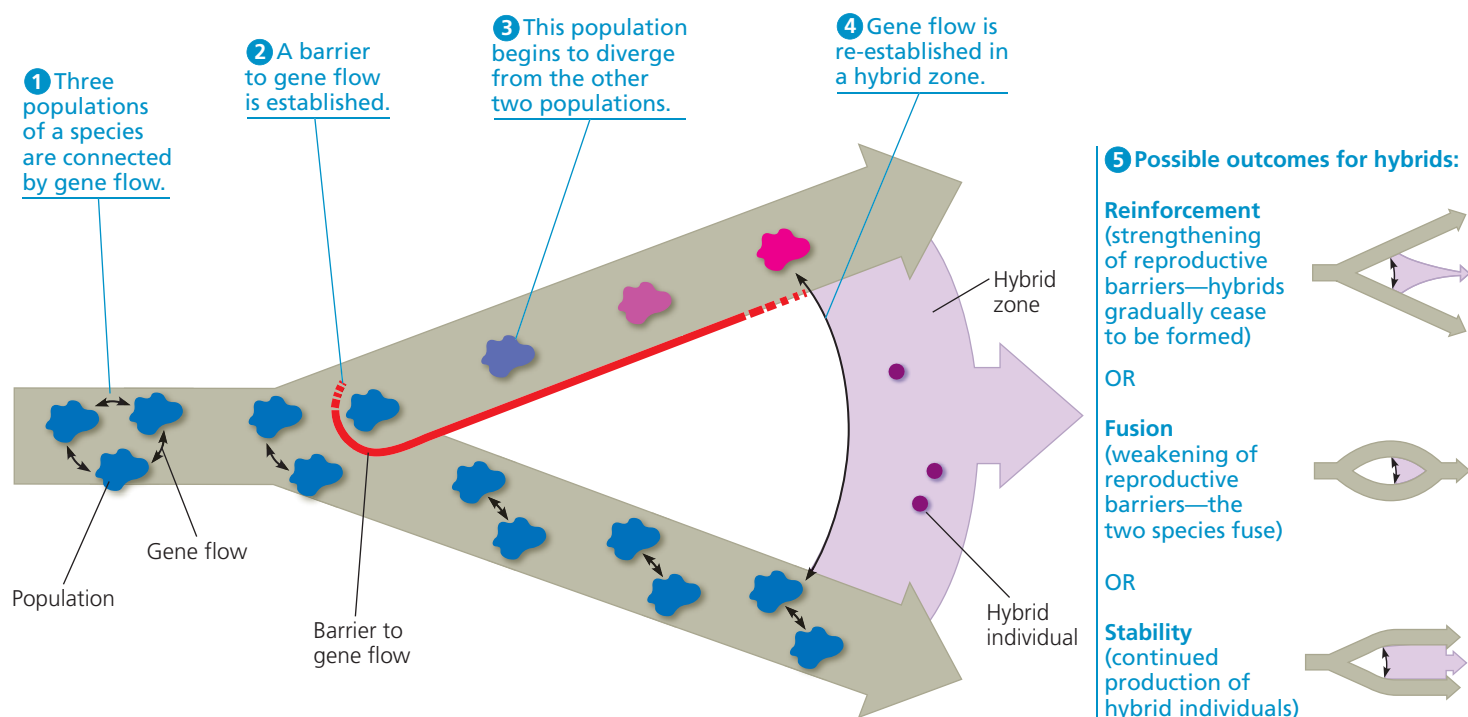
isolated from one another. When two such plant species interbreed, the hybrid zone occurs in a group of disconnected patches, a more complex spatial pattern than the continuous band shown in Figure 24.13. But regardless of whether they have complex or simple spatial patterns, hybrid zones form when two species lacking complete barriers to reproduction come into contact. Once formed, how does a hybrid zone change over time?

Hybrid Zones over Time

Studying a hybrid zone is like observing a natural experiment on speciation. Will the hybrids become reproductively isolated from their parents and form a new species, as occurred by polyploidy in the goatsbeard plant of the Pacific Northwest? If not, there are three possible outcomes for the hybrid zone over time: reinforcement of barriers, fusion of species, or stability (Figure 24.14). Reproductive barriers between species may be reinforced over time (limiting the formation of hybrids) or weakened over time (causing the separating species to fuse into one species). Or hybrids may continue to be produced, creating a long-term and stable hybrid zone. Let’s examine what studies in the field suggest about these three possibilities.

Reinforcement: Strengthening Reproductive Barriers

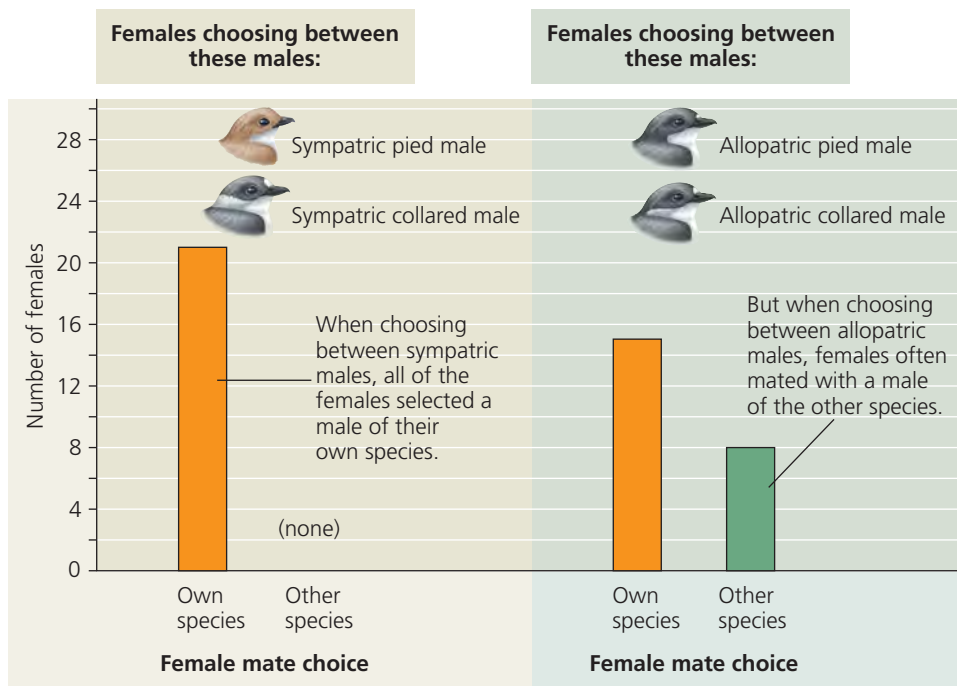
When hybrids are less fit than members of their parent species, as in the *Bombina* example, we might expect natural selection to strengthen prezygotic barriers to reproduction, thus reducing



▲ **Figure 24.14** Formation of a hybrid zone and possible outcomes for hybrids over time.

The thick colored arrows represent the passage of time.

WHAT IF? Predict what might happen if gene flow were re-established at step 3 in this process.



▲ **Figure 24.15 Reinforcement of barriers to reproduction in closely related species of European flycatchers.**

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.

As an example, let's consider the evidence for reinforcement in two closely related species of European flycatcher, the pied flycatcher and the collared flycatcher. In allopatric populations of these birds, males of the two species closely resemble one another. But in sympatric populations, the males of the two species look very different: Male pied flycatchers are a dull brown, whereas male collared flycatchers have enlarged patches of white. Female pied and collared 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 (Figure 24.15). Thus, barriers to reproduction appear to be stronger in birds from sympatric populations than in birds from allopatric populations, as you would predict if reinforcement is occurring. Similar results have been observed in a number of organisms, including fishes, insects, plants, and other birds. But interestingly, reinforcement does *not* appear to be at work in the case of the *Bombina* toads, as we'll discuss shortly.

Fusion: Weakening Reproductive Barriers

Next let's consider the case in which two species contact one another in a hybrid zone, but the barriers to reproduction are

not strong. 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.

Such a situation may be occurring among some of the Lake Victoria cichlids we discussed earlier. In the past 30 years, about 200 of the former 600 species of Lake Victoria cichlids have vanished. Some of these species were driven to extinction by an introduced predator, the Nile perch. But many species not eaten by Nile perch also have disappeared—perhaps in some cases by species fusion. Many pairs of ecologically similar cichlid 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). Researchers think that murky waters caused by pollution may have reduced the ability of females to use color to distinguish males of their own species from males of closely related species. If further evidence supports this hypothesis, it would seem that pollution in Lake Victoria has produced a cascade of related effects. First, by decreasing the ability of females to distinguish males of their own species, pollution has increased the frequency of mating between members of species that had been isolated reproductively from one another. Second, as a result of these matings, many hybrids have been produced, leading to fusion of the parent species' gene pools and a loss of species (Figure 24.16).

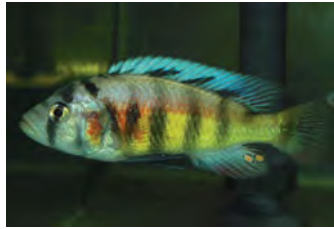
Similar events may be affecting the polar bear (*Ursus maritimus*). Fossils and genetic analyses indicate that polar bears evolved from North American populations of grizzly bears (*U. arctos*) between 100,000 and 200,000 years ago. In recent decades, global warming has reduced the extent of the Arctic Ocean ice packs from which polar bears hunt for seals and other prey. As their ice-pack habitat disappears (placing them at risk of extinction), polar bears are more likely to be found on land, where they may encounter grizzly bears. Hybrid offspring of polar bears and grizzly bears in the wild have been documented (see Figure 24.4). As polar bear habitat continues to disappear, increasing numbers of such hybrids may cause the gene pools of these species to begin to fuse, thus contributing to the possible eventual extinction of the polar bear.



Pundamilia nyererei



Pundamilia pundamilia



Pundamilia "turbid water,"
hybrid offspring from a location
with turbid water

▲ **Figure 24.16 Fusion: The breakdown of reproductive barriers.** Increasingly cloudy water in Lake Victoria over the past 30 years 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.

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.

Recall that hybrids are at a strong disadvantage in the *Bombina* hybrid zone. As a result, the offspring of individuals that prefer to mate with members of their own species should survive or reproduce better than the unfit hybrid offspring of individuals that mate indiscriminately with members of the other species. This suggests that reinforcement should occur, strengthening reproductive barriers and thereby limiting the production of hybrid toads. But in more than 20 years of study, no evidence for reinforcement has been found, and hybrids continue to be produced.

What could explain this finding? One possibility 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. Such movements lead to the continued production of hybrids, potentially overwhelming the selection for increased reproductive isolation inside the zone. If the hy-

brid 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.

In short, 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 what would happen 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

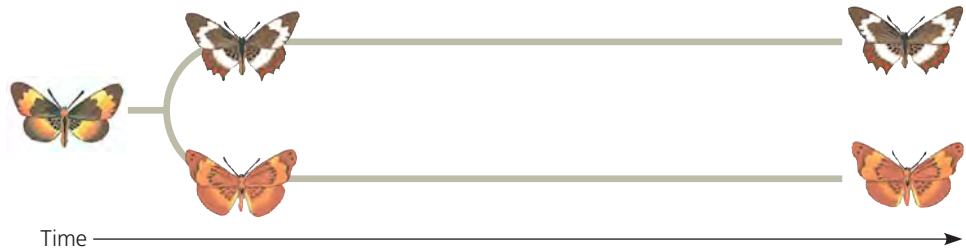
Speciation can occur rapidly or slowly and can result from changes in few or many genes

Darwin faced many unanswered questions when he began to ponder that "mystery of mysteries"—speciation. As you read in Chapter 22, he found answers to some of those questions when he realized that evolution by natural selection helped explain both the diversity of life and the adaptations of organisms. But biologists since Darwin have continued to ask fundamental questions about speciation. For example, 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 beginning to emerge.

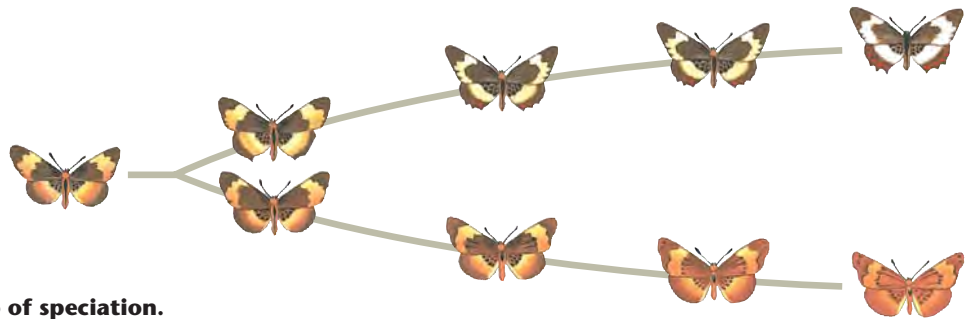
The Time Course of Speciation

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.

(a) In a punctuated pattern, new species change most as they branch from a parent species and then change little for the rest of their existence.



(b) Other species diverge from one another much more gradually over time.



▲ **Figure 24.17** Two models for the tempo of speciation.

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. Paleontologists Niles Eldredge, of the American Museum of Natural History, and Stephen Jay Gould, of Harvard University, coined the term **punctuated equilibria** to describe these periods of apparent stasis punctuated by sudden change (Figure 24.17a). Other species do not show a punctuated pattern; instead, they change more gradually over long periods of time (Figure 24.17b).

What do 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 the first 50,000 years of its existence—just 1% of its total lifetime. Time periods this short (in geologic terms) often cannot be distinguished in fossil strata, in part because the rate of sediment accumulation is 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 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.

Speciation Rates

The punctuated pattern suggests that once the process of speciation begins, it can be completed relatively rapidly—a suggestion supported by a growing number of studies.

For example, research conducted at Indiana University suggests that rapid speciation 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 answer this question, the researchers performed an



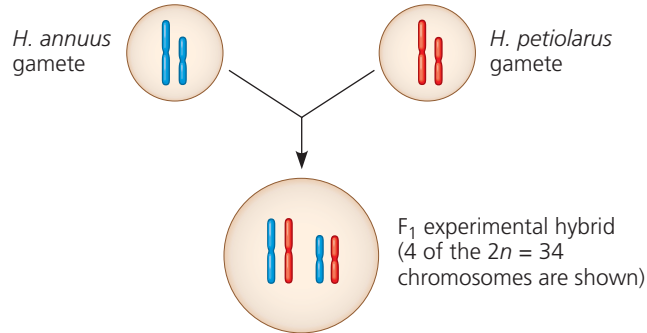
▲ **Figure 24.18** A hybrid sunflower species and its dry sand dune habitat. The wild sunflower *Helianthus anomalus* originated via the hybridization of two other sunflowers, *H. annuus* and *H. petiolaris*, which live in nearby but moister environments.

▼ Figure 24.19

INQUIRY

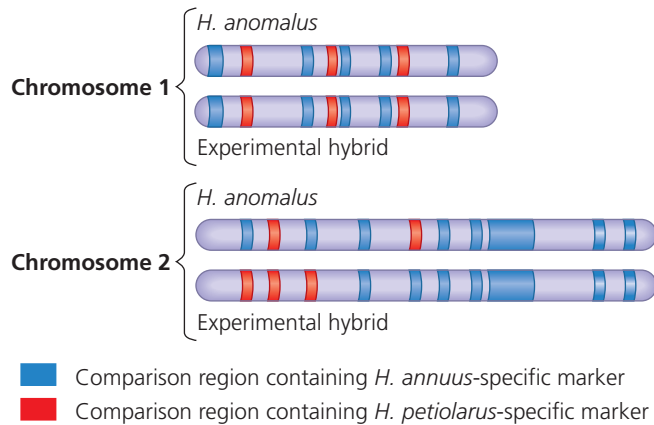
How does hybridization lead to speciation in sunflowers?

EXPERIMENT At Indiana University, 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 (F₁) generation, each chromosome of the experimental hybrids consisted entirely of DNA from one or the other parent species. The researchers then tested whether the F₁ 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 F₁ 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 F₁ generation 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 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.

SOURCE 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 results.

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*.

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. For example, in a survey of data from 84 groups of plants and animals, the interval between speciation events 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 rarely took less than 500,000 years.

What can we learn from such data? First, the data suggest that on average, millions of years may pass before a newly formed species will itself give rise to another new species. As we'll see in Chapter 25, this result has implications for how long it takes life on Earth to recover from mass extinction events. Second, the extreme variability in the time it takes new species to form indicates that organisms do not have a "speciation clock" ticking inside them, causing them to produce new species at regular time 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 an isolated 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 change when a new species forms?

In a few cases, the evolution of reproductive isolation is due to a change in a single gene. For example, in Japanese snails of the genus *Euhadra*, a change in a single gene can result 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 shows a similar example).

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.

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*. Douglas Schemske, of Michigan State University, and colleagues have shown that 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 F₁ hybrids and then performing repeated backcrosses of these F₁ hybrids to each parent species, Schemske and colleagues 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.

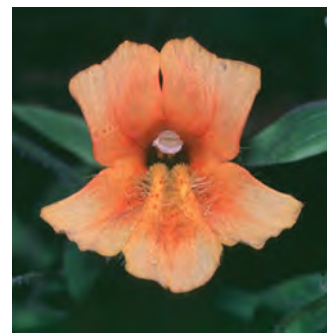
In other organisms, the speciation process is influenced by larger numbers of genes and gene interactions. For example, hybrid sterility between two subspecies of the fruit fly *Drosophila pseudoobscura* results from gene interactions among at least four loci, and postzygotic isolation in the sunflower 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 seemingly 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 land-dwelling mammals; see Figure 22.20). Furthermore, 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.



(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

▲ 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.

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?

CONCEPT CHECK 24.4

- Speciation can occur rapidly between diverging populations, yet the length of time between speciation events is often more than a million years. Explain this apparent contradiction.
- Summarize evidence that the *yup* locus acts as a prezygotic barrier to reproduction in two species of monkey flowers. Do these results demonstrate that the *yup* locus alone controls barriers to reproduction between these species? Explain.
- MAKE CONNECTIONS** Compare Figure 13.11 (p. 259) with Figure 24.19 (p. 503). What cellular process could cause the hybrid chromosomes to contain DNA from both parent species? Explain.

For suggested answers, see Appendix A.

24 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 24.1

The biological species concept emphasizes reproductive isolation (pp. 488–492)

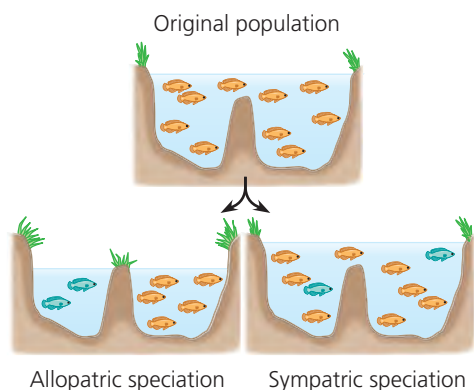
- A biological **species** is a group of populations whose individuals have the potential to interbreed and produce viable, fertile offspring with each other but not with members of other species. The **biological species concept** emphasizes reproductive isolation through prezygotic and postzygotic barriers that separate gene pools.
- Although helpful in thinking about how speciation occurs, the biological species concept has limitations. For instance, it cannot be applied to organisms known only as fossils or to organisms that reproduce only asexually. Thus, scientists use other species concepts, such as the **morphological species concept**, in certain circumstances.

? Explain the importance of gene flow to the biological species concept.

CONCEPT 24.2

Speciation can take place with or without geographic separation (pp. 493–498)

- 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 prezygotic or postzygotic 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 habitat shifts and sexual selection.



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

CONCEPT 24.3

Hybrid zones reveal factors that cause reproductive isolation (pp. 498–501)

- 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. 501–504)

- 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.
- New developments in genetics have enabled researchers to identify specific genes involved in some cases of speciation. Results show that speciation can be driven by 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

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. The *largest* unit within which gene flow can readily occur is a
 - a. population.
 - b. species.
 - c. genus.
 - d. hybrid.
 - e. phylum.
2. 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?
 - a. habitat isolation
 - b. temporal isolation
 - c. behavioral isolation
 - d. gametic isolation
 - e. postzygotic barriers
3. According to the punctuated equilibria model,
 - a. natural selection is unimportant as a mechanism of evolution.
 - b. given enough time, most existing species will branch gradually into new species.
 - c. 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.
 - d. most evolution occurs in sympatric populations.
 - e. speciation is usually due to a single mutation.

LEVEL 2: APPLICATION/ANALYSIS

4. 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 have good survival and reproduction.
 - The two forms live in similar habitats.
 - The two forms have many genes in common.
 - The two forms have similar food requirements.
 - The two forms are very similar in coloration.
5. Which of the following factors would *not* contribute to allopatric speciation?
- A population becomes geographically isolated from the parent population.
 - The separated population is small, and genetic drift occurs.
 - The isolated population is exposed to different selection pressures than the ancestral population.
 - Different mutations begin to distinguish the gene pools of the separated populations.
 - Gene flow between the two populations is extensive.
6. Plant species A has a diploid 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
- 12.
 - 14.
 - 16.
 - 28.
 - 56.

LEVEL 3: SYNTHESIS/EVALUATION

7. Suppose that a group of male pied flycatchers migrated from a region where there were no collared flycatchers to a region where both species were present (see Figure 24.15). Assuming events like this are very rare, which of the following scenarios is *least* likely?
- The frequency of hybrid offspring would increase.
 - Migrant pied males would produce fewer offspring than would resident pied males.
 - Pied females would rarely mate with collared males.
 - Migrant males would mate with collared females more often than with pied females.
 - The frequency of hybrid offspring would decrease.

8. EVOLUTION CONNECTION

What is 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?

9. SCIENCE, TECHNOLOGY, AND SOCIETY

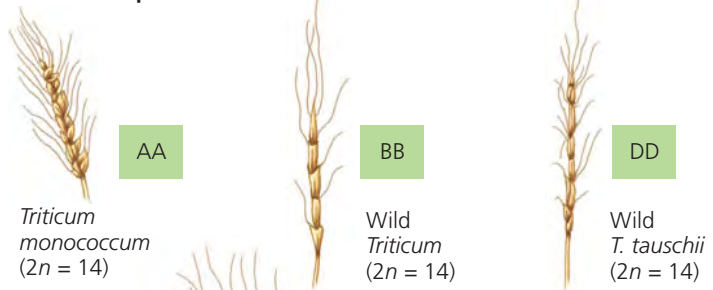
In the United States, the rare red wolf (*Canis lupus*) has been known to hybridize with coyotes (*Canis latrans*), which are much more numerous. Although red wolves and coyotes differ in terms of morphology, DNA, and behavior, genetic evidence suggests that living red wolf individuals are actually hybrids. Red wolves are designated as an endangered species and hence receive legal protection under the Endangered Species Act. Some people think that their endangered status should be withdrawn because the remaining red wolves are hybrids, not members of a “pure” species. Do you agree? Why or why not?

10. SCIENTIFIC INQUIRY

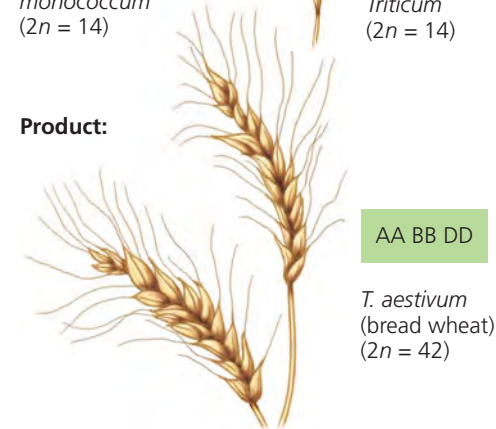
DRAW IT In this chapter, you read that bread wheat (*Triticum aestivum*) is an allohexaploid, containing two sets of chromosomes from each of three different parent species. Genetic analysis suggests that the three species pictured following this question each contributed chromosome sets to *T. aestivum*. (The capital letters here represent sets of chromosomes rather than individual genes.) Evidence also indicates that the first polyploidy event was a spontaneous hybridiza-

tion of the early cultivated wheat species *T. monococcum* and a wild *Triticum* grass species. Based on this information, draw a diagram of one possible chain of events that could have produced the allohexaploid *T. aestivum*.

Ancestral species:



Product:



11. WRITE ABOUT A THEME

The Genetic Basis of Life In sexually reproducing species, each individual begins life with DNA inherited 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.

For selected answers, see Appendix A.

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