

Two closely related species of parrot, the scarlet macaw (*Ara chloroptera*) and the blue and yellow macaw (*Ara arauna*), perching together in the Amazon jungle of Peru.



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STUDY PLAN

21.1 What Is a Species?

The morphological species concept is a practical way to identify species

The biological and phylogenetic species concepts derive from evolutionary theory

Many species exhibit substantial geographical variation

21.2 Maintaining Reproductive Isolation

Prezygotic isolating mechanisms prevent the production of hybrid individuals

Postzygotic isolating mechanisms reduce the success of hybrid individuals

21.3 The Geography of Speciation

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Polyploidy is a common mechanism of sympatric speciation in plants

Chromosome alterations can foster speciation

21 Speciation

WHY IT MATTERS

In 1927, nearly 100 years after Darwin boarded the *Beagle*, a young German naturalist named Ernst Mayr embarked on his own journey, to the highlands of New Guinea. He was searching for rare “birds of paradise,” no trace of which had been seen in Europe since plume hunters had returned years before with ornate and colorful feathers that were used to decorate ladies’ hats (**Figure 21.1**). On his trek through the remote Arfak Mountains, Mayr identified 137 bird species (including many birds of paradise) based on differences in their size, plumage, color, and other external characteristics.

To Mayr’s surprise, the native Papuans—who were untrained in the ways of Western science, but who hunted these birds for food and feathers—had their own names for 136 of the 137 species he had identified. The close match between the two lists confirmed Mayr’s belief that the *species* is a fundamental level of organization in nature. Each species has a unique combination of genes underlying its distinctive appearance and habits. Thus, people who observe them closely—whether indigenous hunters or Western scientists—can often distinguish one species from another.



Bruce Beehler

Figure 21.1

Birds of paradise. A male Count Raggi's bird of paradise (*Paradisaea raggiana*) has clearly attracted the attention of a female (the smaller, less colorful bird) with his showy plumage and conspicuous display. There are 43 known bird of paradise species, 35 of them found only on the island of New Guinea.

Mayr also discovered some remarkable patterns in the geographical distributions of the bird species in New Guinea. For example, each mountain range he explored was home to some species that lived nowhere else. Closely related species often lived on different mountaintops, separated by deep valleys of unsuitable habitat. In 1942, Mayr published the book *Systematics and the Origin of Species*, in which he described the role of geography in the evolution of new species; the book quickly became a cornerstone of the modern synthesis (which was outlined in Section 19.3).

What mechanisms produce distinct species? As you discovered in Chapter 20, microevolutionary processes alter the pattern and extent of genetic and phenotypic variation within populations. When these processes differ between populations, the populations will diverge, and they may eventually become so different that we recognize them as distinct species. Although Darwin's famous book was titled *On the Origin of Species*, he didn't dwell on the question of *how* new species arise. But the concept of **speciation**—the process of species formation—was implicit in his insight that similar species often share inherited characteristics and a common ancestry. Darwin also recognized that “descent with modification” had generated the amazing diversity of organisms on Earth.

Today evolutionary biologists view speciation as a *process*, a series of events that occur through time. However, they usually study the *products* of speciation, species that are alive today. Because they can rarely witness the process of speciation from start to finish,

scientists make inferences about it by studying organisms in various stages of species formation. In this chapter, we consider four major topics: how biologists define and recognize species; how species maintain their genetic identity; how the geographical distributions of organisms influence speciation; and how different genetic mechanisms produce new species.

21.1 What Is a Species?

Like the hunters of the Arfak Mountains, most of us recognize the different species that we encounter every day. We can distinguish a cat from a dog and sunflowers from roses. The concept of species is based on our perception that Earth's biological diversity is packaged in discrete, recognizable units, and not as a continuum of forms grading into one another. As evolutionary scientists learn more about the causes of microevolution, they refine our understanding of what a species really is.

The Morphological Species Concept Is a Practical Way to Identify Species

Biologists often describe new species on the basis of visible anatomical characteristics, a process that dates back to Linnaeus' classification of organisms in the eighteenth century (described in Chapter 23). This approach is based on the **morphological species concept**, the idea that all individuals of a species share measurable traits that distinguish them from individuals of other species.

The morphological species concept has many practical applications. For example, paleobiologists use morphological criteria to identify the species of fossilized organisms (see Chapter 22). And because we can observe the external traits of organisms in nature, field guides to plants and animals list diagnostic (that is, distinguishing) physical characters that allow us to recognize them (**Figure 21.2**).

Nevertheless, relying exclusively on a morphological approach can present problems. Consider the variation in the shells of *Cepaea nemoralis* (shown earlier in Figure 20.2). How could anyone imagine that so variable a collection of shells represents just one species

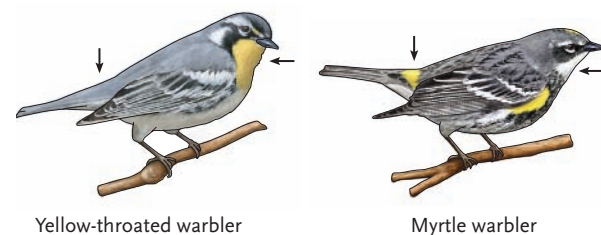


Figure 21.2

Diagnostic characters. Yellow-throated warblers (*Dendroica dominica*) and myrtle warblers (*Dendroica coronata*) can be distinguished by the color of feathers on the throat and rump.

of snail? Moreover, morphology does not help us distinguish some closely related species that are nearly identical in appearance. Finally, morphological species definitions tell us little about the evolutionary processes that produce new species.

The Biological and Phylogenetic Species Concepts Derive from Evolutionary Theory

The **biological species concept** emphasizes the dynamic nature of species. Ernst Mayr defined biological species as “groups of . . . interbreeding natural populations that are reproductively isolated from [do not produce fertile offspring with] other such groups.” The concept is based on reproductive criteria and is easy to apply, at least in principle: if the members of two populations interbreed and produce fertile offspring *under natural conditions*, they belong to the same species; their fertile offspring will, in turn, produce the next generation of that species. If two populations do not interbreed in nature, or fail to produce fertile offspring when they do, they belong to different species.

The biological species concept defines species in terms of population genetics and evolutionary theory. The first half of Mayr’s definition notes the genetic *cohesiveness* of species: populations of the same species experience gene flow, which mixes their genetic material. Thus, we can think of a species as one large gene pool, which may be subdivided into local populations.

The second part of the biological species concept emphasizes the genetic *distinctness* of each species. Because populations of different species are reproductively isolated, they cannot exchange genetic information. In fact, the process of speciation is frequently defined as the evolution of reproductive isolation between populations.

The biological species concept also explains why individuals of a species generally look alike: members of the same gene pool share genetic traits that determine their appearance. Individuals of different species generally do not resemble one another as closely because they share fewer genetic characteristics. In practice, biologists often use similarities or differences in morphological traits as convenient markers of genetic similarity or reproductive isolation.

However, the biological species concept does not apply to the many forms of life that reproduce asexually, including most bacteria; some protists, fungi, and plants; and a few animals. In these species, individuals don’t interbreed, so it is pointless to ask whether different populations do. Similarly, we cannot use the biological species concept to study extinct organisms, because we have little or no data on their reproductive habits. These species must all be defined using morphological or biochemical criteria. Yet, despite its limitations, the biological species concept currently provides the best evolutionary definition of a sexually reproducing species.

Recognizing the limitations of the biological species concept, some researchers have proposed a **phylogenetic species concept**. Using both morphological and genetic sequence data, scientists first reconstruct the evolutionary tree for the populations of interest. They then define a phylogenetic species as a cluster of populations—the tiniest twigs on the tree—that emerge from the same small branch. Thus, a phylogenetic species comprises populations that share a recent evolutionary history. We will consider this approach for defining species as well as more inclusive evolutionary groups in Chapter 23.

Many Species Exhibit Substantial Geographical Variation

Populations change in response to shifting environments, and separate populations of a species frequently differ both genetically and phenotypically. Neighboring populations often have shared characteristics because they live in similar environments, exchange individuals, and experience comparable patterns of natural selection. Widely separated populations, by contrast, may live under different conditions and experience different patterns of selection; because gene flow is less likely to occur between distant populations, their gene pools and phenotypes often differ.

When geographically separated populations of a species exhibit dramatic, easily recognized phenotypic variation, biologists may identify them as different **subspecies** (Figure 21.3), which are local variants of a species. Individuals from different subspecies usually interbreed where their geographical distributions

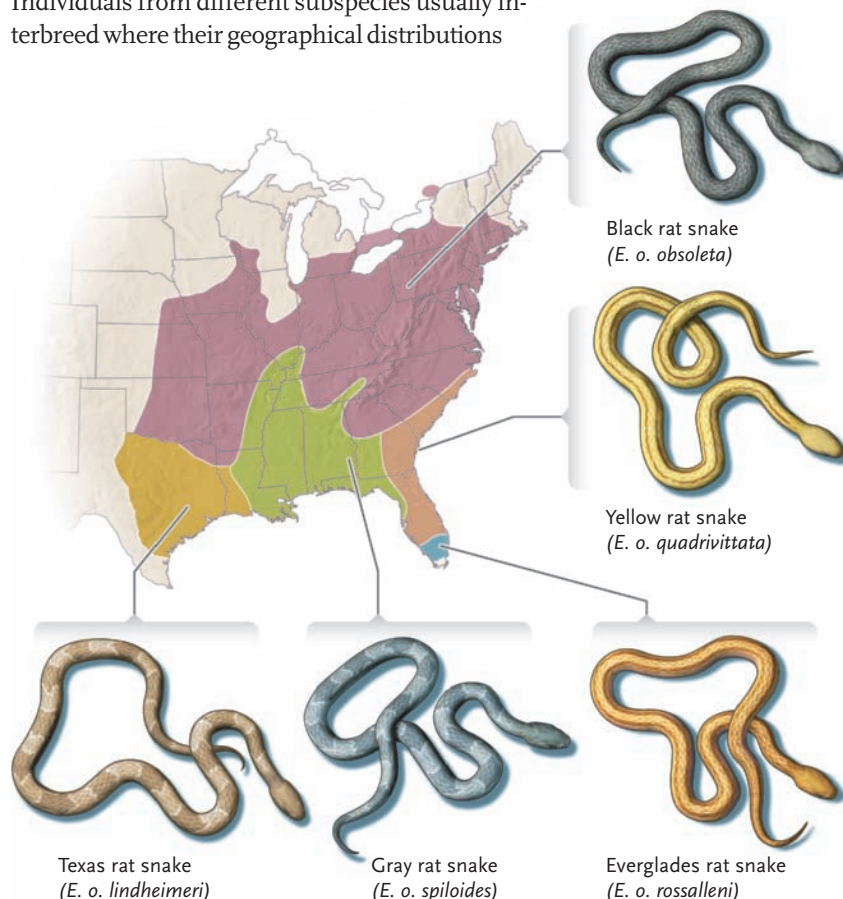
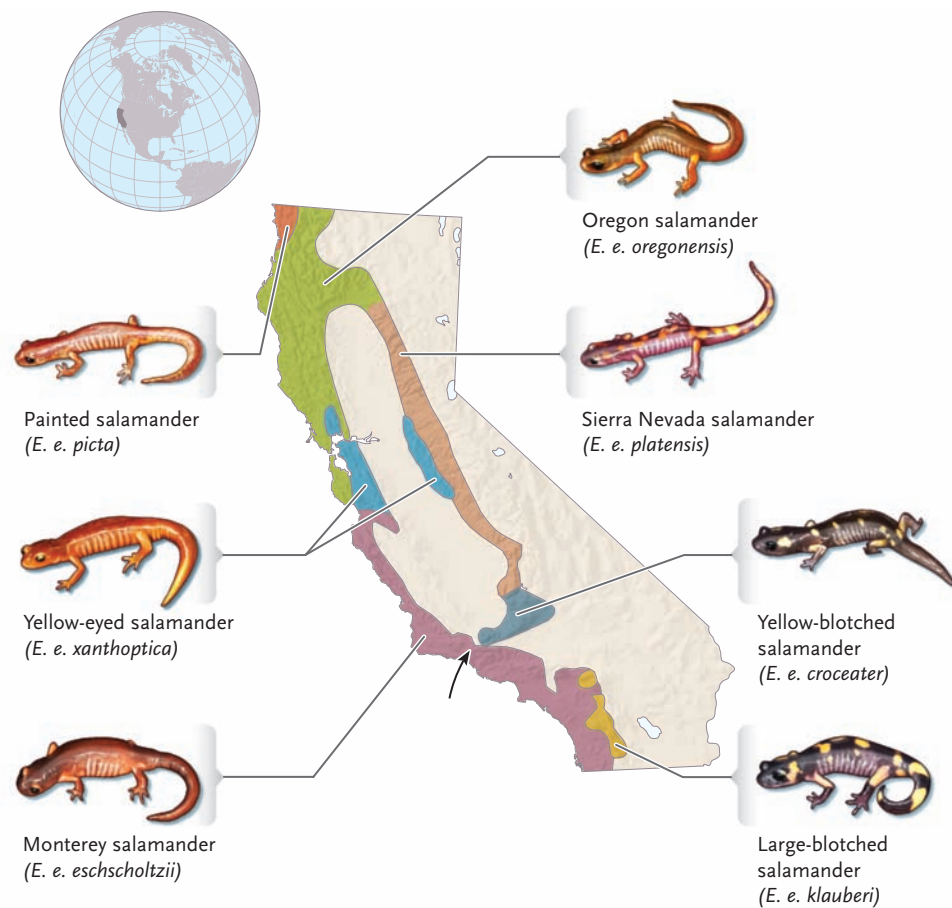


Figure 21.3 Subspecies. Five subspecies of rat snake (*Elaphe obsoleta*) in eastern North America differ in color and in the presence or absence of stripes or blotches.

Figure 21.4

Ring species. Six of the seven subspecies of the salamander *Ensatina eschscholtzii* are distributed in a ring around California's Central Valley. Subspecies often interbreed where their geographical distributions overlap. However, the two subspecies that nearly close the ring in the south (marked with an arrow), the Monterey salamander and the yellow-blotched salamander, rarely interbreed.



meet, and their offspring often exhibit intermediate phenotypes. Biologists sometimes use the word “race” as shorthand for the term “subspecies.”

Various patterns of geographical variation have provided great insight into the speciation process. Two of the best-studied patterns are *ring species* and *clinal variation*.

Ring Species. Some plant and animal species have a ring-shaped geographical distribution that surrounds uninhabitable terrain. Adjacent populations of these so-called **ring species** can exchange genetic material directly, but gene flow between distant populations occurs only through the intermediary populations.

The lungless salamander *Ensatina eschscholtzii*, an example of a ring species, is widely distributed in the coastal mountains and the Sierra Nevada of California, but it cannot survive in the hot, dry Central Valley (**Figure 21.4**). Seven subspecies differ in biochemical traits, color, size, and ecology. Individuals from adjacent subspecies often interbreed where their geographical distributions overlap, and intermediate phenotypes are fairly common. But at the southern end of the Central Valley, adjacent subspecies rarely interbreed. Apparently, they have differentiated to such an extent that they can no longer exchange genetic material directly.

Are the southernmost populations of this salamander subspecies or different species? A biologist who saw *only* the southern populations, which coexist without interbreeding, might define them as separate species. However, they still have the potential to exchange genetic material through the intervening populations that form the ring. Hence, biologists recognize these populations as belonging to the same species. Most likely, the southern subspecies are in an intermediate stage of species formation.

Clinal Variation. When a species is distributed over a large, environmentally diverse area, some traits may exhibit a **cline**, a pattern of smooth variation along a geographical gradient. Clinal variation usually results from gene flow between adjacent populations that are each adapting to slightly different conditions. For example, many birds and mammals in the northern hemisphere show clinal variation in body size (**Figure 21.5**) and the relative length of their appendages: in general, populations living in colder environments have larger bodies and shorter appendages, a pattern that is usually interpreted as a mechanism to conserve heat (see Chapter 46). If a cline extends over a large geographical gradient, populations at the opposite ends may be very different.

Despite the geographical variation that many species exhibit, most closely related species are genetically and morphologically different from each other. In the next section, we consider the mechanisms that maintain the genetic distinctness of closely related species by preventing their gene pools from mixing.

STUDY BREAK

1. How does the morphological species concept differ from the biological species concept?
2. What is clinal variation?

21.2 Maintaining Reproductive Isolation

Reproductive isolation is central to the biological species concept. A **reproductive isolating mechanism** is a biological characteristic that prevents the gene pools of two species from mixing. Biologists classify reproductive isolating mechanisms into two categories (summarized in **Table 21.1**): **prezygotic isolating mechanisms** exert their effects before the production of a zygote, or fertilized egg, and **postzygotic isolating mechanisms** operate after zygote formation. These isolating mechanisms are not mutually exclusive; two or more of them may operate simultaneously.

Prezygotic Isolating Mechanisms Prevent the Production of Hybrid Individuals

Biologists have identified five mechanisms that can prevent interspecific (between species) matings or fertilizations, and thus prevent the production of hybrid (mixed species) offspring. These five prezygotic mechanisms are *ecological*, *temporal*, *behavioral*, *mechanical*, and *gametic isolation*.

Species living in the same geographical region may experience **ecological isolation** if they live in different habitats. For example, lions and tigers were both common in India until the mid-nineteenth century, when hunters virtually exterminated the Asian lions. However, because lions live in open grasslands and tigers in dense forests, the two species did not encounter one another and did not interbreed. Lion-tiger hybrids are sometimes born in captivity, but do not occur under natural conditions.

Species living in the same habitat can experience **temporal isolation** if they mate at different times of day or different times of year. For example, the fruit flies *Drosophila persimilis* and *Drosophila pseudo-obscura* overlap extensively in their geographical distributions, but they do not interbreed, in part because *D. persimilis* mates in the morning and *D. pseudo-obscura* in the

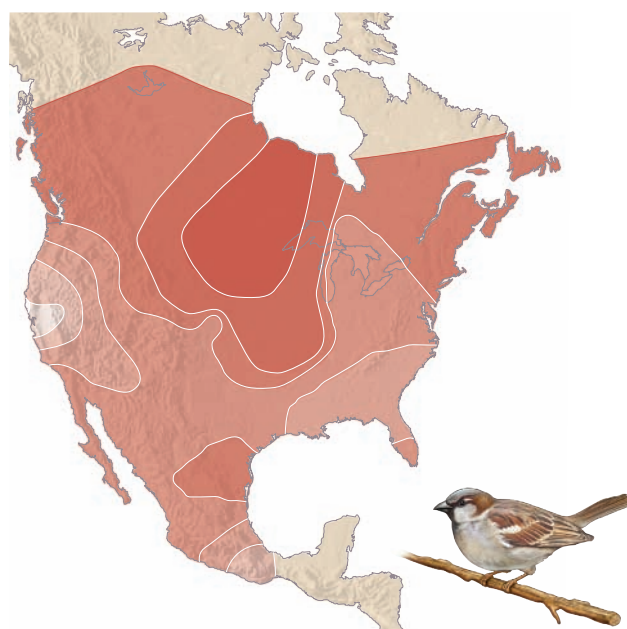
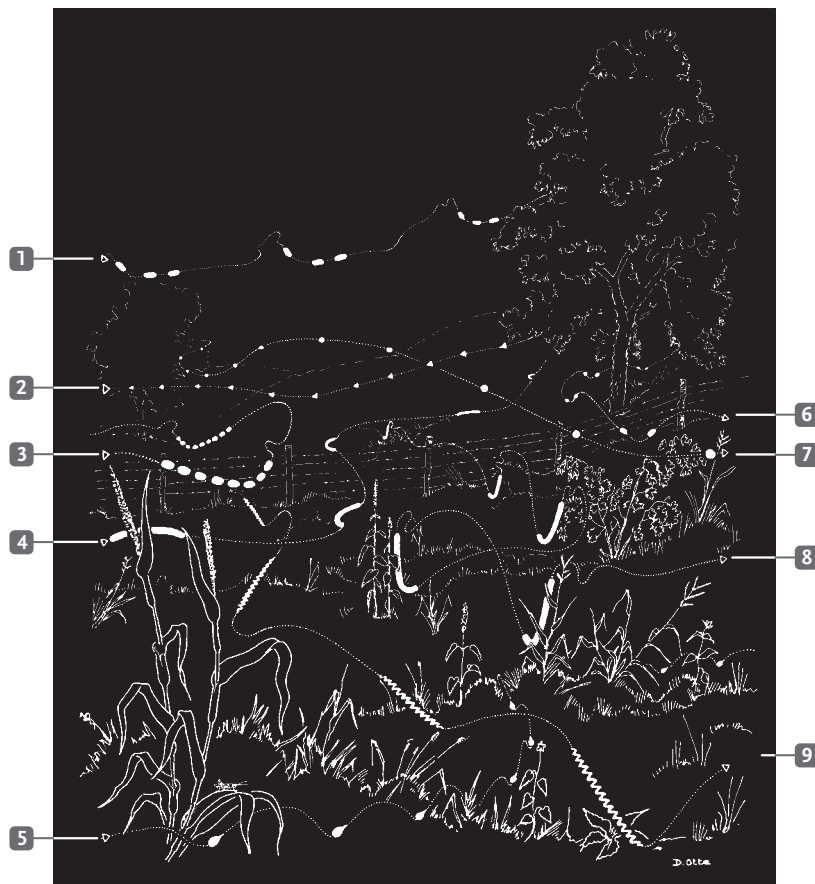


Figure 21.5
Clinal variation. House sparrows (*Passer domesticus*) exhibit clinal variation in overall body size, which was summarized from measurements of 16 skeletal features. Darker shading indicates larger size.

Table 21.1 Reproductive Isolating Mechanisms

Timing Relative to Fertilization	Mechanism	Mode of Action
Prezygotic (“pre mating”) mechanisms	Ecological isolation	Species live in different habitats
	Temporal isolation	Species breed at different times
	Behavioral isolation	Species cannot communicate
	Mechanical isolation	Species cannot physically mate
	Gametic isolation	Species have nonmatching receptors on gametes
Postzygotic (“post mating”) mechanisms	Hybrid inviability	Hybrid offspring do not complete development
	Hybrid sterility	Hybrid offspring cannot produce gametes
	Hybrid breakdown	Hybrid offspring have reduced survival or fertility



KEY

1 <i>P. consimilis</i>	4 <i>P. collustrans</i>	7 <i>P. ignitus</i>
2 <i>P. brimleyi</i>	5 <i>P. marginellus</i>	8 <i>P. pyralis</i>
3 <i>P. carolinus</i>	6 <i>P. consanguineus</i>	9 <i>P. granulatus</i>

Figure 21.6

Behavioral reproductive isolation. Male fireflies (*Photinus* species) use bioluminescent signals to attract potential mates. The different flight paths and flashing patterns of males in nine North American species are represented here. Females respond only to the display given by males of their own species.

(Courtesy of James E. Lloyd. Miscellaneous Publications of the Museum of Zoology of the University of Michigan, 130:1–195, 1966.)

afternoon. Two species of pine in California are reproductively isolated where their geographical distributions overlap: even though both rely on the wind to carry male gametes (pollen grains) to female gametes (ova) in other cones, *Pinus radiata* releases pollen in February and *Pinus muricata* releases pollen in April.

Many animals rely on specific signals, which often differ dramatically between species, to identify the species of a potential mate. **Behavioral isolation** results when the signals used by one species are not recognized by another. For example, female birds rely on the song, color, and displays of males to identify members of their own species. Similarly, female fireflies identify males by their flashing patterns (Figure 21.6). These behaviors (collectively called *courtship displays*) are often so complicated that signals sent by one species are like a foreign language that another species simply does not understand.

Mate choice by females and sexual selection (discussed in Section 20.3) generally drive the evolution of mate recognition signals. Females often spend substantial energy in reproduction, and choosing an appropriate mate—that is, a male of her own species—is critically important for the production of successful young. By contrast, a female that mates with a male from a different species is unlikely to leave any surviving offspring at all. Over time, the number of males with recognizable traits, as well as the number of females able to recognize the traits, increases in the population.

Differences in the structure of reproductive organs or other body parts—**mechanical isolation**—may prevent individuals of different species from interbreeding. In particular, many plants have anatomical features that allow only certain pollinators, usually particular bird or insect species, to collect and distribute pollen (see Chapter 27). For example, the flowers and nectar of two native California plants, the monkey-flowers *Mimulus lewisii* and *Mimulus cardinalis*, attract different animal pollinators (Figure 21.7). *Mimulus lewisii* is pollinated by bumblebees. It has shallow pink flowers with broad petals that provide a landing platform for the bees. Bright yellow streaks on the petals serve as “nectar guides,” directing bumblebees to the short nectar tube and reproductive parts, which are located among the petals. Bees enter the flowers to drink their concentrated nectar, and they pick up and deliver pollen as they brush against the reproductive parts of the flowers. *Mimulus cardinalis*, by contrast, is pollinated by hummingbirds. It has long red flowers with no yellow streaks, and the reproductive parts extend above the petals. The red color attracts hummingbirds but lies outside the color range detected by bumblebees. The nectar of *M. cardinalis* is more dilute than that of *M. lewisii* but is produced in much greater quantity, making it easier for hummingbirds to

Mimulus lewisii



Mimulus cardinalis



Figure 21.7

Mechanical reproductive isolation. Because of differences in floral structure, two species of monkey-flower attract different animal pollinators. *Mimulus lewisii* attracts bumblebees and *Mimulus cardinalis* attracts hummingbirds.

ingest. When a hummingbird visits *M. cardinalis* flowers, it pushes its long bill down the nectar tube, and its forehead touches the reproductive parts, picking up and delivering pollen. Recent research has demonstrated that where the two monkey-flower species grow side-by-side, animal pollinators restrict their visits to either one species or the other 98% of the time, providing nearly complete reproductive isolation.

Even when individuals of different species mate, **gametic isolation**, an incompatibility between the sperm of one species and the eggs of another, may prevent fertilization. Many marine invertebrates release gametes into the environment for external fertilization. The sperm and eggs of each species recognize one another's complementary surface proteins (see Chapter 47), but the surface proteins on the gametes of different species don't match. In animals with internal fertilization, sperm of one species may not survive and function within the reproductive tract of another. Interspecific matings between some *Drosophila* species, for example, induce a reaction in the female's reproductive tract that blocks "foreign" sperm from reaching eggs. Parallel physiological incompatibilities between a pollen tube and a stigma prevent interspecific fertilization in some plants.

Postzygotic Isolating Mechanisms Reduce the Success of Hybrid Individuals

If prezygotic isolating mechanisms between two closely related species are incomplete or ineffective, sperm from one species sometimes fertilizes an egg of the other species. In such cases the two species will be reproductively isolated if their offspring, called interspecific (between species) hybrids, have lower fitness than those produced by intraspecific (within species) matings. Three postzygotic isolating mechanisms—*hybrid inviability*, *hybrid sterility*, and *hybrid breakdown*—can reduce the fitness of hybrid individuals.

Many genes govern the complex processes that transform a zygote into a mature organism. Hybrid individuals have two sets of developmental instructions, one from each parent species, which may not interact properly for the successful completion of embryonic development. As a result, hybrid organisms frequently die as embryos or at an early age, a phenomenon called **hybrid inviability**. For example, domestic sheep and goats can mate and fertilize one another's ova, but the hybrid embryos always die before coming to term, presumably because the developmental programs of the two parent species are incompatible.

Although some hybrids between closely related species develop into healthy and vigorous adults, they may not produce functional gametes. This **hybrid sterility** often results when the parent species differ in the number or structure of their chromosomes, which cannot pair properly during meiosis. Such hybrids have zero fitness because they leave no descendants. The most familiar example is a mule, the product of mating be-



Figure 21.8
Interspecific hybrids. Horses and zebroids (hybrid offspring of horses and zebras) run in a mixed herd. Zebroids are usually sterile.

tween a female horse ($2n = 64$) and a male donkey ($2n = 62$). Zebroids, the offspring of matings between horses and zebras, are also usually sterile (**Figure 21.8**).

Some first-generation hybrids (F_1 ; see Section 12.1) are healthy and fully fertile. They can breed with other hybrids and with both parental species. However, the second generation (F_2), produced by matings between F_1 hybrids, or between F_1 hybrids and either parental species, may exhibit reduced survival or fertility, a phenomenon known as **hybrid breakdown**. For example, experimental crosses between *Drosophila* species may produce functional hybrids, but their offspring experience a high rate of chromosomal abnormalities and harmful types of genetic recombination. Thus, reproductive isolation is maintained between the species because there is little long-term mixing of their gene pools.

STUDY BREAK

1. What is the difference between prezygotic and postzygotic isolating mechanisms?
2. When a male duck of one species performed a courtship display to a female of another species, she interpreted his behavior as aggressive rather than amorous. What type of reproductive isolating mechanism does this scenario illustrate?

21.3 The Geography of Speciation

As Ernst Mayr recognized, geography has a huge impact on whether gene pools have the opportunity to mix. Biologists define three modes of speciation, based on the geographical relationship of populations as they become

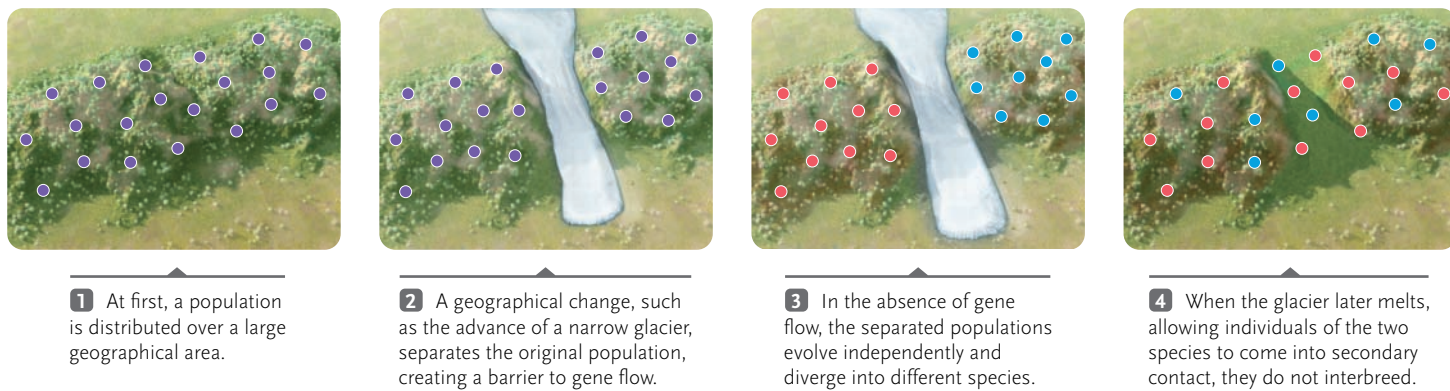


Figure 21.9
The model of allopatric speciation and secondary contact.

reproductively isolated: *allopatric speciation* (*allo* = different; *patria* = homeland), *parapatric speciation* (*para* = beside), and *sympatric speciation* (*sym* = together).

Allopatric Speciation Occurs between Geographically Separated Populations

Allopatric speciation may take place when a physical barrier subdivides a large population or when a small population becomes separated from a species' main geographical distribution. Probably the most common mode of speciation in large animals, allopatric speciation occurs in two stages. First, two populations become *geographically* separated, preventing gene flow between them. Then, as the populations experience distinct mutations as well as different patterns of natural selection and genetic drift, they may accumulate genetic differences that isolate them *reproductively*.

Geographical separation sometimes occurs when a barrier divides a large population into two or more units (**Figure 21.9**). For example, hurricanes may create new channels that divide low coastal islands and the populations inhabiting them. Uplifting mountains or landmasses as well as advancing glaciers can also pro-

duce barriers that subdivide populations. The uplift of the Isthmus of Panama, caused by movements of Earth's crust about five million years ago (see the *Focus on Research* in Chapter 22), separated a once-continuous shallow sea into the eastern tropical Pacific Ocean and the western tropical Atlantic Ocean. Populations of marine organisms were subdivided by this event, and pairs of closely related species now live on either side of this divide (**Figure 21.10**).

In other cases, small populations may become isolated at the edge of a species' geographical distribution. Such peripheral populations often differ genetically from the central population because they are adapted to somewhat different environments. Once a small population is isolated, genetic drift and natural selection as well as limited gene flow from the parent population foster further genetic differentiation. In time, the accumulated genetic differences may lead to reproductive isolation.

Populations on oceanic islands represent extreme examples of this phenomenon. Founder effects, an example of genetic drift (see Section 20.3), make the populations genetically distinct. And on oceanic archipelagos, such as the Galápagos and Hawaiian islands, individuals from one island may colonize nearby islands, found-

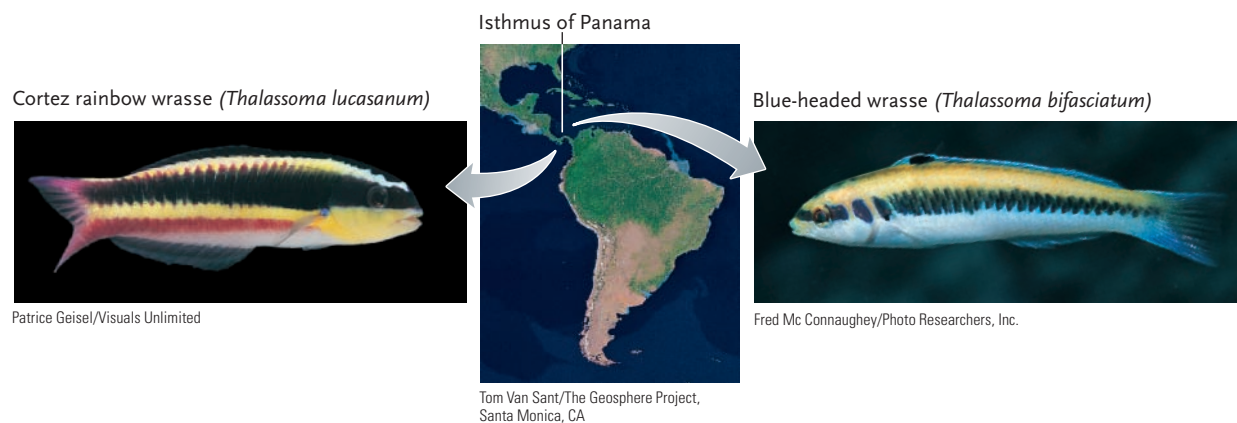


Figure 21.10
Geographical separation. The uplift of the Isthmus of Panama divided an ancestral wrasse population. The Cortez rainbow wrasse now occupies the eastern Pacific Ocean, and the blue-headed wrasse now occupies the western Atlantic Ocean.

ing populations that differentiate into distinct species. Each island may experience multiple invasions, and the process may be repeated many times within the archipelago, leading to the evolution of a **species cluster**, a group of closely related species recently descended from a common ancestor (**Figure 21.11**). The nearly 800 species of fruit flies on the Hawaiian Islands, described in *Focus on Research*, form several species clusters.

Sometimes, allopatric populations reestablish contact when a geographical barrier is eliminated or breached (see Figure 21.9, step 4). This *secondary contact* provides a test of whether or not the populations have diverged into separate species. If their gene pools did not differentiate much during geographical separation, the populations will interbreed and merge. But if the populations have differentiated enough to be reproductively isolated, they have become separate species.

During the early stages of secondary contact, prezygotic reproductive isolation may be incomplete. Some members of each population may mate with individuals from the other, producing viable, fertile offspring, in areas called **hybrid zones**. Although some hybrid zones have persisted for hundreds or thousands of years (**Figure 21.12**), they are generally narrow, and ecological or geographical factors maintain the separation of the gene pools for the majority of individuals in both species.

If hybrid offspring have lower fitness than those produced within each population, natural selection will favor individuals that mate only with members of their own population. Recent studies of *Drosophila* suggest that this phenomenon, called **reinforcement**, enhances reproductive isolation that had begun to develop while the populations were geographically separated. Thus, natural selection may promote the evolution of prezygotic isolating mechanisms.

Parapatric Speciation May Occur between Adjacent Populations

Sometimes a single species is distributed across a discontinuity in environmental conditions, such as a major change in soil type. Although organisms on one side of the discontinuity may interbreed freely with those on the other side, natural selection may favor different alleles on either side, limiting gene flow. In such cases, **parapatric speciation**—speciation arising between adjacent populations—may occur if hybrid offspring have low relative fitness.

Some strains of bent grass (*Agrostis tenuis*), a common pasture plant in Great Britain, have the physiological ability to grow on mine tailings where the soil is heavily polluted by copper or other metals. Plants of the copper-tolerant strains grow well on polluted soils, but plants of the pasture strain do not. Conversely, copper-tolerant plants don't survive as well as pasture plants on unpolluted soils. These strains often grow within a few meters of each other where polluted and unpolluted soils form an intricate mosaic. Because

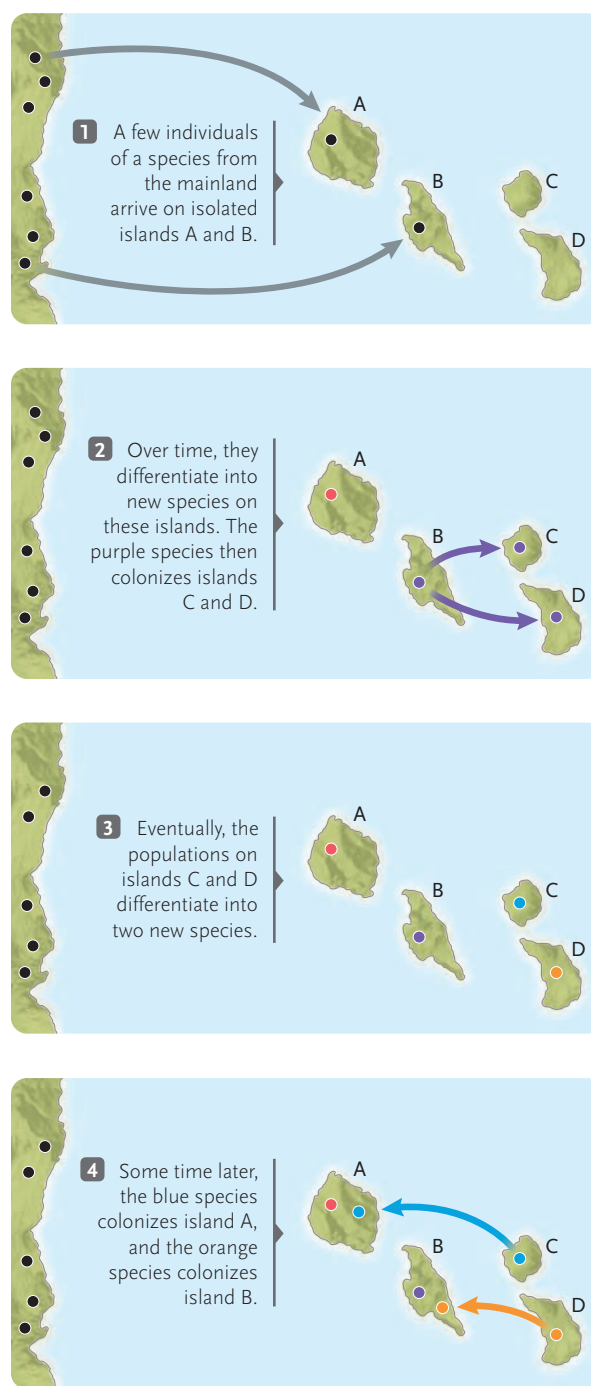


Figure 21.11

Evolution of a species cluster on an archipelago. Letters identify four islands in a hypothetical archipelago, and colored dots represent different species. The ancestor of all the species is represented by black dots on the mainland. At the end of the process, islands A and B are each occupied by two species, and islands C and D are each occupied by one species, all of which evolved on the islands.

bent grass is wind-pollinated, pollen is readily transferred from one strain to another.

Thomas McNeilly and Janis Antonovics of University College of North Wales crossed these strains in the laboratory and determined that they are still fully interfertile. However, copper-tolerant plants flower about one week earlier than nearby pasture plants, which promotes prezygotic (temporal) isola-

FOCUS ON RESEARCH

Basic Research: Speciation in Hawaiian Fruit Flies

After Darwin published his analyses of island species, evolutionary biologists realized that oceanic archipelagos provide “natural laboratories” for studies of speciation. The islands of the Hawaiian archipelago have been geographically isolated throughout their history, lying at least 3200 km (1900 miles) from the nearest continents or other islands (**Figure a**). They were built by undersea volcanic eruptions over hundreds of thousands of years and emerged from the sea from northwest to southeast: Kauai is at least 5 million years old, and Hawaii, the “Big Island,” is less than 1 million years old. Individual islands differ in maximum elevation and include a wide range of habitats, from dry zones of sparse vegetation to wet tracts of lush forest.

Resident species must have arrived from distant mainland localities or evolved on the islands from colonizing ancestors. The islands’ isolation, differ-

ent ages, and geographical and ecological complexity provide environmental conditions that foster repeated interisland colonizations followed by allopatric speciation events. Thus, it is not surprising that species clusters have evolved in several groups of organisms (including flowering plants, insects, and birds).

Nearly 800 species of fruit flies have been identified on the archipelago, and most species live on only one island. Biologists used many characters to identify the different fruit fly species, including external and internal anatomy, cell structure, chromosome structure, ecology, and mating behavior. Their data suggest that the vast majority of native Hawaiian species arose from one ancestral species that colonized the archipelago long ago, probably from eastern Asia. After repeated speciation events, the fruit flies of the Hawaiian Islands represent more than 25% of all known fruit fly species.

Hampton Carson, now of the University of Hawaii, has spearheaded studies on the evolutionary relationships of Hawaiian fruit flies. He and his colleagues have gathered data on hundreds of fly species—a daunting task. Most species are sexually dimorphic. Although the females of different species may be similar in appearance, the males of even closely related species differ in virtually every aspect of their external anatomy: body size, head shape, and the structure of their eyes, antennae, mouthparts, bristles, legs, and wings. Their mating behavior and choice of mating sites also vary dramatically.

Nevertheless, closely related species on different islands occupy comparable habitats and associate with related plant species. Carson suggests that speciation in these flies resulted from the evolution of different genetically determined *mating systems*, the behaviors and sexual characteristics that males display when seeking a mate. The mating systems serve as prezygotic isolating mechanisms.

The 100 or more species of “picture-wing” *Drosophila*, relatively large flies with patterns on their wings, illustrate the evolution of a species cluster. Carson and his colleagues used similarities and differences in the banding patterns on

the flies’ giant salivary chromosomes (described in the *Focus on Research* in Chapter 13), to trace the evolutionary origin of species on the younger islands by identifying their closest relatives on the older islands. Their analysis of 26 species on Hawaii, the youngest island, suggests that flies from the older islands colonized Hawaii at least 19 different times, and each founder population evolved into a new species there. Additional species apparently evolved when lava flows on Hawaii subdivided existing populations.

Among the picture-wing fruit flies, some interspecies matings result in hybrid sterility or hybrid breakdown. But for the majority of species, prezygotic reproductive isolation is maintained by differences in their mating systems. For example, *Drosophila silvestris* and *Drosophila heteroneura*, which produce healthy and fertile hybrids in the laboratory, have similar geographical distributions; however, differences in courtship behavior and in the shape of the males’ heads, a characteristic that females use to recognize males of their own species (**Figure b**), keep these two species reproductively isolated. In nature, they hybridize only in one small geographical area.

The work of Carson and his colleagues suggests that most speciation in Hawaiian *Drosophila* has resulted from founder effects. When a fertile female—or a small group of males and females—moves to a new island, this founding population responds to novel selection pressures in its new environment. Sexual selection then exaggerates distinctive morphological and behavioral characteristics, maintaining the population’s reproductive isolation from its new neighbors. The tremendous variety of Hawaiian fruit flies has undoubtedly been produced by repeated colonizations of newer islands by flies from older islands and by the back-colonization of older islands by newly evolved species. Thus, they represent what evolutionary biologists describe as an *adaptive radiation*, a cluster of closely related species that are ecologically different (as described further in Chapter 22).

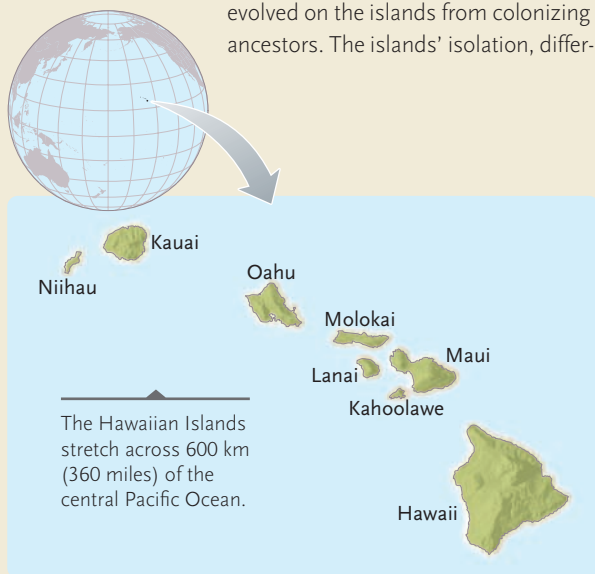
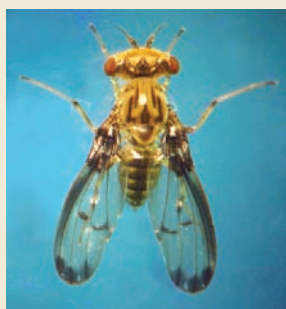


Figure a
The Hawaiian Islands

Drosophila heteroneura



Drosophila silvestris

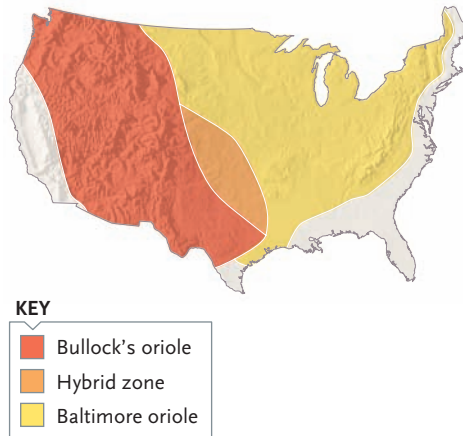


Figure b
Two *Drosophila* species in which the males’ head shapes differ.

Bullock's oriole



© H. Clarke/VIREO/Academy of Natural Sciences



Baltimore oriole



Robert C. Simpson/Nature Stock

Figure 21.12

Hybrid zones. Males of the Baltimore oriole (*Icterus galbula*) and Bullock's oriole (*Icterus bullockii*) differ in color and courtship song. The populations have maintained a hybrid zone for hundreds of years, and once were considered subspecies of the same species. The American Ornithologists' Union recognized them as separate species in 1997. They now hybridize less frequently than they once did, leading some researchers to suggest that their reproductive isolation evolved recently.

tion of the two strains (**Figure 21.13**). If the flowering times become further separated, the two strains may attain complete reproductive isolation and become separate species.

Some biologists argue that the places where parapatric populations of bent grass interbreed are really hybrid zones where allopatric populations have established secondary contact. Unfortunately, there is no way to determine whether the hybridizing populations were parapatric or allopatric in the past. Thus, a thorough evaluation of the parapatric speciation hypothesis must await the development of techniques that enable biologists to distinguish clearly between the products of allopatric and parapatric speciation.

Sympatric Speciation Occurs within One Continuously Distributed Population

In **sympatric speciation**, reproductive isolation evolves between distinct subgroups that arise within one population. Models of sympatric speciation do not require that the populations be either geographically or environmentally separated as their gene pools diverge. We examine below general models of sympatric speciation in animals and plants; the genetic basis of sympatric speciation is one of the topics we consider in the next section.

Insects that feed on just one or two plant species are among the animals most likely to evolve by sympatric speciation. These insects generally carry out most important life cycle activities on or near their “host” plants. Adults mate on the host plant; females lay their eggs on it; and larvae feed on the host plant's tissues, eventually developing into adults, which initiate another round of the life cycle. Host plant choice is

genetically determined in many insect species. In others, individuals associate with the host plant species they ate as larvae.

Theoretically, a genetic mutation could suddenly change some insects' choice of host plant. Mutant individuals would shift their life cycle activities to the new host, and then interact primarily with others preferring the same new host, an example of ecological isolation. These individuals would collectively form a separate subpopulation, called a **host race**. Reproductive isolation could evolve between different host races if the individuals of each host race are more likely to mate with members of their own host race than with members of another. Some biologists criticize this model, however, because it assumes that the genes controlling two traits, the insects' host plant choice and their mating preferences, change simultaneously. Moreover, host plant choice is controlled by multiple gene loci in some insect species, and it is clearly influenced by prior experience in others.

The apple maggot (*Rhagoletis pomonella*) is the most thoroughly studied example of possible sympatric speciation in animals (**Figure 21.14**). This fly's natural host plant in eastern North America is the hawthorn (*Crataegus* species), but at least two host races have appeared in little more than 100 years. The larvae of a new host race were first discovered feeding on apples in New York state in the 1860s. In the 1960s, a cherry-feeding host race appeared in Wisconsin.

Recent research has shown that variations at just a few gene loci underlie differences in the feeding preferences of *Rhagoletis* host races; other genetic differences cause the host races to develop at different rates. Moreover, adults of the three races mate during different summer months. Nevertheless, individuals

Figure 21.13 Observational Research

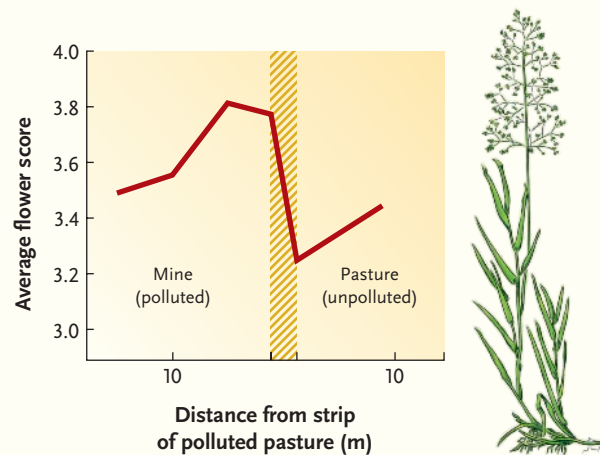
Evidence for Reproductive Isolation in Bent Grass

QUESTION: Do adjacent populations of bent grass (*Agrostis tenuis*) living on different soil types exhibit any signs of reproductive isolation?

HYPOTHESIS: McNeilly and Antonovics hypothesized that adjacent populations of bent grass flowered at slightly different times, which could foster prezygotic reproductive isolation between them.

METHODS: On a late summer day in 1965, the researchers compared the flowers of bent grass growing on polluted soil at a copper mine with those of plants growing on unpolluted soil in a nearby pasture. A meter-wide stretch of polluted pasture (indicated by cross-hatching) formed a boundary between the two populations. Researchers assigned a score to every flower, with immature flowers scored as 3 and mature flowers as 4.

RESULTS: On the day that they were surveyed, flowers of the copper-tolerant plants had higher scores, indicating that they were more mature—and thus would complete pollination earlier—than the flowers of the pasture plants.



CONCLUSION: Because adjacent populations of bent grass flower at slightly different times, temporal reproductive isolation may be developing between them.

show no particular preference for mates of their own host race, at least under simplified laboratory conditions. Thus, although behavioral isolation has not developed between races, ecological and temporal isolation may separate adults in nature. Researchers are still not certain that the different host races are reproductively isolated under natural conditions.

Sympatric speciation often occurs in plants through a genetic phenomenon, **polyploidy**, in which an individual receives one or more *extra* copies of the entire haploid complement of chromosomes (see Section 13.3). As we explain in the next section, polyploidy can lead to speciation because these large-scale genetic changes may prevent polyploid individuals from breed-



Jim Smith, Michigan State University

Figure 21.14

Sympatric speciation in animals. Male and female apple maggots (*Rhagoletis pomonella*) court on a hawthorn leaf. The female will later lay her eggs on the fruit, and the offspring will feed, mate, and lay their eggs on hawthorns as well.

ing with individuals of the parent species. Nearly half of all flowering plant species are polyploid, including many important crops and ornamental species. The genetic mechanisms that produce polyploid individuals in plant populations are well understood; we describe them in detail as part of a larger discussion of the genetics of speciation.

STUDY BREAK

1. What are the two stages required for allopatric speciation?
2. What factor appears to promote parapatric speciation in bent grass?
3. Why might insects from different host races be unlikely to mate with each other?

21.4 Genetic Mechanisms of Speciation

What genetic changes lead to reproductive isolation between populations, and how do these changes arise? In this section we examine three genetic mechanisms that can lead to reproductive isolation: *genetic divergence* between allopatric populations, *polyploidy* in sympatric populations, and *chromosome alterations*, which occur independently of the geographical distributions of populations.

Genetic Divergence in Allopatric Populations Can Lead to Speciation

In the absence of gene flow, geographically separated populations inevitably accumulate genetic differences. Most postzygotic isolating mechanisms probably develop as accidental by-products of mutation, genetic



INSIGHTS FROM THE MOLECULAR REVOLUTION

Monkey-Flower Speciation

Reproductive isolation is the primary criterion that biologists use to distinguish species. A molecular study by H. D. Bradshaw and his coworkers at the University of Washington indicates that the amount of genetic change required to establish reproductive isolation, and thus new species, may be surprisingly small in some cases.

These scientists studied two monkey-flower species, *Mimulus lewisii* and *Mimulus cardinalis*, that experience mechanical reproductive isolation because differences in flower structure keep bumblebees or hummingbirds from carrying pollen from one species to the other (see Figure 21.7). Although these species do not hybridize in nature, they are easily crossed in the laboratory and produce fertile hybrids. The F₂ offspring of the laboratory crosses have flowers with various forms intermediate between the parental *lewisii* and *cardinalis* types, indicating that several gene loci control the traits separating the species. But how many?

Relatively little is known about the genetics of the two monkey-flower spe-

cies, so a direct genetic analysis of their hereditary differences was impractical. Instead, the investigators studied 153 randomly chosen DNA sequences distributed throughout the haploid number of eight chromosomes in the two species. They correlated the distribution of these sequences with the distribution of flower traits in 93 plants of the F₂ generation. Some of the DNA sequences segregated so closely with a particular trait, such as yellow pigment, that they are almost certainly located near that trait in the chromosomes. Because the sequences can pair with complementary DNA in the chromosomes, the investigators used them as “probes” to find the sites in the chromosomes from which they originated. From the close linkage of the sequences to the traits, the investigators could estimate the positions and approximate number of genes that establish reproductive isolation.

Their results indicate that reproductive isolation of *M. lewisii* and *M. cardinalis* results from differences

in eight floral traits—the amount of (1) anthocyanin pigments and (2) carotenoid pigments in petals; (3) flower width; (4) petal width; (5) nectar volume; (6) nectar concentration; and the lengths of the stalks supporting the (7) male and (8) female reproductive parts. Although the investigators could not directly determine the number of genes controlling each trait, the characteristics of the traits, their locations at eight sites on six of the chromosomes, and their pattern of inheritance make it most likely that each trait is controlled by a single gene, giving a likely minimum of eight genes. Thus mutations in as few as eight genes may have established reproductive isolation and speciation in the monkey-flowers.

This research was the first in which random differences in DNA sequences were used to answer the fundamental evolutionary question of how much genetic change is needed to produce a new species.

drift, and natural selection. Note, however, that natural selection cannot promote the evolution of reproductive isolating mechanisms between *allopatric* populations directly: individuals in such populations do not encounter one another and therefore have no opportunity to produce hybrid offspring. And if there are no hybrid offspring, natural selection cannot select against the matings that would have produced them. Nevertheless, natural selection may sometimes foster adaptive changes that create postzygotic reproductive isolation between populations when they later reestablish contact. And, if postzygotic isolating mechanisms reduce the fitness of hybrid offspring, natural selection can reinforce the evolution of prezygotic isolating mechanisms.

How much genetic divergence is necessary for speciation to occur? To understand the genetic basis of speciation in closely related species, researchers first identify the specific causes of reproductive isolation. They then use standard techniques of genetic analysis along with new molecular approaches such as gene mapping and sequencing to analyze the genetic mechanisms that establish reproductive isolation. As explained in *Insights from the Molecular Revolution*, these

techniques now allow researchers to determine the minimum number of genes responsible for reproductive isolation in particular pairs of species.

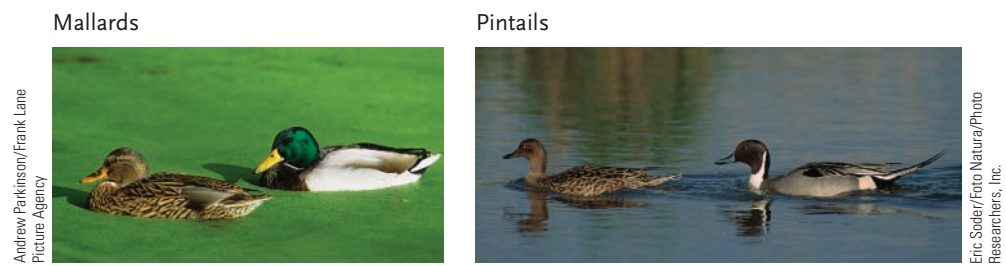
In cases of postzygotic reproductive isolation, mutations in at least a few gene loci establish reproductive isolation. For example, if two common aquarium fishes, swordtails (*Xiphophorus helleri*) and platys (*Xiphophorus maculatus*), mate, two genes induce the development of lethal tumors in their hybrid offspring. When hybrid sterility is the primary cause of reproductive isolation between *Drosophila* species, at least 5 gene loci are responsible. About 55 gene loci contribute to postzygotic reproductive isolation between the toads *Bombina bombina* and *Bombina variegata*.

In cases of prezygotic reproductive isolation, some mechanisms have a surprisingly simple genetic basis. For example, a single mutation reverses the direction of coiling in the shells of some snail species. Snails with shells that coil in opposite directions cannot approach each other closely enough to mate, making reproduction between them mechanically impossible.

Many traits that now function as prezygotic isolating mechanisms may originally have evolved in response to sexual selection (described in Section 20.3).

Figure 21.15

Sexual selection and prezygotic isolation. In closely related species, such as mallard ducks (*Anas platyrhynchos*) and pintails (*Anas acuta*), males have much more distinctive coloration than females, a sure sign of sexual selection at work.



This evolutionary process exaggerates showy structures and courtship behaviors in males, the traits that females use to identify appropriate mates. When two species encounter one another on secondary contact, these traits may also prevent interspecific mating. For example, many closely related duck species exhibit dramatic variation in the appearance of males, but not females (**Figure 21.15**), an almost certain sign of sexual selection. Yet these species hybridize readily in captivity, producing offspring that are both viable and fertile. Speciation in these birds probably resulted from geographical isolation and sexual selection without significant genetic divergence: only a few morphological and behavioral characters are responsible for their reproductive isolation. Thus, sometimes the evolution of reproductive isolation may not require much genetic change at all.

Ployploidy Is a Common Mechanism of Sympatric Speciation in Plants

Ployploidy is common among plants, and it may be an important factor in the evolution of some fish, amphibian, and reptile species. Polyploid individuals can arise

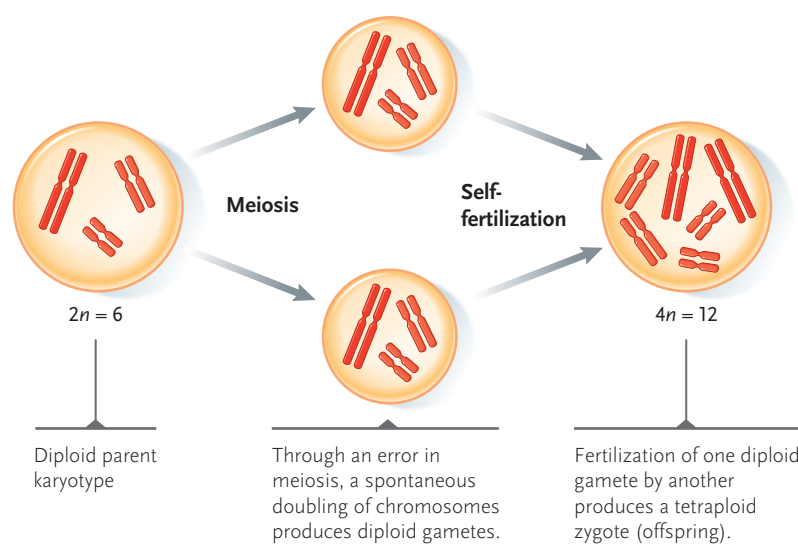


Figure 21.16

Speciation by autopolyploidy in plants. A spontaneous doubling of chromosomes during meiosis produces diploid gametes. If the plant fertilizes itself, a tetraploid zygote will be produced.

from chromosome duplications within a single species (autopolyploidy) or through hybridization of different species (allopolyploidy).

Autopolyploidy. In autopolyploidy (**Figure 21.16**), a diploid ($2n$) individual may produce, for example, tetraploid ($4n$) offspring, each of which has four complete chromosome sets. Autopolyploidy often results when gametes, through an error in either mitosis or meiosis, spontaneously receive the same number of chromosomes as a somatic cell. Such gametes are called **unreduced gametes** because their chromosome number has not been reduced compared with that of somatic cells.

Diploid pollen can fertilize the diploid ovules of a self-fertilizing individual, or it may fertilize diploid ovules on another plant with unreduced gametes. The resulting tetraploid offspring can reproduce either by self-pollination or by breeding with other tetraploid individuals. However, a tetraploid plant cannot produce fertile offspring by hybridizing with its diploid parents. The fusion of a diploid gamete with a normal haploid gamete produces a triploid ($3n$) offspring, which is usually sterile because its odd number of chromosomes cannot segregate properly during meiosis. Thus, the tetraploid is reproductively isolated from the original diploid population. Many species of grasses, shrubs, and ornamental plants, including violets, chrysanthemums, and nasturtiums, are autopolyploids, having anywhere from four to 20 complete chromosome sets.

Allopolyploidy. In allopolyploidy (**Figure 21.17**), two closely related species hybridize and subsequently form polyploid offspring. Hybrid offspring are sterile if the two parent species have diverged enough that their chromosomes do not pair properly during meiosis. However, if the hybrid's chromosome number is doubled, the chromosome complement of the gametes is also doubled, producing homologous chromosomes that *can* pair during meiosis. The hybrid can then produce polyploid gametes and, through self-fertilization or fertilization with other doubled hybrids, establish a population of a new polyploid species. Compared with speciation by genetic divergence, speciation by allopolyploidy is extremely rapid, causing a new species to arise in one generation without geographical isolation.

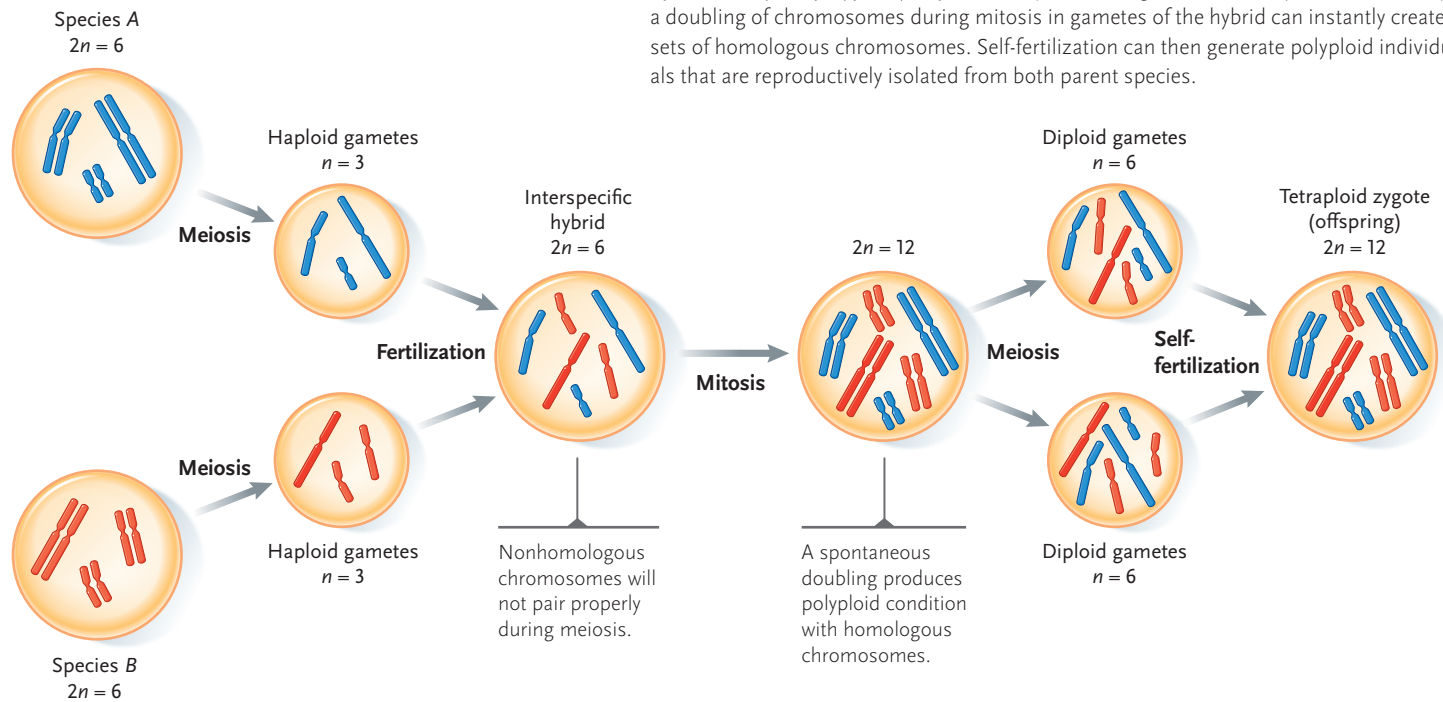


Figure 21.17

Speciation by allopolyploidy in plants. A hybrid mating between two species followed by a doubling of chromosomes during mitosis in gametes of the hybrid can instantly create sets of homologous chromosomes. Self-fertilization can then generate polyploid individuals that are reproductively isolated from both parent species.

Even when sterile, polyploids are often robust, growing larger than either parent species. For that reason, both autopolyploids and allopolyploids have been important to agriculture. For example, the wheat used to make flour (*Triticum aestivum*) has six sets of

chromosomes (**Figure 21.18**). Other polyploid crop plants include plantains (cooking bananas), coffee, cotton, potatoes, sugarcane, and tobacco.

Plant breeders often try to increase the probability of forming an allopolyploid by using chemicals that

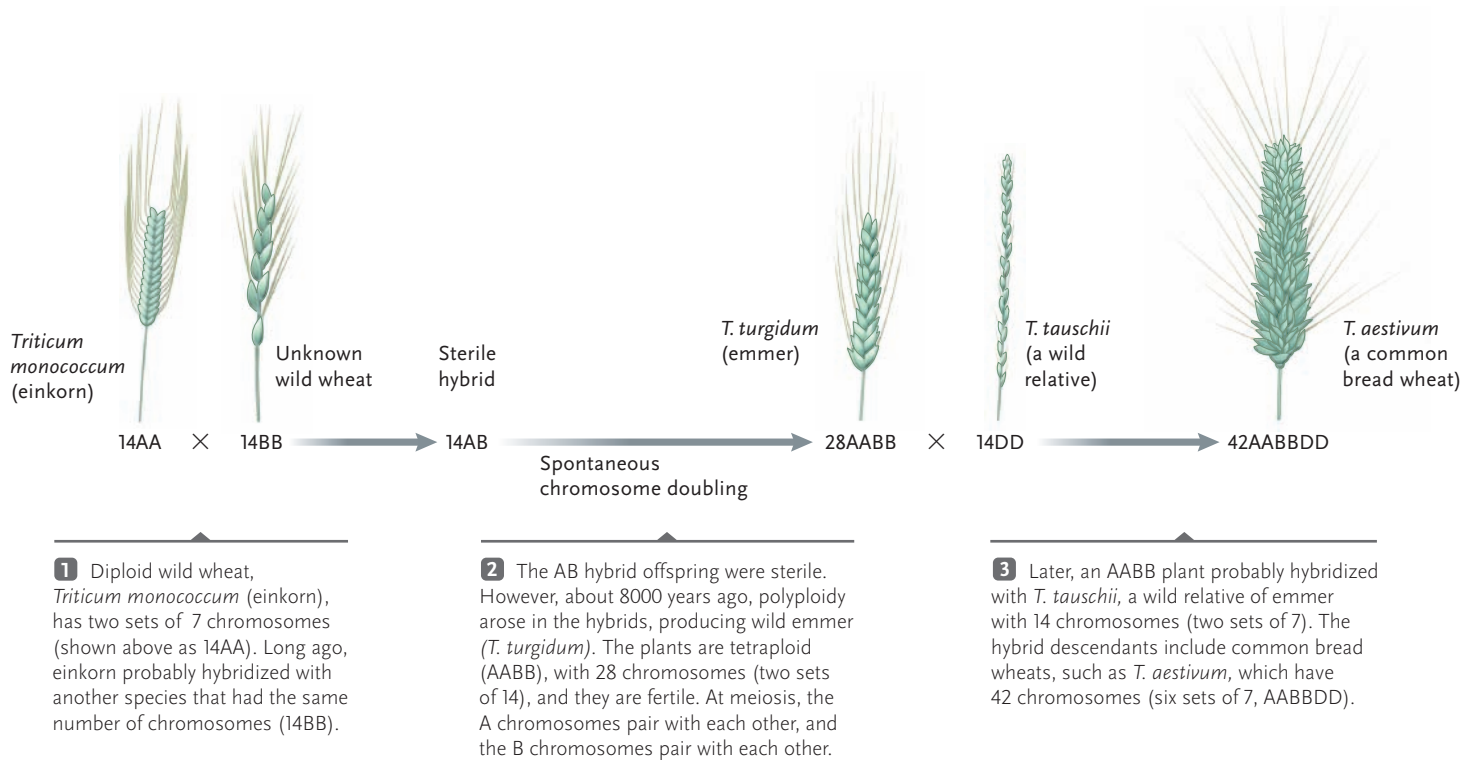


Figure 21.18

The evolution of wheat (*Triticum*). Cultivated wheat grains more than 11,000 years old have been found in the Eastern Mediterranean region. Researchers believe that speciation in wheat occurred through hybridization and polyploidy.

Figure 21.19 Observational Research

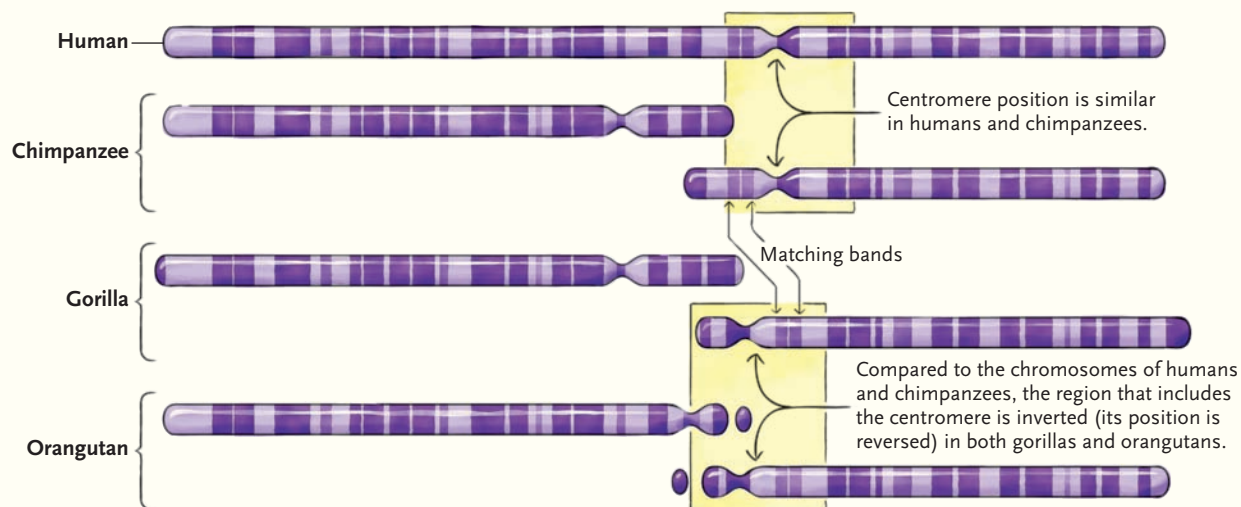
Chromosomal Similarities and Differences among the Great Apes

QUESTION: Does chromosome structure differ between humans and their closest relatives among the great apes?

HYPOTHESIS: Yunis and Prakash hypothesized that chromosome structure would differ markedly between humans and their close relatives among the apes: chimpanzees, gorillas, and orangutans.

METHODS: The researchers used Giemsa stain to visualize the banding patterns on metaphase chromosome preparations from humans, chimpanzees, gorillas, and orangutans. By matching the banding patterns on the chromosomes, the researchers verified that they were comparing the same segments of the genomes in the four species. They then searched for similarities and differences in the structure of the chromosomes.

RESULTS: The analysis of human chromosome 2 reveals that it was produced by the fusion of two smaller chromosomes that are still present in the other three species. Although the position of the centromere in human chromosome 2 matches that of the centromere in one of the chimpanzee chromosomes, in gorillas and orangutans it falls within an inverted segment of the chromosome.



CONCLUSION: Differences in chromosome structure between humans and both gorillas and orangutans are more pronounced than they are between humans and chimpanzees. Structural differences in the chromosomes of these four species may contribute to their reproductive isolation.

foster nondisjunction of chromosomes during mitosis. In the first such experiment, undertaken in the 1920s, scientists crossed a radish and a cabbage, hoping to develop a plant with both edible roots and leaves. Instead, the new species, *Raphanobrassica*, combined the least desirable characteristics of each parent, growing a cabbagelike root and radishlike leaves. Recent experiments have been more successful. For example, plant scientists have produced an allopolyploid grain, triticale, that has the disease-resistance of its rye parent and the high productivity of its wheat parent.

Chromosome Alterations Can Foster Speciation

Other changes in chromosome structure or number may also foster speciation. Closely related species often have a substantial number of chromosome differences between them, including inversions, translocations, deletions, and duplications (described in Section 13.3). These differences may foster postzygotic isolation.

In 1982, Jorge J. Yunis and Om Prakash of the University of Minnesota Medical School compared the

chromosome structures of humans and their closest relatives among the apes—chimpanzees, gorillas, and orangutans—by examining the *banding patterns* in stained chromosome preparations. In all species, banding patterns vary from one chromosome segment to another. When researchers find identical banding patterns in chromosome segments from two or more related species, they know that they are examining comparable portions of the species' genomes. Thus, the banding patterns allow scientists to identify specific chromosome segments and compare their positions in the chromosomes of different species.

Nearly all of the 1000 bands that Yunis and Prakash identified are present in humans and in the three ape species. However, the banding patterns revealed that whole sections of chromosomes have been rearranged over evolutionary time (**Figure 21.19**). For example, humans have a diploid chromosome complement of 46 chromosomes, whereas chimpanzees, gorillas, and orangutans have 48. The difference can be traced to the fusion (that is, the joining together) of two ancestral

chromosomes into chromosome 2 of humans; the ancestral chromosomes are separate in the other three species.

Moreover, banding patterns suggest that the position of the centromere in human chromosome 2 closely matches that of a centromere in one of the chimpanzee chromosomes, reflecting their close evolutionary relationship. But this centromere falls within an inverted region of the chromosome in gorillas and orangutans, reflecting their evolutionary divergence from chimpanzees and humans. (Recall from Section 13.3 that an inverted chromosome segment has a reversed orientation, so the order of genes on it is reversed relative to the order in a segment that is not inverted.) Nevertheless, humans and chimps differ from each other in centromeric inversions in six other chromosomes.

How might such chromosome rearrangements promote speciation? In a paper published in 2003, Arcadi Navarro of the Universitat Pompeu Fabra in Spain and Nick H. Barton of the University of Edin-

UNANSWERED QUESTIONS

Do asexual organisms form species?

As you learned in this chapter, the biological species concept applies only to sexually reproducing organisms because only those organisms can evolve barriers to gene flow (asexual organisms reproduce more or less clonally). Nevertheless, research is starting to show that organisms whose reproduction is almost entirely asexual, such as bacteria, seem to form distinct and discrete clusters in nature. (These clusters could be considered “species.”) That is, bacteria and other asexual forms may be as distinct as the species of birds described by Ernst Mayr in New Guinea. Workers are now studying the many species of bacteria in nature (only a small number of which have been discovered) to see if they indeed fall into distinct groups. If they do, then scientists will need a special theory, independent of reproductive isolation, to explain this distinctness. Scientists are now working on theories of whether the existence of discrete ecological niches in nature might explain the possible discreteness of asexual “species.”

How often does speciation occur allopatrically versus sympatrically or parapatrically?

Scientists do not know how often speciation occurs between populations that are completely isolated geographically (allopatric speciation) compared with how often it occurs in populations that exchange genes (parapatric or sympatric speciation). The relative frequency of these modes of speciation in nature is an active area of research. The ongoing work includes studies on small isolated islands: if an invading species divides into two or more species in this situation, it probably did so sympatrically or parapatrically, since geographical isolation of populations in small islands is unlikely. In addition, biologists are reconstructing the evolutionary history of speciation using molecular tools and correlating this history with the species' geographical distributions. If

this line of research were to show, for example, that the most closely related pairs of species always had geographically isolated distributions, it would imply that speciation was usually allopatric. These lines of research should eventually answer the controversial question of the relative frequency of various forms of speciation.

What are the genetic changes underlying speciation?

Biologists know a great deal about the types of reproductive isolation that prevent gene flow between species, but almost nothing about their genetic bases. Which genes control the difference between flower shape in monkey-flower species? Which genes lead to inviability and sterility of *Drosophila* hybrids? Which genes cause species of ducks to preferentially mate with members of their own species over members of other species? Do the genetic changes that lead to reproductive isolation tend to occur repeatedly at the same genes in a group of organisms, or at different genes? Do the changes occur mostly in protein-coding regions of genes, or in the noncoding regions that control the production of proteins? Were the changes produced by natural selection or by genetic drift? Biologists are now isolating “speciation genes” and sequencing their DNA. With only a handful of such genes known, and all of these causing hybrid sterility or inviability, there will undoubtedly be a lot to learn about the genetics of speciation in the next decade.



Jerry Coyne conducts research on speciation and teaches at the University of Chicago. To learn more about his research go to http://pondside.uchicago.edu/ecol-evol/faculty/coyne_j.html.

burgh in Scotland compared the rates of evolution in protein-coding genes that lie within rearranged chromosome segments of humans and chimpanzees to those in genes outside the rearranged segments. They discovered that proteins evolved more than twice as quickly in the rearranged chromosome segments. Navarro and Barton reasoned that because chromosome rearrangements inhibit chromosome pairing and recombination during meiosis, new genetic variations favored by natural selection would be conserved within the rearranged segments. These variations accumulate over time, contributing to genetic divergence between populations with the rearrangement and those without it. Thus, chromosome rearrangements can be a trigger for speciation: once a chromosome rearrangement becomes established

within a population, that population will diverge more rapidly from populations lacking the rearrangement. The genetic divergence eventually causes reproductive isolation.

In the next chapter we consider the effects of speciation over vast spans of time as we examine paleobiology and patterns of macroevolution.

STUDY BREAK

1. How can natural selection promote reproductive isolation in allopatric populations?
2. What group of organisms has frequently undergone speciation by polyploidy?

Review

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21.1 What Is a Species?

- In practice, most biologists describe, identify, and recognize species on the basis of morphological characteristics that serve as indicators of their genetic similarity to or divergence from other species (Figure 21.2).
- The biological species concept defines species as groups of interbreeding populations that are reproductively isolated from populations of other species in nature. A biological species thus represents a gene pool within which genetic material is potentially shared among populations. The biological species concept cannot be applied to organisms that reproduce only asexually, to those that are extinct, or to geographically separated populations. The phylogenetic species concept defines a species as a group of populations with a recently shared evolutionary history.
- Most species exhibit geographical variation of phenotypic and genetic traits. When marked geographical variation in phenotypes is discontinuous, biologists sometimes name subspecies (Figure 21.3). In ring species, populations are distributed in a ring around unsuitable habitat (Figure 21.4). Many species exhibit clinal variation of characteristics, which change smoothly over a geographical gradient (Figure 21.5).

Animation: Morphological differences within a species

21.2 Maintaining Reproductive Isolation

- Reproductive isolating mechanisms are characteristics that prevent two species from interbreeding.
- Prezygotic isolating mechanisms either prevent individuals of different species from mating or prevent fertilization between their gametes. Prezygotic isolation occurs because species live in different habitats, breed at different times, use different courtship behavior (Figure 21.6), or differ anatomically (Figure 21.7). Prezygotic isolation can also result from genetic and physiological incompatibilities between male and female gametes.

- Postzygotic isolating mechanisms reduce the fitness of interspecific hybrids through hybrid inviability, hybrid sterility (Figure 21.8), or hybrid breakdown.

Animation: Reproductive isolating mechanisms

Animation: Temporal isolation among cicadas

21.3 The Geography of Speciation

- The model of allopatric speciation proposes that speciation results from divergent evolution in geographically separated populations (Figures 21.9–21.11). If allopatric populations accumulate enough genetic differences, they will be reproductively isolated upon secondary contact. Nevertheless, some species hybridize over small areas of secondary contact (Figure 21.12).
- The model of parapatric speciation suggests that reproductive isolation can evolve between parts of a population that occupy opposite sides of an environmental discontinuity (Figure 21.13).
- A model of sympatric speciation in insects suggests that reproductive isolation may evolve between host races that rarely contact one another under natural conditions (Figure 21.14). Sympatric speciation commonly occurs in flowering plants by allopolyploidy.

Animation: Models of speciation

Animation: Allopatric speciation on an archipelago

Animation: Sympatric speciation in wheat

21.4 Genetic Mechanisms of Speciation

- Allopatric populations inevitably accumulate genetic differences, some of which contribute to their reproductive isolation. Reproductive isolating mechanisms evolve as by-products of genetic changes that occur during divergence. Prezygotic isolating mechanisms may evolve in populations experiencing secondary contact (Figure 21.15).
- We cannot yet generalize about how many gene loci participate in the process of speciation, but at least several gene loci are usually involved.

- Speciation by polyploidy in flowering plants involves the duplication of an entire chromosome complement through nondisjunction of chromosomes during meiosis or mitosis. Polyploids can arise among the offspring of a single species (autopolyploidy; Figure 21.16) or, more commonly, after hybridization between closely related species (allopolyploidy; Figures 21.17 and 21.18).
- Chromosome alterations can promote speciation by fostering the genetic divergence of, and reproductive isolation between, populations with different numbers of chromosomes or different chromosome structure (Figure 21.19).

Questions

Self-Test Questions

- The biological species concept defines species on the basis of:
 - reproductive characteristics.
 - biochemical characteristics.
 - morphological characteristics.
 - behavioral characteristics.
 - all of the above
- Biologists can apply the biological species concept *only* to species that:
 - reproduce asexually.
 - lived in the past.
 - are allopatric to each other.
 - hybridize in captivity.
 - reproduce sexually.
- A characteristic that exhibits smooth changes in populations distributed along a geographical gradient is called a:
 - ring species.
 - subspecies.
 - cline.
 - hybrid breakdown.
 - subspecies.
- If two species of holly (genus *Ilex*) flower during different months, their gene pools may be kept separate by:
 - mechanical isolation.
 - ecological isolation.
 - gametic isolation.
 - temporal isolation.
 - behavioral isolation.
- Prezygotic isolating mechanisms:
 - reduce the fitness of hybrid offspring.
 - generally prevent individuals of different species from producing zygotes.
 - are found only in animals.
 - are found only in plants.
 - are observed only in organisms that reproduce asexually.
- In the model of allopatric speciation, the geographical separation of two populations:
 - is sufficient for speciation to occur.
 - occurs only after speciation is complete.
 - allows gene flow between them.
 - reduces the relative fitness of hybrid offspring.
 - inhibits gene flow between them.
- Adjacent populations that produce hybrid offspring with low relative fitness may be undergoing:
 - clinal isolation.
 - parapatric speciation.
 - allopatric speciation.
 - sympatric speciation.
 - geographical isolation.
- An animal breeder, attempting to cross a llama with an alpaca for finer wool, found that the hybrid offspring rarely lived more than a few weeks. This outcome probably resulted from:
 - genetic drift.
 - prezygotic reproductive isolation.
 - postzygotic reproductive isolation.
 - sympatric speciation.
 - polyploidy.
- Which of the following could be an example of allopolyploidy?
 - One parent has 32 chromosomes, the other has 10, and their offspring have 42.
 - Gametes and somatic cells have the same number of chromosomes.
 - Chromosome number increases by one in a gamete and in the offspring it produces.
 - Chromosome number decreases by one in a gamete and in the offspring it produces.
 - Chromosome number in the offspring is exactly half of what it is in the parents.
- Which of the following genetic characteristics is shared by humans and chimpanzees?
 - They have the same number of chromosomes.
 - The position of the centromere on human chromosome 2 matches the position of a centromere on a chimpanzee chromosome.
 - A fusion of ancestral chromosomes formed chromosome 2.
 - Centromeres on all of their chromosomes fall within inverted chromosome segments.
 - all of the above

Questions for Discussion

- All domestic dogs are classified as members of the species *Canis familiaris*. But it is hard to imagine how a tiny Chihuahua could breed with a gigantic Great Dane. Do you think that artificial selection for different breeds of dogs will eventually create different dog species?
- Human populations often differ dramatically in external morphological characteristics. On what basis are all human populations classified as a single species?
- If intermediate populations in a ring species go extinct, eliminating the possibility of gene flow between populations at the two ends of the ring, would you now identify those remaining populations as full species? Explain your answer.

Experimental Analysis

Design an experiment to test whether populations of birds on different islands belong to the same species.

Evolution Link

How do human activities (such as destruction of natural habitats, diversion of rivers, and the construction of buildings) influence the chances that new species of plants and animals will evolve in the future? Frame your answer in terms of the geographical and genetic factors that foster speciation.

How Would You Vote?

Often, when a species is at the brink of extinction, some individuals are captured and brought to zoos for captive breeding programs. Some people object to this practice. They say that keeping a species alive in a zoo is a distraction from more meaningful conservation efforts, and captive animals seldom are successfully re-stored to the wild. Do you support captive breeding of highly endangered species? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.