

22

The Origin of Species

Concept Outline

22.1 Species are the basic units of evolution.

The Nature of Species. Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups and that maintain connectedness over geographic distances.

22.2 Species maintain their genetic distinctiveness through barriers to reproduction.

Prezygotic Isolating Mechanisms. Some breeding barriers prevent the formation of zygotes.

Postzygotic Isolating Mechanisms. Other breeding barriers prevent the proper development or reproduction of the zygote after it forms.

22.3 We have learned a great deal about how species form.

Reproductive Isolation May Evolve as a By-Product of Evolutionary Change. Speciation can occur in the absence of natural selection, but reproductive isolation generally occurs more quickly when populations are adapting to different environments.

The Geography of Speciation. Speciation occurs most readily when populations are geographically isolated. Sympatric speciation can occur by polyploidy and, perhaps, by other means.

22.4 Clusters of species reflect rapid evolution.

Darwin's Finches. Thirteen species of finches, all descendants of one ancestral finch, occupy diverse niches.

Hawaiian *Drosophila*. More than a quarter of the world's fruit fly species are found on the Hawaiian Islands.

Lake Victoria Cichlid Fishes. Isolation has led to extensive species formation among these small fishes.

New Zealand Alpine Buttercups. Repeated glaciations have fostered waves of species formation in alpine plants.

Diversity of Life through Time. The number of species has increased through time, despite a number of mass extinction events.

The Pace of Evolution. The idea that evolution occurs in spurts is controversial.

Problems with the Biological Species Concept. This concept is not as universal as previously thought.



FIGURE 22.1

A group of Galápagos iguanas bask in the sun on their isolated island. How does geographic isolation contribute to the formation of new species?

Although Darwin titled his book *On the Origin of Species*, he never actually discussed what he referred to as that “mystery of mysteries” of how one species gives rise to another. Rather, his argument concerned evolution by natural selection; that is, how one species evolves through time to adapt to its changing environment. Although of fundamental importance to evolutionary biology, the process of adaptation does not explain how one species becomes another (figure 22.1); much less can it explain how one species can give rise to many descendant species. As we shall see, adaptation may be involved in this process of **speciation**, but it need not be.

22.1 Species are the basic units of evolution.

The Nature of Species

Before we can discuss how one species gives rise to another, we need to understand exactly what a species is. Even though definition of what constitutes a species is of fundamental importance to evolutionary biology, this issue has still not been completely settled and is currently the subject of considerable research and debate. However, any concept of a species must account for two phenomena: the distinctiveness of species that occur together at a single locality, and the connection that exists among populations of the same species that are geographically separated.

The Distinctiveness of Sympatric Species

Put out a birdfeeder on your balcony or back porch and you will attract a wide variety of different types of birds (especially if you put out a variety of different kinds of foods). In the midwestern United States, for example, you might routinely see cardinals, blue jays, downy woodpeckers, house finches—even hummingbirds in the summer (figure 22.2). Although it might take a few days of careful observation, you would soon be able to readily distinguish the many different species. The reason is that species that occur together (termed **sympatric** from the Greek *sym* for “same” and *patria* for “species”) are distinctive entities that are phenotypically different, utilize different parts of the habitat, and behave separately. This observation is generally true not only for birds, but also for most other types of organisms in most places.

Occasionally, two species occur together that appear to be nearly identical, and are thus called **sibling species**. In most cases, however, our inability to distinguish the two reflects our own reliance on vision as our primary sense. When the mating calls or chemicals exuded by such species are examined, they usually reveal great differences. In other words, even though we have trouble separating them, the animals themselves have no such difficulties!

Geographic Variation within Species

Within the units classified as species, populations that occur in different areas may be more or less distinct from one another. Such groups of distinctive individuals may be classified taxonomically as **subspecies** or **varieties** (the vague term “race” has a similar connotation, but is no longer commonly used). In areas where these populations approach one another, individuals often exhibit combinations of features characteristic of both populations. In other words, even though geographically distant populations may appear distinct, they usually are connected by intervening populations that are intermediate in their characteristics (figure 22.3).

The Biological Species Concept

What can account both for the distinctiveness of sympatric species and the connectedness of geographic populations of the same species? One obvious possibility is that each species exchanges genetic material only with other members of its species. If sympatric species commonly ex-

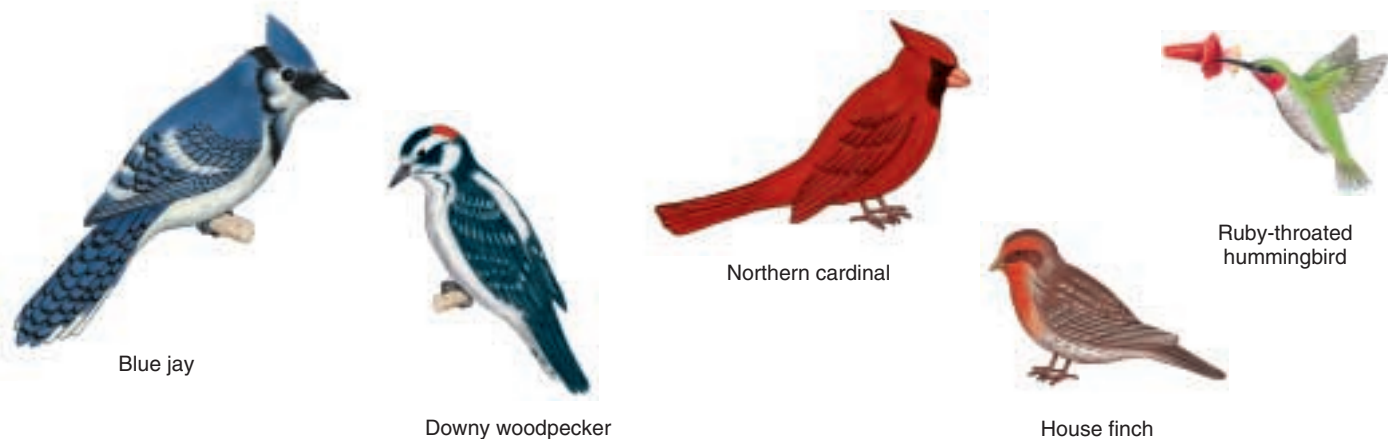


FIGURE 22.2

Common birds in the midwestern United States. No one would doubt that these birds are distinct species. Each can be distinguished from the others by many ecological, behavioral, and phenotypic traits.

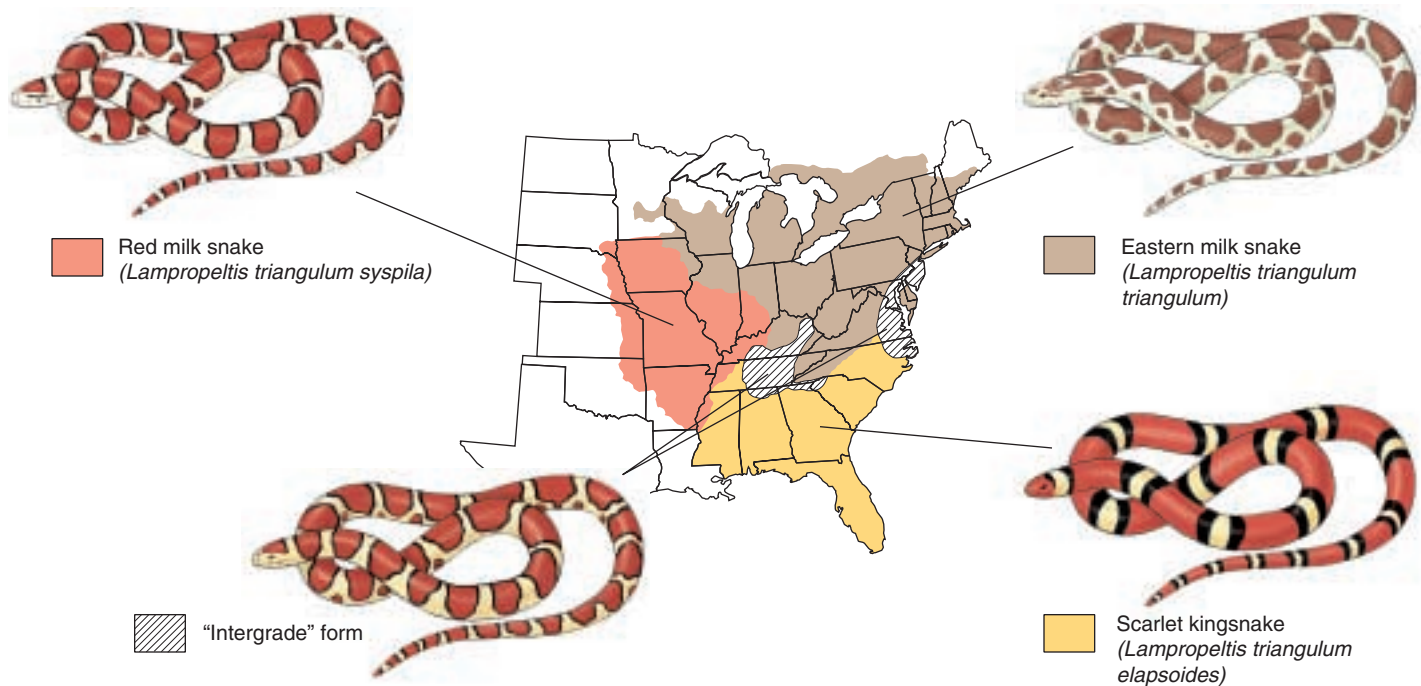


FIGURE 22.3
Geographic variation in the milk snake, *Lampropeltis triangulum*. Although each subspecies appears phenotypically quite distinctive from the others, they are connected by populations that are phenotypically intermediate.

changed genes, we might expect such species to rapidly lose their distinctions as the **gene pools** of the different species became homogenized. Conversely, the ability of geographically distant populations to share genes through the process of gene flow may keep these populations integrated as members of the same species. Based on these ideas, the evolutionary biologist Ernst Mayr coined the **biological species concept** which defines species as:

“. . . groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups.”

In other words, the biological species concept says that a species is all individuals that are capable of interbreeding and producing fertile offspring. Conversely, individuals that cannot produce fertile offspring are said to be **reproductively isolated** and, thus, members of different species.

Occasionally, members of different species will interbreed, a process termed **hybridization**. If the species are reproductively isolated, either no offspring will result, or if offspring are produced, they will be either unhealthy or sterile. In this way, genes from one species generally will not be able to enter the gene pool of another species.

Problems with Applying the Biological Species Concept

The biological species concept has proven to be an effective way of understanding the existence of species in nature. Nonetheless, the concept has some practical difficulties.

For example, it can be difficult to apply the concept to populations that do not occur together in nature (and are thus said to be **allopatric**). Because individuals of these populations do not encounter each other, it is not possible to observe whether they would interbreed naturally. Although experiments can determine whether fertile hybrids can be produced, this information is not enough. The reason is that many species that will coexist without interbreeding in nature will readily hybridize in the artificial settings of the laboratory or zoo. Consequently, evaluating whether allopatric populations constitute different species is ultimately a judgment call.

In addition, the concept is more limited than its name would imply. Many organisms are asexual and reproduce without mating; reproductive isolation has no meaning for such organisms.

Moreover, despite its name, the concept is really a zoological species concept and applies less readily to plants. Even among animals, the biological species concept appears to apply more successfully to some groups than to others. As we will see in section 22.4, biologists are currently reevaluating this and other approaches to the study of species.

Species are groups of organisms that are distinct from other co-occurring species and that are interconnected geographically. The ability to exchange genes appears to be a hallmark of such species.

22.2 Species maintain their genetic distinctiveness through barriers to reproduction.

Prezygotic Isolating Mechanisms

How do species keep their separate identities? Reproductive isolating mechanisms fall into two categories: **prezygotic isolating mechanisms**, which prevent the formation of zygotes; and **postzygotic isolating mechanisms**, which prevent the proper functioning of zygotes after they form. In the following sections we will discuss various isolating mechanisms in these two categories and offer examples that illustrate how the isolating mechanisms operate to help species retain their identities.

Ecological Isolation

Even if two species occur in the same area, they may utilize different portions of the environment and thus not hybridize because they do not encounter each other. For example, in India, the ranges of lions and tigers overlapped until about 150 years ago. Even when they did, however, there were no records of natural hybrids. Lions stayed mainly in the open grassland and hunted in groups called prides; tigers tended to be solitary creatures of the forest (figure 22.4). Because of their ecological and behavioral differences, lions and tigers rarely came into direct contact with each other, even though their ranges overlapped over thousands of square kilometers.

In another example, the ranges of two toads, *Bufo woodhousei* and *B. americanus*, overlap in some areas. Although these two species can produce viable hybrids, they usually do not interbreed because they utilize different portions of the habitat for breeding. Whereas *B. woodhousei* prefers to breed in streams, *B. americanus* breeds in rainwater puddles. Similarly, the ranges of two species of dragonflies overlap in Florida. However, the dragonfly *Progomphus obscurus* lives near rivers and streams, and *P. alachuenis* lives near lakes.

Similar situations occur among plants. Two species of oaks occur widely in California: the valley oak, *Quercus lobata*, and the scrub oak, *Q. dumosa*. The valley oak, a graceful deciduous tree that can be as tall as 35 meters, occurs in the fertile soils of open grassland on gentle slopes and valley floors. In contrast, the scrub oak is an evergreen shrub, usually only 1 to 3 meters tall, which often forms the kind of dense scrub known as chaparral. The scrub oak is found on steep slopes in less fertile soils. Hybrids between these different oaks do occur and are fully fertile, but they are rare. The sharply distinct habitats of their parents limit their occurrence together, and there is no intermediate habitat where the hybrids might flourish.



(a)



(b)



(c)

FIGURE 22.4

Lions and tigers are ecologically isolated. The ranges of lions and tigers used to overlap in India. However, lions and tigers do not hybridize in the wild because they utilize different portions of the habitat. (a) Lions live in open grassland. (b) Tigers are solitary animals that live in the forest. (c) Hybrids, such as this tigon, have been successfully produced in captivity, but hybridization does not occur in the wild.

Behavioral Isolation

In chapter 27, we will consider the often elaborate courtship and mating rituals of some groups of animals. Related species of organisms such as birds often differ in their courtship rituals, which tends to keep these species distinct in nature even if they inhabit the same places (figure 22.5). For example, mallard and pintail ducks are perhaps the two most common freshwater ducks in North America. In captivity, they produce completely fertile offspring, but in nature they nest side-by-side and only rarely hybridize.

More than 500 species of flies of the genus *Drosophila* live in the Hawaiian Islands. This is one of the most remarkable concentrations of species in a single animal genus found anywhere. The genus occurs throughout the world, but nowhere are the flies more diverse in external appearance or behavior than in Hawaii. Many of these flies differ greatly from other species of *Drosophila*, exhibiting characteristics that can only be described as bizarre.

The Hawaiian species of *Drosophila* are long-lived and often very large compared with their relatives on the mainland. The females are more uniform than the males, which are often bizarrely distinctive. The males display complex territorial behavior and elaborate courtship rituals.

The mating behavior patterns among Hawaiian species of *Drosophila* are of great importance in maintaining the distinctiveness of the individual species. For example, despite the great differences between them, *D. heteroneura* and *D. silvestris* are very closely related. Hybrids between them are fully fertile. The two species occur together over a wide area on the island of Hawaii, yet hybridization has been observed at only one locality. The very different and complex behavioral characteristics of these flies obviously play a major role in maintaining their distinctiveness.

Other Prezygotic Isolating Mechanisms

Temporal Isolation. *Lactuca graminifolia* and *L. canadensis*, two species of wild lettuce, grow together along roadsides throughout the southeastern United States. Hybrids between these two species are easily made experimentally and are completely fertile. But such hybrids are rare in nature because *L. graminifolia* flowers in early spring and *L. canadensis* flowers in summer. When their blooming periods overlap, as they do occasionally, the two species do form hybrids, which may become locally abundant.

Many species of closely related amphibians have different breeding seasons that prevent hybridization between the species. For example, five species of frogs of the genus *Rana* occur together in most of the eastern United States, but hybrids are rare because the peak breeding time is different for each of them.



FIGURE 22.5
Differences in courtship rituals can isolate related bird species. These Galápagos blue-footed boobies select their mates only after an elaborate courtship display. This male is lifting his feet in a ritualized high-step that shows off his bright blue feet. The display behavior of other species of boobies, some of which also occur in the Galápagos, is much different.

Mechanical Isolation. Structural differences prevent mating between some related species of animals. Aside from such obvious features as size, the structure of the male and female copulatory organs may be incompatible. In many insect and other arthropod groups, the sexual organs, particularly those of the male, are so diverse that they are used as a primary basis for classification.

Similarly, flowers of related species of plants often differ significantly in their proportions and structures. Some of these differences limit the transfer of pollen from one plant species to another. For example, bees may pick up the pollen of one species on a certain place on their bodies; if this area does not come into contact with the receptive structures of the flowers of another plant species, the pollen is not transferred.

Prevention of Gamete Fusion. In animals that shed their gametes directly into water, eggs and sperm derived from different species may not attract one another. Many land animals may not hybridize successfully because the sperm of one species may function so poorly within the reproductive tract of another that fertilization never takes place. In plants, the growth of pollen tubes may be impeded in hybrids between different species. In both plants and animals the operation of such isolating mechanisms prevents the union of gametes even following successful mating.

Prezygotic isolating mechanisms lead to reproductive isolation by preventing the formation of hybrid zygotes.

Postzygotic Isolating Mechanisms

All of the factors we have discussed up to this point tend to prevent hybridization. If hybrid matings do occur and zygotes are produced, many factors may still prevent those zygotes from developing into normally functioning, fertile individuals. Development in any species is a complex process. In hybrids, the genetic complements of two species may be so different that they cannot function together normally in embryonic development. For example, hybridization between sheep and goats usually produces embryos that die in the earliest developmental stages.

Leopard frogs (*Rana pipiens* complex) of the eastern United States are a group of similar species, assumed for a long time to constitute a single species (figure 22.6). However, careful examination revealed that although the frogs appear similar, successful mating between them is rare because of problems that occur as the fertilized eggs develop. Many of the hybrid combinations cannot be produced even in the laboratory.

Examples of this kind, in which similar species have been recognized only as a result of hybridization experi-

ments, are common in plants. Sometimes the hybrid embryos can be removed at an early stage and grown in an artificial medium. When these hybrids are supplied with extra nutrients or other supplements that compensate for their weakness or inviability, they may complete their development normally.

Even if hybrids survive the embryo stage, however, they may not develop normally. If the hybrids are weaker than their parents, they will almost certainly be eliminated in nature. Even if they are vigorous and strong, as in the case of the mule, a hybrid between a horse and a donkey, they may still be sterile and thus incapable of contributing to succeeding generations. Sterility may result in hybrids because the development of sex organs may be abnormal, the chromosomes derived from the respective parents may not pair properly, or from a variety of other causes.

Postzygotic isolating mechanisms are those in which hybrid zygotes fail to develop or develop abnormally, or in which hybrids cannot become established in nature.



FIGURE 22.6

Postzygotic isolation in leopard frogs. Numbers indicate the following species in the geographical ranges shown:

(1) *Rana pipiens*; (2) *Rana blairi*; (3) *Rana utricularia*; (4) *Rana berlandieri*. These four species resemble one another closely in their external features. Their status as separate species was first suspected when hybrids between them produced defective embryos in some combinations. Subsequent research revealed that the mating calls of the four species differ substantially, indicating that the species have both pre- and postzygotic isolating mechanisms.

22.3 We have learned a great deal about how species form.

One of the oldest questions in the field of evolution is: how does one ancestral species become divided into two descendant species? If species are defined by the existence of reproductive isolation, then the process of speciation equates with the evolution of reproductive isolating mechanisms. How do reproductive isolating mechanisms evolve?

Reproductive Isolation May Evolve as a By-Product of Evolutionary Change

Most reproductive isolating mechanisms initially arise for some reason other than to provide reproductive isolation. For example, a population that colonizes a new habitat may evolve adaptations for living in that habitat. As a result, individuals from that population might never encounter individuals from the ancestral population. Even if they do meet, the population in the new habitat may have evolved new phenotypes or behavior so that members of the two populations no longer recognize each other as potential mates (figure 22.7). For this reason, some biologists believe that the term “isolating mechanisms” is misguided, because it implies that the traits evolved specifically for the purpose of genetically isolating a species, which in most cases is probably incorrect.

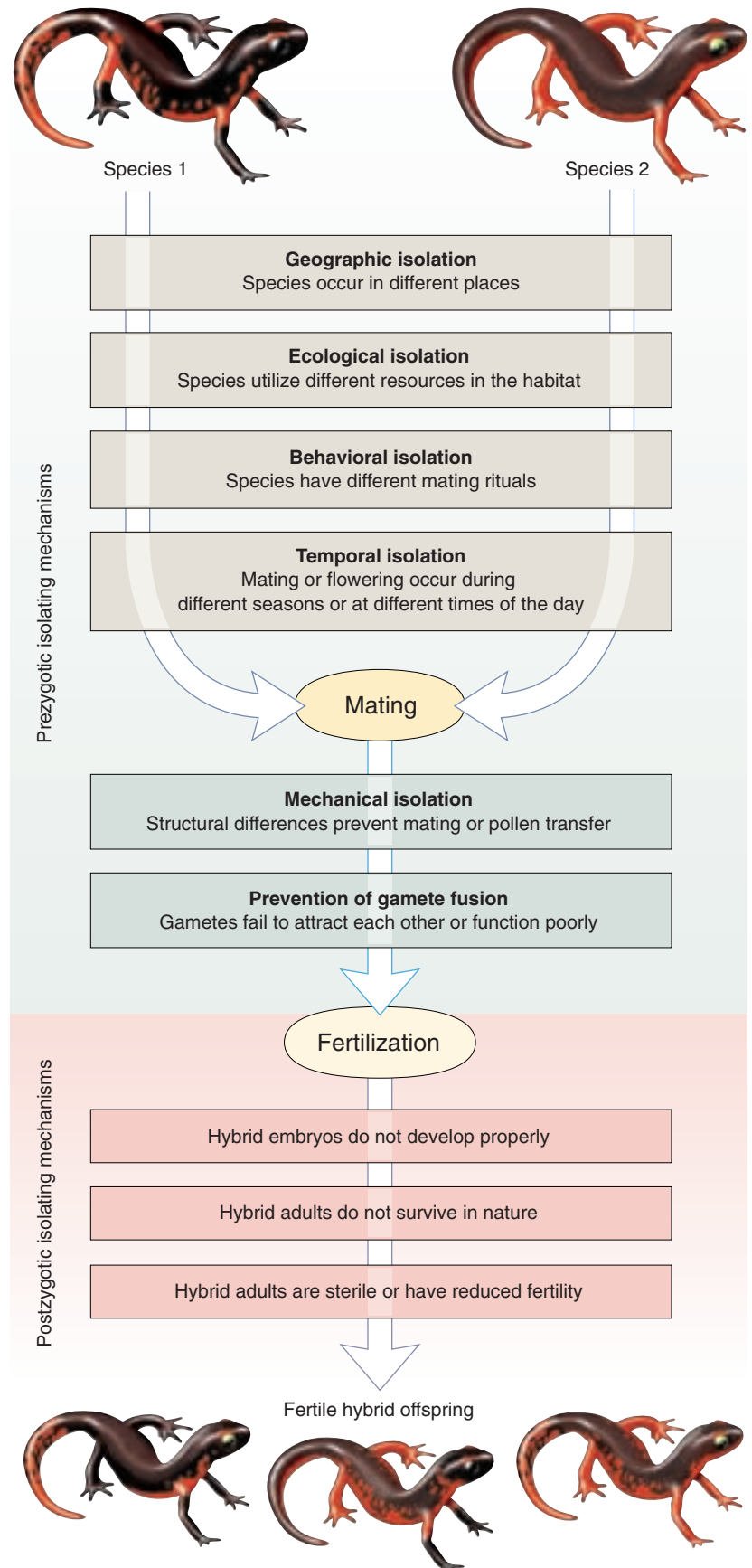


FIGURE 22.7
Reproductive isolating mechanisms. A variety of different mechanisms can prevent successful reproduction between individuals of different species.

Selection May Reinforce Isolating Mechanisms

The formation of species is a continuous process, one that we can understand because of the existence of intermediate stages at all levels of differentiation. If populations that are partly differentiated come into contact with one another, they may still be able to interbreed freely, and the differences between them may disappear over the course of time as genetic exchange homogenizes the populations. Conversely, if the populations are reproductively isolated, then no genetic exchange will occur and the two populations will be different species.

However, there is an intermediate situation in which reproductive isolation has partially evolved, but is not complete. As a result, hybridization will occur at least occasionally. If they are partly sterile, or not as well adapted to the existing habitats as their parents, these hybrids will be at a disadvantage. As a result, selection would favor any alleles in the parental populations that prevented hybridization because individuals that avoided hybridizing would be more successful in passing their genes on to the next generation. The result would be the continual improvement of prezygotic isolating mechanisms until the two populations were completely reproductively isolated. This process is termed **reinforcement** because initially incomplete isolating mechanisms are reinforced by natural selection until they are completely effective.

Reinforcement is by no means inevitable, however. When incompletely isolated populations come together, gene flow immediately begins to occur between the species. Although hybrids may be inferior, they are not, in this case, completely inviable or infertile (if they were, then the species would be reproductively isolated); hence, when these hybrids reproduce with members of either population, they will serve as a conduit of genetic exchange from one population to the other. As a result, the two populations will tend to lose their genetic distinctiveness. Thus, a race ensues: can reproductive isolation be perfected before gene flow destroys the differences between the populations? Experts disagree on the likely outcome, but many believe that reinforcement is the much less common outcome.

The Role of Natural Selection in Speciation

What role does natural selection play in the speciation process? Certainly, the process of reinforcement is driven by natural selection favoring the perfection of reproductive isolation. But, as we have seen, reinforcement may not be common. Is natural selection necessarily involved in the initial evolution of isolating mechanisms?

Random Changes May Cause Reproductive Isolation

As we discussed in chapter 20, populations may diverge for purely random reasons. Genetic drift in small populations, founder effects, and population bottlenecks all may lead to changes in traits that cause reproductive isolation. For example, in the Hawaiian Islands, closely related species of *Drosophila* often differ greatly in their courtship behavior. Colonization of new islands by these fruit flies probably involves a founder effect, in which one or a few fruit flies—perhaps only a single pregnant female—is blown by strong winds to a new island. Changes in courtship behavior between ancestor and descendant populations may be the result of such founder events. Given long enough periods of time, any two isolated populations will diverge due to genetic drift. In some cases, this random divergence may affect traits responsible for reproductive isolation, and speciation will have occurred.

Adaptation and Speciation

Nonetheless, adaptation and speciation are probably related in many cases. As species adapt to different circumstances, they will accumulate many differences that may lead to reproductive isolation. For example, if one population of flies adapts to wet conditions and another to dry conditions, then the populations will evolve a variety of differences in physiological and sensory traits; these differences may promote ecological and behavioral isolation and may cause any hybrids they produce to be poorly adapted to either habitat.

Selection might also act directly on mating behavior. Male *Anolis* lizards, for example, court females by extending a colorful flap of skin, called a “dewlap,” that is located under their throat (figure 22.8). The ability of one lizard to see the dewlap of another lizard depends not only on the color of the dewlap, but the environment in which they occur. As a result, a light-colored dewlap is most effective in reflecting light in a dim forest, whereas dark colors are more apparent in the bright glare of open habitats. As a result, when these lizards occupy new habitats, natural selection will favor evolutionary change in dewlap color because males whose dewlaps cannot be seen will attract few mates. However, the lizards also distinguish members of their own species from those of other species by the color of the dewlap. Hence, adaptive change in mating behavior could have the incidental consequence of causing speciation.

Laboratory scientists have conducted experiments on fruit flies and other organisms in which they isolate popula-



(a) *Anolis carolinensis*.



(b) *Anolis sagrei*.



(c) *Anolis grahami*.



(d) Species name to come.

FIGURE 22.8

Dewlaps of several different species of Caribbean *Anolis* lizards. Males use their dewlaps in both territorial and courtship displays. Coexisting species almost always differ in their dewlaps, which are used in species recognition. Some dewlaps are easier to see in open habitats, whereas others are more visible in shaded environments.

tions in different laboratory chambers and measure how much reproductive isolation evolves. These experiments indicate that genetic drift by itself can lead to some degree of reproductive isolation, but, in general, reproductive isolation evolves more rapidly when the populations are forced to adapt to different laboratory environments (such as temperature or food type).

Reproductive isolating mechanisms can evolve either through random changes or as an incidental by-product of adaptive evolution. Under some circumstances, however, natural selection can directly select for traits that increase the reproductive isolation of a species.

The Geography of Speciation

Speciation is a two-part process. First, initially identical populations must diverge and, second, reproductive isolation must evolve to maintain these differences. The difficulty with this process, as we have seen, is that the homogenizing effect of gene flow between populations will constantly be acting to erase any differences that may arise, either by genetic drift or natural selection. Of course, gene flow only occurs between populations that are in contact. Consequently, evolutionary biologists have long recognized that speciation is much more likely in geographically isolated populations.

Allopatric Divergence Is the Primary Means of Speciation

Ernst Mayr was the first biologist to strongly make the case for allopatric speciation. Marshalling data from a wide variety of organisms and localities, Mayr was clearly able to demonstrate that geographically separated populations appear much more likely to have evolved substantial differences leading to speciation. For example, the Papuan kingfisher, *Tanysiptera hydrocharis*, varies little throughout its wide range in New Guinea despite the

great variation in the island's topography and climate. By contrast, isolated populations on nearby islands are strikingly different from each other and from the mainland population (figure 22.9).

Many other examples indicate that speciation can occur in allopatry. Given that one would expect isolated populations to diverge over time by either drift or selection, this result is not surprising. Rather, the question becomes: Is geographic isolation required for speciation to occur?

Whether Speciation Can Occur in Sympatry Is Controversial

As we saw in chapter 20, disruptive selection can cause a population to contain individuals exhibiting two different phenotypes. One might think that if selection were strong enough, these two phenotypes would evolve into different species. However, before the two phenotypes could become different species, they would have to evolve reproductive isolating mechanisms. Because the two phenotypes would initially not be reproductively isolated at all, genetic exchange between individuals of the two phenotypes would tend to prevent genetic divergence in mating preferences or other isolating mechanisms. As a result, the two pheno-

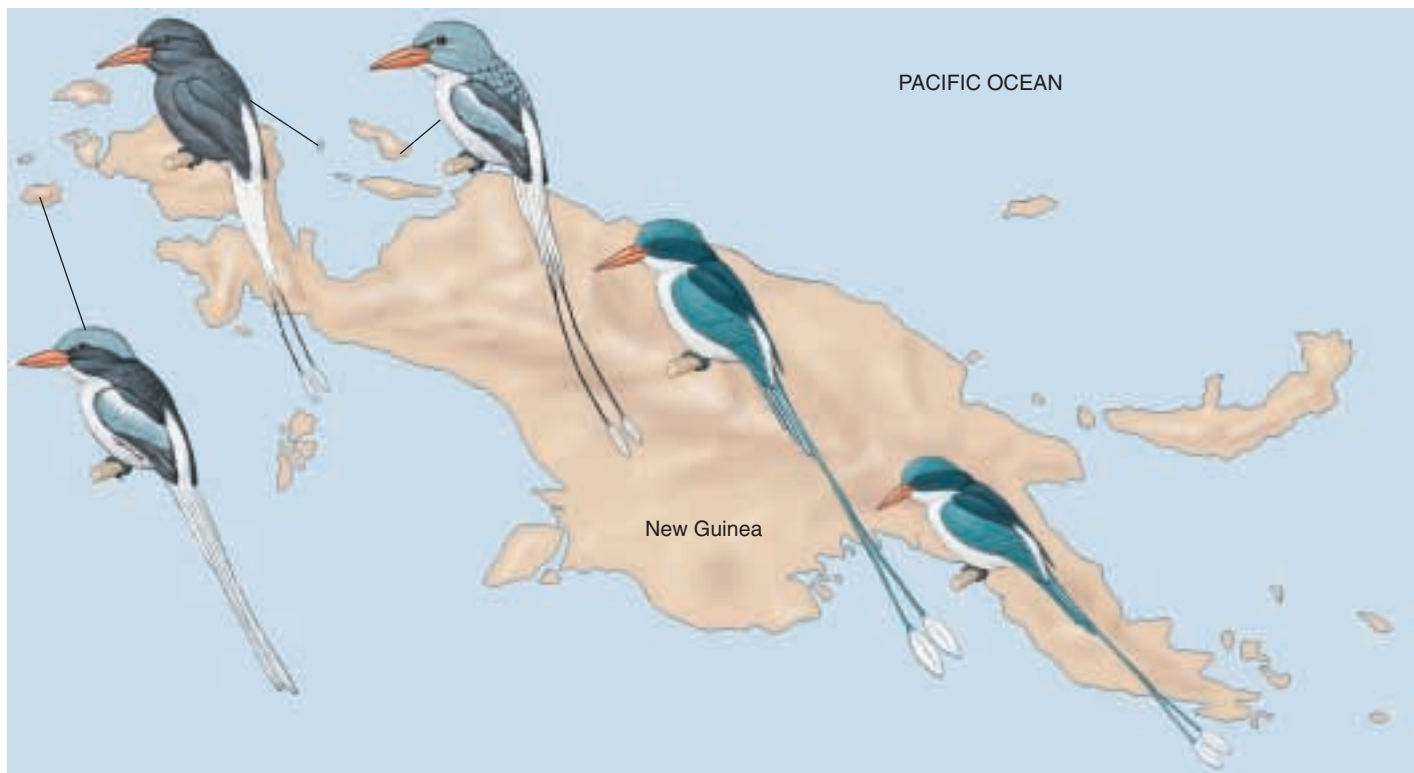


FIGURE 22.9

Phenotypic differentiation in the Papuan kingfisher in New Guinea. Isolated island populations (*above left*) are quite distinctive, showing variation in tail feather structure and length, plumage coloration, and bill size, whereas kingfishers on the mainland (*above right*) show little variation.

FIGURE 22.10

Differences between species can result from a few genes that have major effects. (a) *Mimulus lewisii* has pale pink flowers and concentrated nectar, which are optimal for attracting bumblebees to serve as pollinators. (b) By contrast, *M. cardinalis* has the red flowers and copious dilute nectar typical of hummingbird-pollinated plants. Differences in flower shape and color are the result of a few genes of large effect.



(a) *Mimulus lewisii*



(b) *Mimulus cardinalis*

types would be retained as polymorphisms within a single population. For this reason, most biologists consider sympatric speciation a rare event.

Nonetheless, in recent years, a number of cases have appeared that appear difficult to interpret in any way other than sympatric speciation. For example, the volcanic crater lake Barombi Mbo in Cameroon is extremely small and ecologically homogeneous, with no opportunity for within-lake isolation. Nonetheless, 11 species of closely related cichlid fish occur in the lake; all of the species are more closely related evolutionarily to each other than to any species outside of the crater. The most reasonable explanation is that an ancestral species colonized the crater and subsequently speciated in sympatry multiple times.

Genetic Changes Underlying Speciation

How much divergence does it take to create a new species? How many gene changes does it take? Since Darwin, the traditional view has been that new species arise by the accumulation of many small genetic differences. While there is little doubt that many species have formed in this gradual way, new techniques of molecular biology suggest that in at least some cases, the evolution of a new species may involve very few genes. Studying two species of monkeyflower found in the western United States, researchers found that only a few genes separate the two species, even though at first glance the two species appear to be very different (figure 22.10). Using gene technologies like those described in chapter 19, the researchers found that all of the major differences in the flowers, including not only flower shape and color, but also nectar production, were attributable to several genes, each of which had great phenotypic effects. Because individual genes have such powerful effects, species as different as these two can evolve in relatively few steps.

The Role of Polyploidy in Species Formation

Among plants, fertile individuals often arise from sterile ones through **polyploidy**, which doubles the chromosome number of the original sterile hybrid individual. A polyploid cell, tissue, or individual has more than two sets of chromosomes. Polyploid cells and tissues occur spontaneously and reasonably often in all organisms, although in many they are soon eliminated. A hybrid may be sterile simply because its sets of chromosomes, derived from male and female parents of different species, do not pair with one another. If the chromosome number of such a hybrid doubles, the hybrid, as a result of the doubling, will have a duplicate of each chromosome. In that case, the chromosomes will pair, and the fertility of the polyploid hybrid individual may be restored. It is estimated that about half of the approximately 260,000 species of plants have a polyploid episode in their history, including many of great commercial importance, such as bread wheat, cotton, tobacco, sugarcane, bananas, and potatoes. As you might imagine, the advantages a polyploid plant offers for natural selection can be substantial as a result of their great levels of genetic variation; hence, the significance of polyploidy in the evolution of plants.

Because polyploid plants cannot reproduce with their ancestors, reproductive isolation can evolve in one step. Consequently, speciation by polyploidy is one uncontroversial means of sympatric speciation. Although much rarer than in plants, speciation by polyploidy is also known from a variety of animals, including insects, fish, and salamanders.

Speciation occurs much more readily in the absence of gene flow among populations. However, speciation can occur in sympatry by means of polyploidy, and perhaps in other cases also.

22.4 Clusters of species reflect rapid evolution.

Darwin's Finches

One of the most visible manifestations of evolution is the existence of groups of closely related species that have recently evolved from a common ancestor by occupying different habitats. This type of **adaptive radiation** occurred among the 13 species of Darwin's finches on the Galápagos Islands. Presumably, the ancestor of Darwin's finches reached these islands before other land birds, and all of the types of habitats where birds occur on the mainland were unoccupied. As the new arrivals moved into these vacant ecological niches and adopted new lifestyles, they were subjected to diverse sets of selective pressures. Under these circumstances, and aided by the geographic isolation afforded by the many islands of the Galápagos archipelago, the ancestral finches rapidly split into a series of diverse populations, some of which evolved into separate species. These species now occupy many different kinds of habitats on the Galápagos Islands (figure 22.11), habitats comparable to those several distinct groups of birds occupy on the mainland. The 13 species comprise four groups:

1. **Ground finches.** There are six species of *Geospiza* ground finches. Most of the ground finches feed on seeds. The size of their bills is related to the size of the seeds they eat. Some of the ground finches feed primarily on cactus flowers and fruits and have a longer, larger, more pointed bill than the others.
2. **Tree finches.** There are five species of insect-eating tree finches. Four species have bills that are suitable for feeding on insects. The woodpecker finch has a chisel-like beak. This unusual bird carries around a twig or a cactus spine, which it uses to probe for insects in deep crevices.
3. **Warbler finch.** This unusual bird plays the same ecological role in the Galápagos woods that warblers play on the mainland, searching continually over the leaves and branches for insects. It has a slender, warbler-like beak.
4. **Vegetarian finch.** The very heavy bill of this bud-eating bird is used to wrench buds from branches.

Darwin's finches, all derived from one similar mainland species, have radiated widely on the Galápagos Islands in the absence of competition.

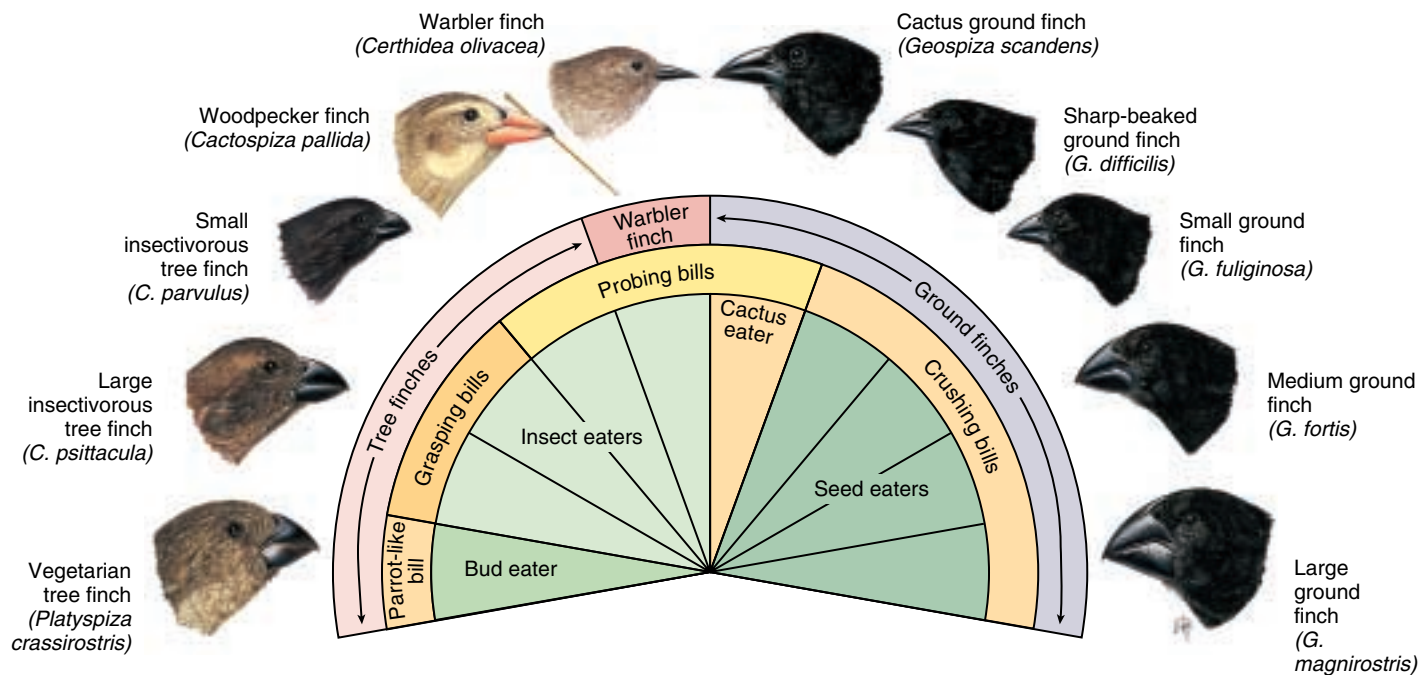


FIGURE 22.11

Darwin's finches. Ten of the 13 Galápagos species of Darwin's finches occur on Isla Santa Cruz, one of the Galápagos Islands. These species show differences in bills and feeding habits. The bills of several of these species resemble those of distinct families of birds on the mainland. This condition presumably arose when the finches evolved new species in habitats lacking small birds. The woodpecker finch uses cactus spines to probe in crevices of bark and rotten wood for food. Scientists believe all of these birds derived from a single common ancestor.

Hawaiian *Drosophila*

Our second example of a cluster of species is the fly genus *Drosophila* on the Hawaiian Islands, which we mentioned earlier as an example of behavioral isolation. There are at least 1250 species of this genus throughout the world, and more than a quarter are found only in the Hawaiian Islands (figure 22.12). New species of *Drosophila* are still being discovered in Hawaii, although the rapid destruction of the native vegetation is making the search more difficult. Aside from their sheer number, Hawaiian *Drosophila* species are unusual because of the morphological and behavioral traits discussed earlier. No comparable species of *Drosophila* are found anywhere else in the world.

A second, closely related genus of flies, *Scaptomyza*, also forms a species cluster in Hawaii, where it is represented by as many as 300 species. A few species of *Scaptomyza* are found outside of Hawaii, but the genus is better represented there than elsewhere. In addition, species intermediate between *Scaptomyza* and *Drosophila* exist in Hawaii, but nowhere else. The genera are so closely related that scientists have suggested that all of the estimated 800 species of these two genera that occur in Hawaii may have derived from a single common ancestor.

The native Hawaiian flies are closely associated with the remarkable native plants of the islands and are often abundant in the native vegetation. Evidently, when their ancestors first reached these islands, they encountered many “empty” habitats that other kinds of insects and other animals occupied elsewhere. The evolutionary opportunities the ancestral *Drosophila* flies found were similar to those the ancestors of Darwin’s finches in the Galápagos Islands encountered, and both groups evolved in a similar way. Many of the Hawaiian *Drosophila* species are highly selective in their choice of host plants for their larvae and in the part of the plant they use. The larvae of various species live in rotting stems, fruits, bark, leaves, or roots, or feed on sap.

New islands have continually arisen from the sea in the region of the Hawaiian Islands. As they have done so, they appear to have been invaded successively by the various *Drosophila* groups present on the older islands. New species have evolved as new islands have been colonized. The Hawaiian species of *Drosophila* have had even greater evolutionary opportunities than Darwin’s finches because of their restricted ecological niches and the variable ages of the islands. They clearly tell one of the most unusual evolutionary stories found anywhere in the world.



(a) *Drosophila mulli*



(b) *Drosophila digressa*

FIGURE 22.12

Hawaiian *Drosophila*. The hundreds of species that have evolved on the Hawaiian Islands are extremely variable in appearance, although genetically almost identical.

The adaptive radiation of about 800 species of the flies *Drosophila* and *Scaptomyza* on the Hawaiian Islands, probably from a single common ancestor, is one of the most remarkable examples of intensive species formation found anywhere on earth.

Lake Victoria Cichlid Fishes

Lake Victoria is an immense shallow freshwater sea about the size of Switzerland in the heart of equatorial East Africa, until recently home to an incredibly diverse collection of over 300 species of cichlid fishes.

Recent Radiation

This cluster of species appears to have evolved recently and quite rapidly. By sequencing the cytochrome *b* gene in many of the lake's fish, scientists have been able to estimate that the first cichlids entered Lake Victoria only 200,000 years ago, colonizing from the Nile. Dramatic changes in water level encouraged species formation. As the lake rose, it flooded new areas and opened up new habitat. Many of the species may have originated after the lake dried down 14,000 years ago, isolating local populations in small lakes until the water level rose again.

Cichlid Diversity

These small, perchlike fishes range from 2 to 10 inches in length, and the males come in endless varieties of colors. The most diverse assembly of vertebrates known to science, the Lake Victoria cichlids defy simple description. We can gain some sense of the vast range of types by looking at how different species eat. There are mud biters, algae scrapers, leaf chewers, snail crushers, snail shellers (who pounce on slow-crawling snails and spear

their soft parts with long curved teeth before the snail can retreat into its shell), zooplankton eaters, insect eaters, prawn eaters, and fish eaters. Scale-scraping cichlids rasp slices of scales off of other fish. There are even cichlid species that are “pedophages,” eating the young of other cichlids.

Cichlid fish have a remarkable trait that may have been instrumental in this evolutionary radiation: a second set of functioning jaws occurs in the throats of cichlid fish (figure 22.13)! The ability of these jaws to manipulate and process food has freed the oral jaws to evolve for other purposes, and the result has been the incredible diversity of ecological roles filled by these fish.

Abrupt Extinction

Much of this diversity is gone. In the 1950s, the Nile perch, a commercial fish with a voracious appetite, was introduced on the Ugandan shore of Lake Victoria. Since then it has spread through the lake, eating its way through the cichlids. By 1990 all the open-water cichlid species were extinct, as well as many living in rocky shallow regions. Over 70% of all the named Lake Victoria cichlid species had disappeared, as well as untold numbers of species that had yet to be described.

Very rapid speciation occurred among cichlid fishes isolated in Lake Victoria, but widespread extinction followed when the isolation ended.

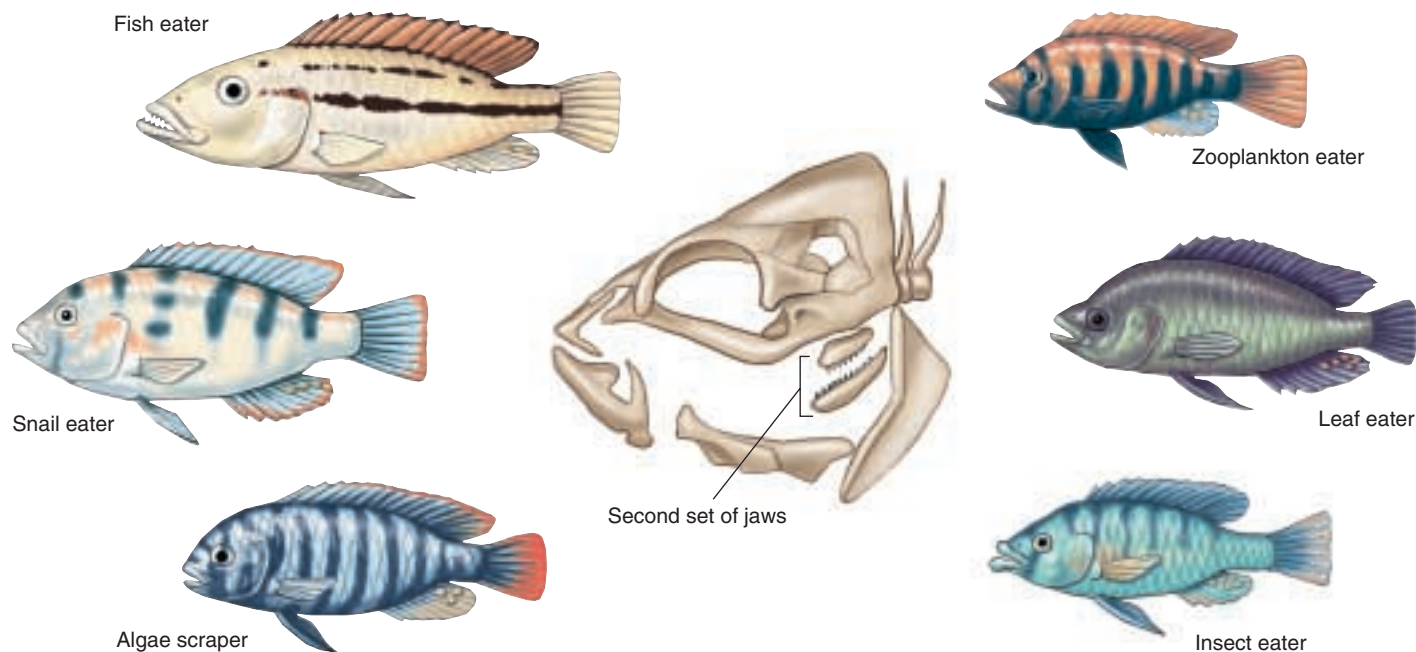


FIGURE 22.13

Cichlid fishes of Lake Victoria. These fishes have evolved adaptations to use a variety of different habitats. The second set of jaws located in the throat of these fish has provided evolutionary flexibility, allowing oral jaws to be modified in many ways.

New Zealand Alpine Buttercups

Adaptive radiations as we have described in Galápagos finches, Hawaiian *Drosophila*, and cichlid fishes seem to be favored by *periodic isolation*. Finches and *Drosophila* invade new islands, local species evolve, and they in turn reinvade the home island, in a cycle of expanding diversity. Similarly, cichlids become isolated by falling water levels, evolving separate species in isolated populations that later are merged when the lake's water level rises again.

A clear example of the role periodic isolation plays in species formation can be seen in the alpine buttercups (genus *Ranunculus*) which grow among the glaciers of New Zealand (figure 22.14). More species of alpine buttercup grow on the two islands of New Zealand than in all of North and South America combined. Detailed studies by the Canadian taxonomist Fulton Fisher revealed that the evolutionary mechanism responsible for inducing this diversity is recurrent isolation associated with the recession of glaciers. The 14 species of alpine *Ranunculus* occupy five distinctive habitats within glacial areas: *snowfields* (rocky crevices among outcrops in permanent snowfields at 7000 to 9000 feet elevation); *snowline fringe* (rocks at lower margin of snowfields between 4000 and 7000 ft); *stony debris* (scree slopes of exposed loose rocks at 2000 to 6000 ft); *sheltered situations* (shaded by rock or shrubs at 1000 to 6000 ft); and *boggy habitats* (sheltered slopes and hollows, poorly drained tussocks at elevations between 2500 and 5000 ft).

Ranunculus speciation and diversification has been promoted by repeated cycles of glacial advance and retreat. As the glaciers retreat, populations become isolated on mountain peaks, permitting speciation (figure 22.15). In the next advance, these new species can expand throughout the mountain range, coming into contact with their close relatives. In this way, one initial species could give rise to many



FIGURE 22.14

A New Zealand alpine buttercup. Fourteen species of alpine *Ranunculus* grow among the glaciers and mountains of New Zealand, including this *R. lyallii*, the giant buttercup.

descendants. Moreover, on isolated mountaintops during glacial retreats, species have convergently evolved to occupy similar habitats; these distantly related but ecologically similar species have then been brought back into contact in subsequent glacial advances.

Recurrent isolation promotes species formation.

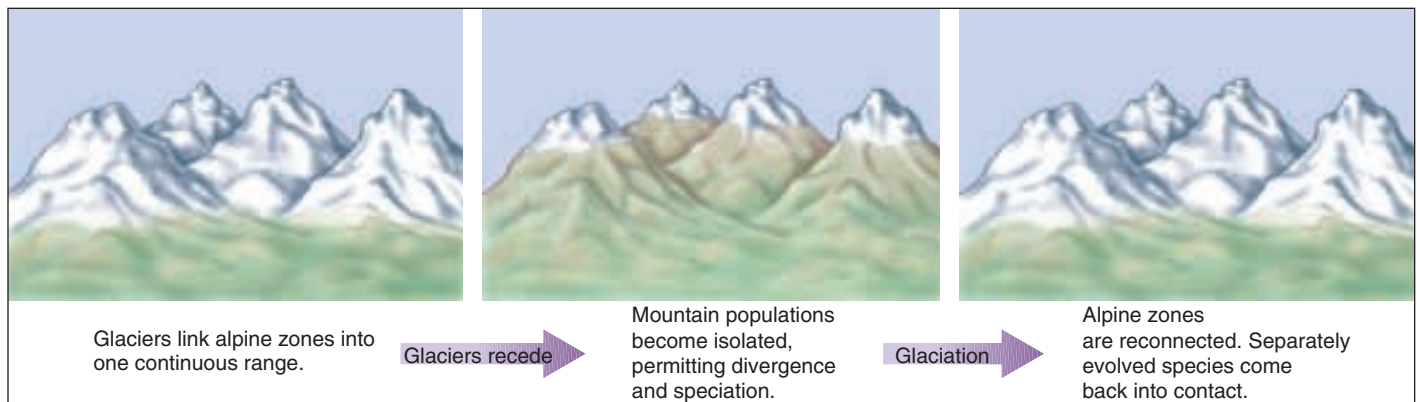


FIGURE 22.15

Periodic glaciation encouraged species formation among alpine buttercups in New Zealand. The formation of extensive glaciers during the Pleistocene linked the alpine zones of many mountains together. When the glaciers receded, these alpine zones were isolated from one another, only to become reconnected with the advent of the next glacial period. During periods of isolation, populations of alpine buttercups diverged in the isolated habitats.

Diversity of Life through Time

Although eukaryotes evolved nearly 3 billion years ago, the diversity of life didn't increase substantially until approximately 550 million years ago. Then, almost all of the extant types of animals evolved in a geologically short period termed the "Cambrian explosion." In addition to organisms whose descendants are recognizable today, a wide variety of

other types of organisms also evolved (figure 22.16). The biology of these creatures, which quickly disappeared without leaving any descendants, is poorly understood. The Cambrian explosion seems to have been a time of evolutionary experimentation and innovation, in which many types of organisms appeared, but most were quickly weeded out. What prompted this explosion of diversity is still a subject of considerable controversy.



FIGURE 22.16

Diversity of animals that evolved during the Cambrian explosion. In addition to the appearance of the ancestors of many present-day groups, such as insects and vertebrates, a variety of bizarre creatures evolved that left no descendants, such as *Wiwaxia*, *Marrella*, *Opabinia*, and the aptly named *Hallucigenia*. The natural history of these species is open to speculation. Key: (1) *Amiskwia*, (2) *Odontogriphus*, (3) *Eldonia*, (4) *Halichondrites*, (5) *Anomalocaris canadensis*, (6) *Pikaia*, (7) *Canadia*, (8) *Marrella splendens*, (9) *Opabinia*, (10) *Ottoia*, (11) *Wiwaxia*, (12) *Yoboia*, (13) *Xiangiangia*, (14) *Aysbeaia*, (15) *Sidneyia*, (16) *Dinomischus*, (17) *Hallucigenia*.

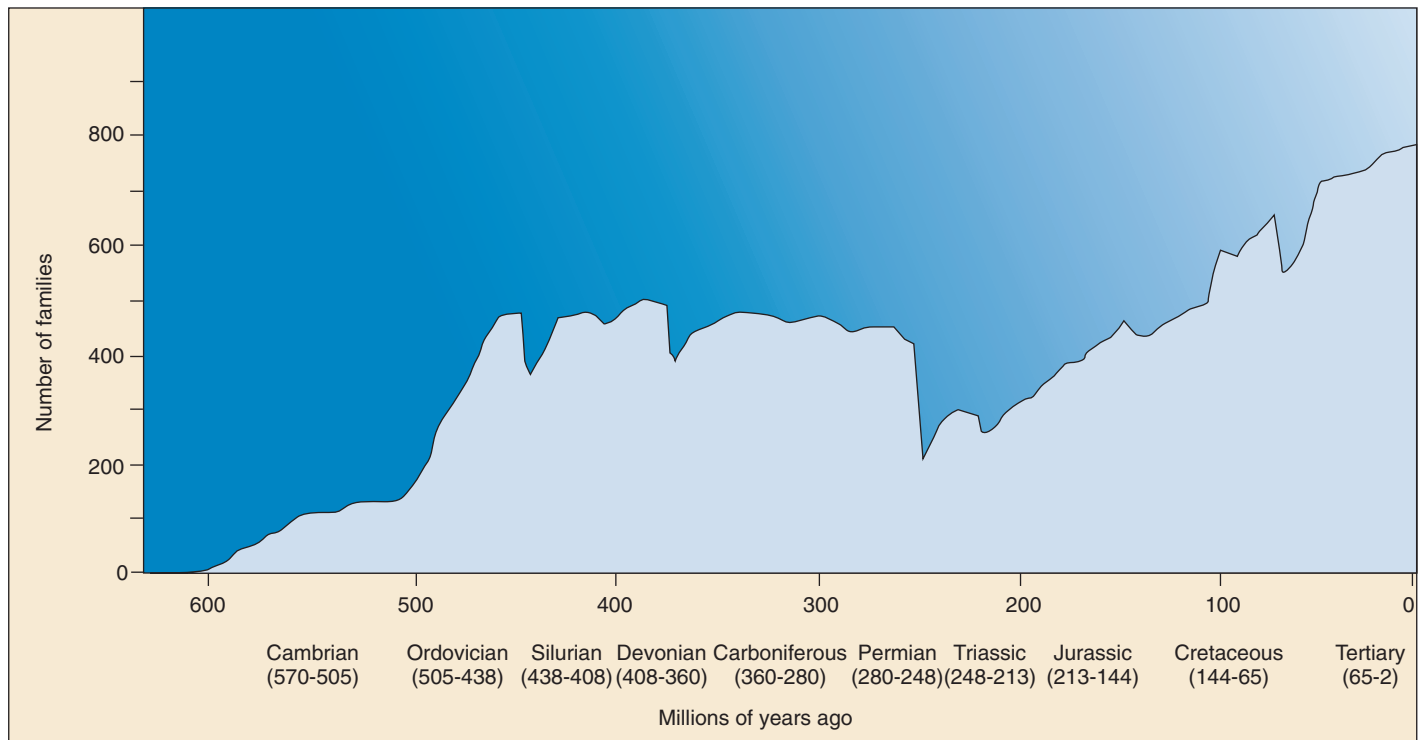


FIGURE 22.17

Diversity through time. Taxonomic diversity of families of marine animals since the Cambrian Period. The fossil record is most complete for marine organisms because they are more readily fossilized than terrestrial species. Families are shown, rather than species, because many species are known from only one specimen, thus introducing error into estimates of time of extinction.

Trends in Species Diversity

The number of species in the world has increased vastly since the Cambrian. However, the trend has been far from consistent (figure 22.17). After a rapid rise, the number of species reached a plateau for about 200 million years ago; since then, the number has risen steadily.

Interspersed in these patterns, however, have been a number of major setbacks, termed **mass extinctions**, in which the number of species has greatly decreased. Five major mass extinctions have been identified, the most severe of which occurred at the end of the Permian Period, approximately 225 million years ago, at which time more than half of all families and as many as 96% of all species may have perished.

The most famous and well-studied extinction, though not as drastic, occurred at the end of the Cretaceous Period (63 million years ago), at which time the dinosaurs and a variety of other organisms went extinct. Recent studies have provided support for the hypothesis that this extinction event was triggered by a large asteroid which slammed into the earth, perhaps causing global forest fires and obscuring the sun for months by throwing particles into the air. This mass extinction did have one positive effect, though: with the disappearance of dinosaurs, mammals,

which previously had been small and inconspicuous, quickly experienced a vast evolutionary radiation, which ultimately produced a wide variety of organisms, including elephants, tigers, whales, and humans. Indeed, a general observation is that biological diversity tends to rebound quickly after mass extinctions, reaching comparable levels of species richness, even if the organisms making up that diversity are not the same.

A Sixth Extinction

The number of species in the world in recent times is greater than it has ever been. Unfortunately, that number is decreasing at an alarming rate due to human activities. Some estimate that as many as one-fourth of all species will become extinct in the next 50 years, a rate of extinction not seen on earth since the Cretaceous mass extinction.

The number of species has increased through time, although not at constant rates. Several major extinction events have substantially, though briefly, reduced the number of species.

The Pace of Evolution

Different kinds of organisms evolve at different rates. Mammals, for example, evolve relatively slowly. On the basis of a relatively complete fossil record, it has been estimated that an average value for the duration of a “typical” mammal species, from formation of the species to its extinction, might be about 200,000 years. American paleontologist George Gaylord Simpson has pointed out that certain groups of animals, such as lungfishes, are apparently evolving even more slowly than mammals. In fact, Simpson estimated that there has been little evolutionary change among lungfishes over the past 150 million years, and even slower rates of evolution occur in other groups.

Evolution in spurts?

Not only does the rate of evolution differ greatly from group to group, but evolution within a group apparently proceeds rapidly during some periods and relatively slowly during others. The fossil record provides evidence for such variability in evolutionary rates, and evolutionists are very interested in understanding the factors that account for it. In 1972, paleontologists Niles Eldredge of the American Museum of Natural History in New York and Stephen Jay Gould of Harvard University proposed that evolution normally proceeds in spurts. They claimed that the evolutionary process is a series of **punctuated equilibria**. Evolutionary innovations would occur and give rise to new lines; then these lines might persist unchanged for a long time, in “equilibrium.” Eventually there would be a new spurt of evolution, creating a “punctuation” in the fossil record. Eldredge and Gould contrast their theory of punctuated equilibrium with that of **gradualism**, or gradual evolutionary change, which they claimed was what Darwin and most earlier students of evolution had considered normal (figure 22.18).

Eldredge and Gould proposed that **stasis**, or lack of evolutionary change, would be expected in large populations experiencing stabilizing selection over long periods of time. In contrast, rapid evolution of new species might occur if populations colonized new areas. Such populations would be small, isolated, and possibly already differing from their parental population as a result of the founder effect. This, combined with selective pressures

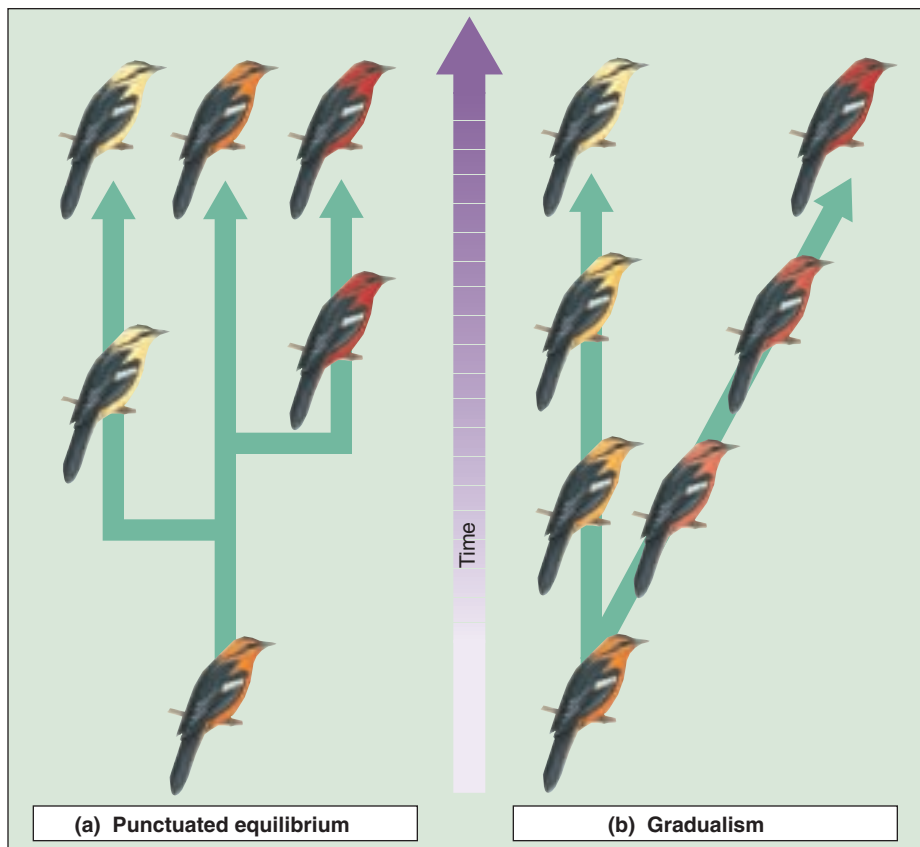


FIGURE 22.18

Two views of the pace of macroevolution. (a) Punctuated equilibrium surmises that species formation occurs in bursts, separated by long periods of quiet, while (b) gradualism surmises that species formation is constantly occurring.

from a new environment, could bring about rapid change.

Unfortunately, the distinctions are not as clear-cut as implied by this discussion. Some well-documented groups such as African mammals clearly have evolved gradually, and not in spurts. Other groups, like marine bryozoa, seem to show the irregular pattern of evolutionary change the punctuated equilibrium model predicts. It appears, in fact, that gradualism and punctuated equilibrium are two ends of a continuum. Although some groups appear to have evolved solely in a gradual manner and others only in a punctuated mode, many other groups appear to show evidence of both gradual and punctuated episodes at different times in their evolutionary history.

The punctuated equilibrium model assumes that evolution occurs in spurts, between which there are long periods in which there is little evolutionary change. The gradualism model assumes that evolution proceeds gradually, with successive change in a given evolutionary line.

Problems with the Biological Species Concept

Since the biological species concept was first proposed by Ernst Mayr in the 1940s, it has been the predominant idea of how to recognize and define species. However, in recent years, workers from a variety of fields have begun to question how universally applicable the concept really is.

The Extent of Hybridization

The crux of the matter concerns hybridization. Biological species are reproductively isolated, so that hybridization should be rare. If hybridization is common, one would expect one of two quick outcomes: either reinforcement would occur, leading to the perfection of isolating mechanisms and an end to hybridization, or the two populations would merge together into a single homogeneous gene pool.

However, in recent years biologists have detected much greater amounts of hybridization than previously realized between populations that seem to neither be experiencing reinforcement nor losing their specific identities. Botanists have always been aware that species can often experience substantial amounts of hybridization. One study found that more than 50% of the plant species surveyed in California were not well defined by genetic isolation. For example, the fossil record indicates that balsam poplars and cottonwoods have been phenotypically distinct for 12 million years, but throughout this time, they have routinely produced hybrids. Consequently, for many years, many botanists have felt that the biological species concept only applies to animals.

What is becoming increasingly evident, however, is that hybridization is not all that uncommon in animals, either. One recent survey indicated that almost 10% of the world's 9500 bird species are known to have hybridized in nature. Recent years have seen the documentation of more and more cases in which substantial hybridization occurs between animal species. Again, the Galápagos finches provide a particularly well-studied example. Three species on the island of Daphne Major—the medium ground finch, the cactus finch, and the small ground finch—are clearly distinct morphologically and occupy different ecological niches. Careful studies over the past 20 years by Peter and Rosemary Grant found that, on average, 2% of the medium ground finches and 1% of the cactus finches mated with other species every year. Furthermore, hybrid offspring appeared to be at no

disadvantage either in terms of survival or subsequent reproduction. This is not a trivial amount of genetic exchange, and one might expect to see the species coalescing into one variable population, but the species are nonetheless maintaining their distinctiveness.

Alternatives to the Biological Species Concept

This is not to say hybridization is rampant throughout the animal world. As the bird survey indicated, 90% of bird species are not known to hybridize, and even fewer probably experience significant amounts of hybridization. Still, it is a common enough occurrence to cast doubt about whether reproductive isolation is the only force maintaining the integrity of species.

An alternative hypothesis is that the distinctions among species are maintained by natural selection. The idea is that each species has adapted to its own specific part of the environment. Stabilizing selection then maintains the species' adaptations; hybridization has little effect because alleles introduced into the gene pool from other species quickly would be eliminated by natural selection.

We have already seen in chapter 20 that the interaction between gene flow and natural selection can have many outcomes. In some cases, strong selection can overwhelm any effects of gene flow, but in other situations, gene flow can prevent populations from eliminating less successful alleles from a population. As a general explanation, then, natural selection is not likely to have any fewer exceptions than the biological species concept, although it may prove more successful for certain types of organisms or habitats.

A variety of other ideas have been put forward to establish criteria for defining species. Many of these are specific to a particular type of organism and none has universal applicability. In truth, it may be that there is no single explanation for what maintains the identity of species. Given the incredible variation evident in plants, animals, and microorganisms in all aspects of their biology, it is perhaps not surprising that different processes are operating in different organisms. This is an area of active research that demonstrates the dynamic nature of the field of evolutionary biology.

Hybridization has always been recognized to be widespread among plants, but recent research reveals that it is surprisingly high in animals, too. Because of the diversity of living organisms, no single definition of what constitutes a species may be universally applicable.



Summary

Questions

Media Resources

22.1 Species are the basic units of evolution.

- Species are groups of organisms that differ from one another in one or more characteristics and do not hybridize freely when they come into contact in their natural environment. Many species cannot hybridize with one another at all.
 - Species exhibit geographic variation, yet phenotypically distinctive populations are connected by intermediate forms.
- Define the term *sympatry*. Why is sympatric speciation thought by many to be unlikely?
 - What is the biological species concept?

22.2 Species maintain their genetic distinctiveness through barriers to reproduction.

- Among the factors that separate populations and species are geographical, ecological, temporal, behavioral, and mechanical isolation, as well as factors that inhibit the fusion of gametes or the normal development of the hybrid organisms.
 - Some isolating mechanisms (prezygotic) prevent hybrid formation; others (postzygotic) prevent hybrids from surviving and reproducing.
- What is the difference between prezygotic and postzygotic isolating mechanisms?
 - What barriers exist to hybrid formation and success? Which are prezygotic and which are postzygotic isolating mechanisms? Why do some people think the term “isolating mechanism” is misleading?



- Activity: Allopatric Speciation
- Introduction to Speciation
- Sympatric Speciation
- Allopatric Speciation
- Constructing Phylogenies

22.3 We have learned a great deal about how species form.

- Reproductive isolation can arise as populations differentiate by adaptation to different environments, as well as by random genetic drift, founder effects, or population bottlenecks.
 - Natural selection may favor changes in the mating system when a species occupies a new habitat, so that the species becomes reproductively isolated from other species.
 - When two species are not completely reproductively isolated, natural selection may favor the evolution of more effective isolating mechanisms to prevent hybridization, a process termed “reinforcement.”
- How does selection relate to population divergence?
 - How many genes are involved in the speciation process?
 - When are hybrids at a disadvantage? What can be the result of this disadvantage?
 - Define the term *polyploidy*.



- Student Research: Evolution in Ferns

22.4 Clusters of species reflect rapid evolution.

- Clusters of species arise when populations differentiate to fill several niches. On islands, differentiation is often rapid because of numerous open habitats.
 - The pace of evolution is not constant among all organisms. Some scientists believe it occurs in spurts, others argue that it proceeds gradually.
 - Hybridization occurs commonly among plants and even among animals. The biological species concept may not apply to all organisms.
- What is adaptive radiation? What types of habitats encourage it? Why?
 - What is the difference between gradualism and punctuated equilibrium?
 - Why is the biological species concept no longer considered to be universally applicable?



- Evolutionary Trends



- Book Reviews
- Darwin's Dreampond* by Goldschmidt
- The Beak of the Finch* by Weiner