drastically in frequency. In some cases, previously rare alleles in the source population may be a significant fraction of the new population's genetic endowment. This phenomenon is called the **founder effect.**

Founder effects are not rare in nature. Many self-pollinating plants start new populations from a single seed. Founder effects have been particularly important in the evolution of organisms on distant oceanic islands, such as the Hawaiian and Galápagos Islands. Most of the organisms in such areas probably derive from one or a few initial founders. Although rare, such events are occasionally observed, such as when a mass of vegetation carrying several iguanas washed up on the shore of the Caribbean island of Anguilla in 1996, leading to the establishment of a population that still occurs there to this day.

In a similar way, isolated human populations begun by relatively few individuals are often dominated by genetic features characteristic of their founders. Amish populations in the United States, for example, have unusually high frequencies of a number of conditions, such as polydactylism (the presence of a sixth finger).

The bottleneck effect

Even if organisms do not move from place to place, occasionally their populations may be drastically reduced in size. This may result from flooding, drought, epidemic disease, and other natural forces, or from changes in the environment. The few surviving individuals may constitute a random genetic sample of the original population (unless some individuals survive specifically because of their genetic makeup). The resulting alterations and loss of genetic variability have been termed the **bottleneck effect.**

The genetic variation of some living species appears to be severely depleted, probably as the result of a bottleneck effect in the past. For example, the northern elephant seal, which breeds on the western coast of North America and nearby islands, was nearly hunted to extinction in the nineteenth century and was reduced to a single population containing perhaps no more than 20 individuals on the island of Guadalupe off the coast of Baja, California (figure 20.6). As a result of this bottleneck, the species has lost almost all of its genetic variation, even though the seal populations have rebounded and now number in the tens of thousands and breed in locations as far north as near San Francisco.

Any time a population becomes drastically reduced in numbers, such as in endangered species, the bottleneck effect is a potential problem. Even if population size rebounds, the lack of variability may mean that the species remains vulnerable to extinction—a topic we will return to in chapter 59.

Selection favors some genotypes over others

As Darwin pointed out, some individuals leave behind more progeny than others, and the rate at which they do so is affected by phenotype and behavior. We describe the results of this process as **selection** (see figure 20.4*e*). In *artificial selection*, a breeder selects for the desired characteristics. In *natural selection*, environmental conditions determine which individuals in a population produce the most offspring.

For natural selection to occur and to result in evolutionary change, three conditions must be met:

1. **Variation must exist among individuals in a population.** Natural selection works by favoring individuals with some traits over individuals with alternative traits. If no variation exists, natural selection cannot operate.
2. **Variation among individuals must result in differences in the number of offspring surviving in the next generation.** This is the essence of natural selection. Because of their phenotype or behavior, some individuals are more successful than others in producing offspring. Although many traits are phenotypically variable, individuals exhibiting variation do not always differ in survival and reproductive success.
3. **Variation must be genetically inherited.** For natural selection to result in evolutionary change, the selected differences must have a genetic basis. Not all variation has a genetic basis—even genetically identical individuals may be phenotypically quite distinctive if they grow up in different environments. Such environmental effects are

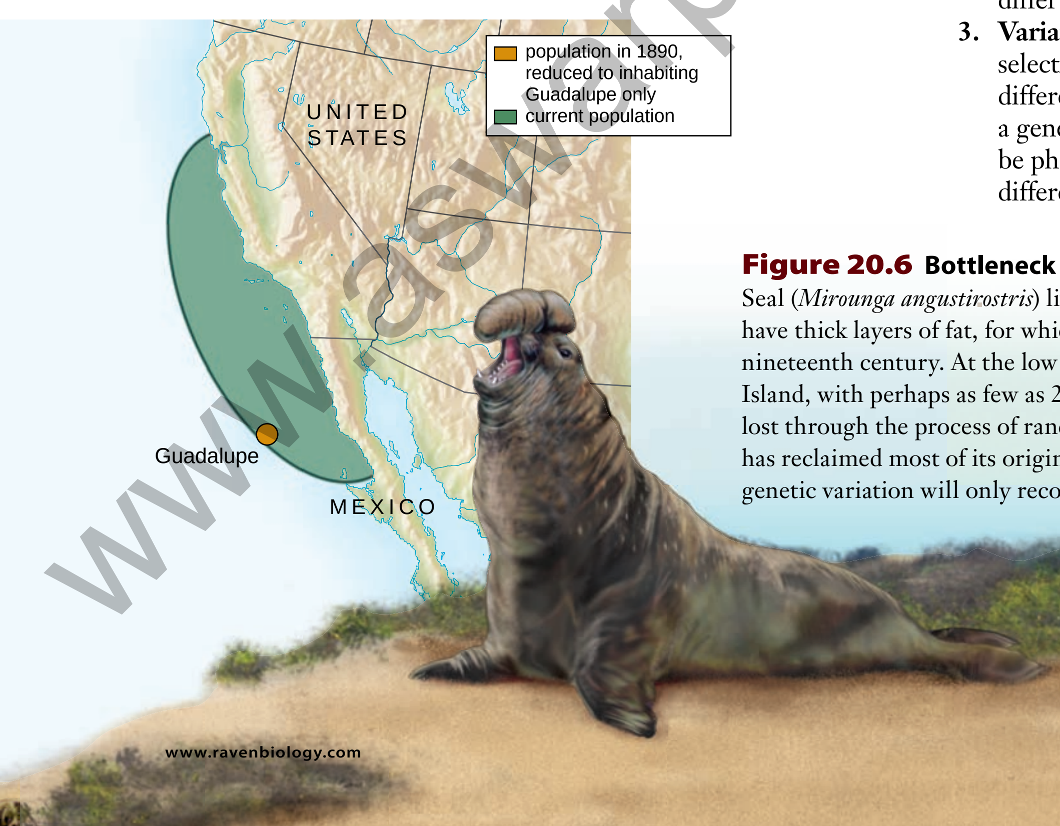


Figure 20.6 Bottleneck effect: case study. Because the Northern Elephant Seal (*Mirounga angustirostris*) lives in very cold waters, these, the world's largest seals, have thick layers of fat, for which they were hunted nearly to extinction late in the nineteenth century. At the low point, only one population remained on Guadalupe Island, with perhaps as few as 20 individuals; during this time, genetic variation was lost through the process of random genetic drift. Since being protected, the species has reclaimed most of its original range and now numbers in the tens of thousands, but genetic variation will only recover slowly over time as mutations accumulate.

common in nature. In many turtles, for example, individuals that hatch from eggs laid in moist soil are heavier, with longer and wider shells, than individuals from nests in drier areas.

When phenotypically different individuals do not differ genetically, then differences in the number of their offspring will not alter the genetic composition of the population in the next generation, and thus, no evolutionary change will have occurred.

It is important to remember that natural selection and evolution are not the same—the two concepts often are incorrectly equated. Natural selection is a process, whereas evolution is the historical record, or outcome, of change through time. Natural selection (the process) can lead to evolution (the outcome), but natural selection is only one of several processes that can result in evolutionary change. Moreover, natural selection can occur without producing evolutionary change; only if variation is genetically based will natural selection lead to evolution.

Selection to avoid predators

The result of evolution driven by natural selection is that populations become better adapted to their environment. Many of the most dramatic documented instances of adaptation involve genetic changes that decrease the probability of capture by a predator. The caterpillar larvae of the common sulphur butterfly *Colias eurytheme* usually exhibit a pale green color, providing excellent camouflage against the alfalfa plants on which they feed. An alternative bright yellow color morph is kept at very low frequency because this color renders the larvae highly visible on the food plant, making it easier for bird predators to see them (see figure 20.4*e*).

One of the most dramatic examples of background matching involves ancient lava flows in the deserts of the American Southwest. In these areas, the black rock formations produced when the lava cooled contrast starkly with the surrounding bright glare of the desert sand. Populations of many species of animals occurring on these rocks—including lizards, rodents, and a variety of insects—are dark in color, whereas sand-dwelling populations in surrounding areas are much lighter (figure 20.7).

Predation is the likely cause for these differences in color. Laboratory studies have confirmed that predatory birds such as owls are adept at picking out individuals occurring on backgrounds to which they are not adapted.

Selection to match climatic conditions

Many studies of selection have focused on genes encoding enzymes, because in such cases the investigator can directly assess the consequences to the organism of changes in the frequency of alternative enzyme alleles.

Often investigators find that enzyme allele frequencies vary with latitude, so that one allele is more common in northern populations, but is progressively less common at more southern locations. A superb example is seen in studies of a fish, the mummichog *(Fundulus heteroclitus)*, which ranges along the eastern coast of North America. In this fish, geographic variation occurs in allele frequencies for the gene that produces the enzyme lactate dehydrogenase, which catalyzes the conversion of pyruvate to lactate (see section 7.8).

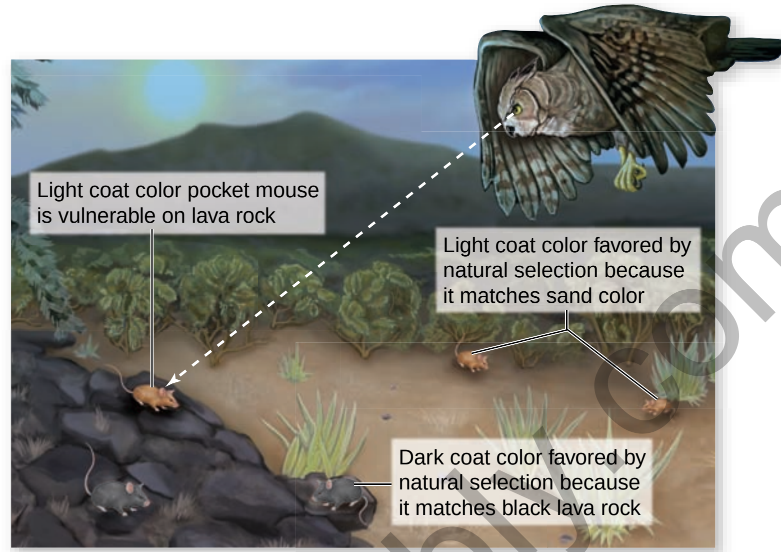


Figure 20.7 Pocket mice from the Tularosa Basin of New Mexico whose color matches their background. Black lava formations are surrounded by desert, and selection favors coat color in pocket mice that matches their surroundings. Genetic studies indicate that the differences in coat color are the result of small differences in the DNA of alleles of a single gene.

Biochemical studies show that the enzymes formed by these alleles function differently at different temperatures, thus explaining their geographic distributions. The form of the enzyme more frequent in the north is a better catalyst at low temperatures than is the enzyme from the south. Moreover, studies indicate that at low temperatures, individuals with the northern allele swim faster, and presumably survive better, than individuals with the alternative allele.

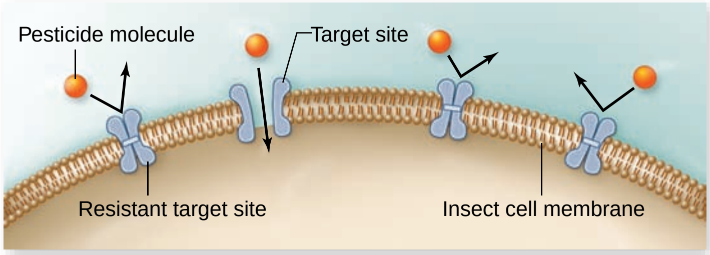
Selection for pesticide and microbial resistance

A particularly clear example of selection in natural populations is provided by studies of pesticide resistance in insects. The widespread use of insecticides has led to the rapid evolution of resistance in more than 500 pest species. The cost of this evolution, in terms of crop losses and increased pesticide use, has been estimated at $3-8 billion per year.

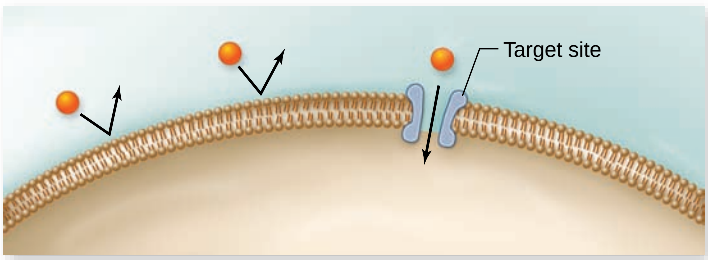
In the housefly, the resistance allele at the *pen* gene decreases the uptake of insecticide, whereas alleles at the *kdr* and *dld-r* genes decrease the number of target sites, thus decreasing the binding ability of the insecticide (figure 20.8). Other alleles enhance the ability of the insects' enzymes to identify and detoxify insecticide molecules.

Single genes are also responsible for resistance in other organisms. For example, Norway rats are normally susceptible to the pesticide warfarin, which diminishes the clotting ability of the rat's blood and leads to fatal hemorrhaging. However, a resistance allele at a single gene reduces the ability of warfarin to bind to its target enzyme and thus renders it ineffective.

Selection imposed by humans has also led to the evolution of resistance to antibiotics in many disease-causing pathogens. For example, *Staphylococcus aureus*, which causes staph infections, was initially treated by penicillin. However, within four years of mass-production of the drug, evolutionary change



a. Insect cells with resistance allele at *pen* gene: decreased uptake of the pesticide.



b. Insect cells with resistance allele at *kdr* gene: decreased number of target sites for the pesticide.

Figure 20.8 Selection for pesticide resistance. Resistance alleles at genes such as *pen* and *kdr* allow insects to be more resistant to pesticides. Insects that possess these resistance alleles have become more common through selection.

in *S. aureus* modified an enzyme so that it would attack penicillin and render it inactive. Since that time, several other drugs have been developed to attack the microbe, and each time resistance has evolved. As a result, staph infections have re-emerged as a major health threat.

Learning Outcomes Review 20.3

Five factors can bring about deviation from the predicted Hardy–Weinberg genotype frequencies. Of these, only selection regularly produces adaptive evolutionary change, but the genetic constitution of populations, and thus the course of evolution, can also be affected by mutation, gene flow, nonrandom mating, and genetic drift.

- ***How do each of these processes cause populations to vary from Hardy-Weinberg equilibrium?***

20.4 *Fitness and Its Measurement*

Learning Outcomes

1. ***Define evolutionary fitness.***
2. ***Explain the different components of fitness.***
3. ***Demonstrate how the success of different phenotypes can be compared by calculating their relative fitness.***

Selection occurs when individuals with one phenotype leave more surviving offspring in the next generation than individuals with an alternative phenotype. Evolutionary biologists quantify reproductive success as **fitness,** the number of surviving offspring left in the next generation.

Fitness is a relative concept; the most fit phenotype is simply the one that produces, on average, the greatest number of offspring.

A phenotype with greater fitness usually increases in frequency

Suppose, for example, that in a population of toads, two phenotypes exist: green and brown. Suppose, further, that green toads leave, on average, 4.0 offspring in the next generation, but brown toads leave only 2.5. By custom, the most fit phenotype is assigned a fitness value of 1.0, and other phenotypes are expressed as relative proportions. In this case, the fitness of the green phenotype would be $4.0/4.0 = 1.000$, and the fitness of the brown phenotype would be $2.5/4.0 = 0.625$. The difference in fitness would therefore be $1.000 - 0.625 = 0.375$. A difference in fitness of 0.375 is quite large; natural selection in this case strongly favors the green phenotype.

If differences in color have a genetic basis, then we would expect evolutionary change to occur; the frequency of green toads should be substantially greater in the next generation. Further, if the fitness of two phenotypes remained unchanged, we would expect alleles for the brown phenotype eventually to disappear from the population.

Inquiry question

? **Why might the frequency of green toads not increase in the next generation, even if color differences have a genetic basis?**

Fitness may consist of many components

Although selection is often characterized as "survival of the fittest," differences in survival are only one component of fitness.

Even if no differences in survival occur, selection may operate if some individuals are more successful than others in attracting mates. In many territorial animal species, for example, large males mate with many females, and small males rarely get to mate. Selection with respect to mating success is termed *sexual selection;* we describe this topic more fully in the discussion of behavioral biology in chapter 54.

In addition, the number of offspring produced per mating is also important. Large female frogs and fish lay more eggs than do smaller females, and thus they may leave more offspring in the next generation.

Fitness is therefore a combination of survival, mating success, and number of offspring per mating. Selection favors phenotypes with the greatest fitness, but predicting fitness from a single component can be tricky because traits favored for one component of fitness may be at a disadvantage for others. As an example, in water striders, larger females lay more eggs per day

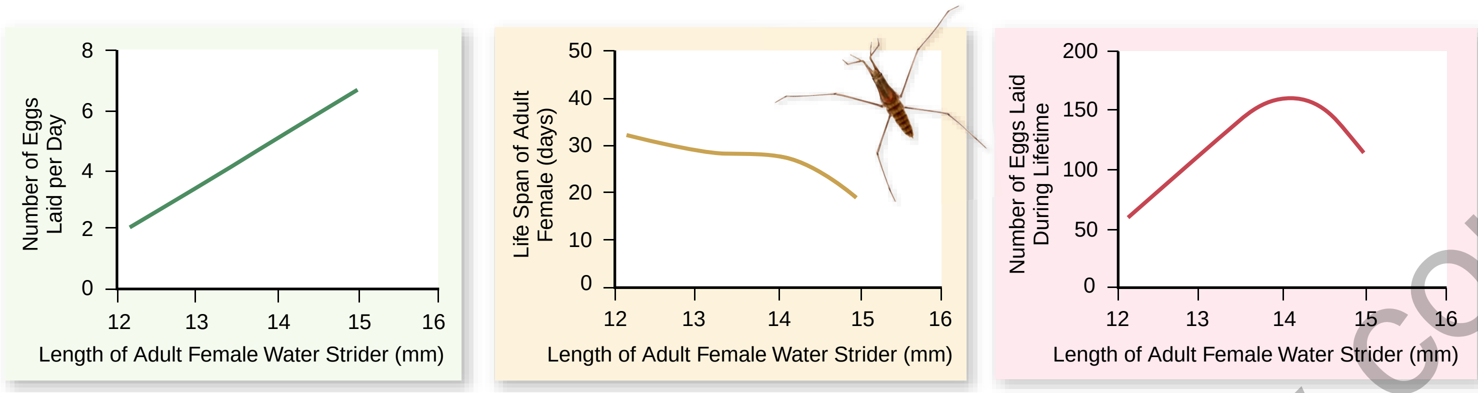


Figure 20.9 Body size and egg-laying in water striders. Larger female water striders lay more eggs per day (left panel), but also survive for a shorter period of time (center panel). As a result, intermediate-sized females produce the most offspring over the course of their entire lives and thus have the highest fitness (right panel).

? **Inquiry question**

What evolutionary change in body size might you expect? If the number of eggs laid per day was not affected by body size, would your prediction change?

(figure 20.9). Thus, natural selection at this stage favors large size. However, larger females also die at a younger age and thus have fewer opportunities to reproduce than smaller females. Overall, the two opposing directions of selection cancel each other out, and the intermediate-sized females leave the most offspring in the next generation.

Learning Outcomes Review 20.4

Fitness is defined by an organism's reproductive success relative to other members of its population. This success is determined by how long it survives, how often it mates, and how many offspring it produces per mating. Relative fitness assigns numerical values to different phenotypes relative to the most fit phenotype.

- ***Is one of these factors always the most important in determining reproductive success? Explain.***

20.5 *Interactions Among Evolutionary Forces*

Learning Outcomes

1. ***Discuss how evolutionary processes can work simultaneously, but in opposing ways.***
2. ***Evaluate what determines the evolutionary outcome when multiple processes are operating simultaneously.***

The amount of genetic variation in a population may be determined by the relative strength of different evolutionary processes. Sometimes these processes act together, and in other cases they work in opposition.

Mutation and genetic drift may counter selection

In theory, if allele *B* mutates to allele *b* at a high enough rate, allele *b* could be maintained in the population, even if natural selection strongly favored allele *B*. In nature, however, mutation rates are rarely high enough to counter the effects of natural selection.

The effect of natural selection also may be countered by genetic drift. Both of these processes may act to remove variation from a population. But selection is a nonrandom process that operates to increase the representation of alleles that enhance survival and reproductive success, whereas genetic drift is a random process in which any allele may increase. Thus, in some cases, drift may lead to a decrease in the frequency of an allele that is favored by selection. In some extreme cases, drift may even lead to the loss of a favored allele from a population.

Remember, however, that the magnitude of drift is inversely related to population size; consequently, natural selection is expected to overwhelm drift, except when populations are very small.

Gene flow may promote or constrain evolutionary change

Gene flow can be either a constructive or a constraining force. On one hand, gene flow can spread a beneficial mutation that arises in one population to other populations. On the other hand, gene flow can impede adaptation within a population by the continual flow of inferior alleles from other populations.

Consider two populations of a species that live in different environments. In this situation, natural selection might favor different alleles—*B* and *b*—in the two populations. In the absence of other evolutionary processes such as gene flow, the frequency of *B* would be expected to reach 100% in one population and 0% in the other. However, if gene flow occurred between the two populations, then the less favored allele would continually be reintroduced into each population. As a result, the frequency of the alleles in the populations would reflect a balance between the rate at which gene flow brings the inferior allele into a population, and the rate at which natural selection removes it.

A classic example of gene flow opposing natural selection occurs on abandoned mine sites in Great Britain. Although mining activities ceased hundreds of years ago, the concentration of metal ions in the soil is still much greater than in surrounding areas. Large concentrations of heavy metals are generally toxic to plants, but alleles at certain genes confer the ability to grow on soils high in heavy metals. The ability to tolerate heavy metals comes at a price, however; individuals with the resistance allele exhibit lower growth rates on nonpolluted soil. Consequently, we would expect the resistance allele to occur with a frequency of 100% on mine sites and 0% elsewhere.

Heavy-metal tolerance has been studied intensively in the slender bent grass *Agrostis tenuis*, in which the resistance allele occurs at intermediate levels in many areas (figure 20.10). The explanation relates to the reproductive system of this grass, in which pollen, the floral equivalent of sperm, is dispersed by the wind. As a result, pollen grains—and the alleles they carry—can move great distances, leading to levels of gene flow between mine sites and unpolluted areas high enough to counteract the effects of natural selection.

In general, the extent to which gene flow can hinder the effects of natural selection should depend on the relative strengths of the two processes. In species in which gene flow is generally strong, such as in birds and wind-pollinated plants, the frequency of the allele less favored by natural selection may be relatively high. In more sedentary species that exhibit low levels of gene flow, such as salamanders, the favored allele should occur at a frequency near 100%.

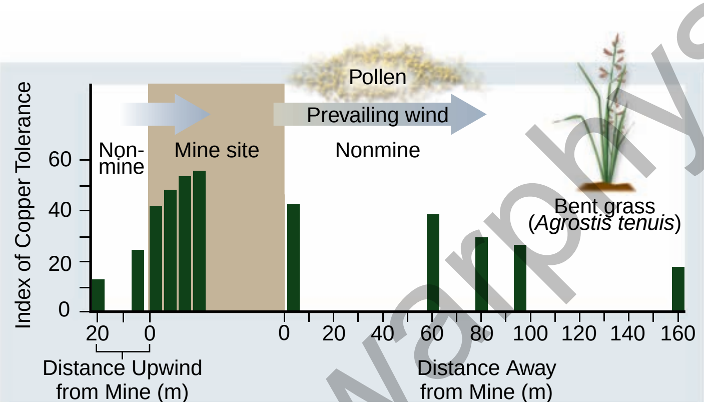


Figure 20.10 Degree of copper tolerance in grass plants on and near ancient mine sites. Individuals with tolerant alleles have decreased growth rates on unpolluted soil. Thus, we would expect copper tolerance to be 100% on mine sites and 0% on non-mine sites. However, prevailing winds blow pollen containing nontolerant alleles onto the mine site and tolerant alleles beyond the site's borders. The amount of pollen received decreases with distance, which explains the changes in levels of tolerance. The index of copper tolerance is calculated as the growth rate of a plant on soil with high concentrations of copper relative to growth rate on soils with low levels of copper; the higher the index, the more tolerant the plant is of heavy metal pollution.

Inquiry question

? **Would you expect the frequency of copper tolerance to be affected by distance from the mine site?**

Learning Outcomes Review 20.5

Allele frequencies sometimes reflect a balance between opposing processes. Gene flow, for example, may increase some alleles while natural selection decreases them. Where several processes are involved, observed frequencies depend on the relative strength of the processes.

- ***Under what circumstances might evolutionary processes operate in the same direction, and what would be the outcome?***

20.6 *Maintenance of Variation*

Learning Outcomes

1. ***Define frequency-dependent selection, oscillating selection, and heterozygote advantage.***
2. ***Explain how these processes affect the amount of genetic variation in a population.***

In the previous pages, natural selection has been discussed as a process that removes variation from a population by favoring one allele over others at a gene locus. However, in some circumstances, selection can do exactly the opposite and actually maintain population variation.

Frequency-dependent selection may favor either rare or common phenotypes

In some circumstances, the fitness of a phenotype depends on its frequency within the population, a phenomenon termed **frequency-dependent selection.** This type of selection favors certain phenotypes depending on how commonly or uncommonly they occur.

Negative frequency-dependent selection

In negative frequency-dependent selection, rare phenotypes are favored by selection. Assuming a genetic basis for phenotypic variation, such selection will have the effect of making rare alleles more common, thus maintaining variation.

Negative frequency-dependent selection can occur for many reasons. For example, it is well known that animals or people searching for something form a "search image." That is, they become particularly adept at picking out certain objects. Consequently, predators may form a search image for common prey phenotypes. Rare forms may thus be preyed upon less frequently.

An example is fish predation on an insect, the water boatman, which occurs in three different colors. Experiments indicate that each of the color types is preyed upon disproportionately when it is the most common one; fish eat more of the common-colored insects than would occur by chance alone (figure 20.11).

Another cause of negative frequency dependence is resource competition. If genotypes differ in their resource requirements, as occurs in many plants, then the rarer genotype will have fewer competitors. When the different resource types are equally abundant, the rarer genotype will be at an advantage relative to the more common genotype.

Positive frequency-dependent selection

Positive frequency-dependent selection has the opposite effect; by favoring common forms, it tends to eliminate variation from a population. For example, predators don't always select common individuals. In some cases, "oddballs" stand out from the rest and attract attention (figure 20.12).

The strength of selection should change through time as a result of frequency-dependent selection. In negative frequency-dependent selection, rare genotypes should become increasingly common, and their selective advantage will decrease correspondingly. Conversely, in positive frequency dependence, the rarer a genotype becomes, the greater the chance it will be selected against.

SCIENTIFIC THINKING

Question: *Does negative frequency-dependent selection maintain variation in a population?*

Hypothesis: *Fish may disproportionately capture water boatmen (a type of aquatic insect) with the most common color.*

Experiment: *Place predatory fish in different aquaria with the different frequencies of the color types in each aquarium.*

Result: *Fish prey disproportionately on the common color in each aquarium. The rare color in each aquarium generally survives best.*

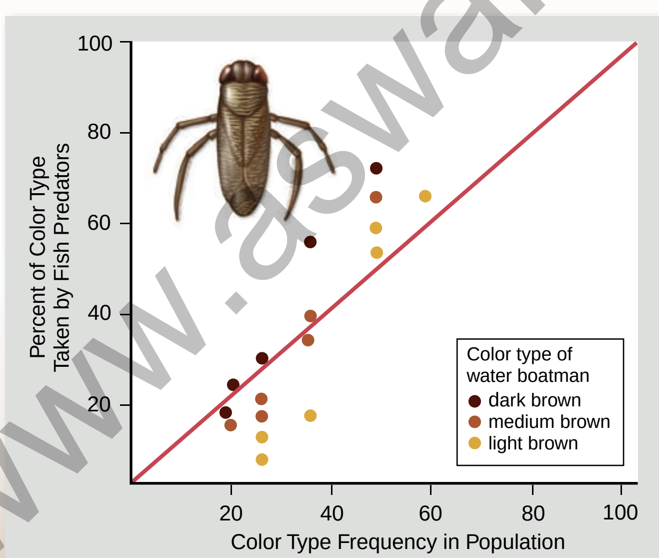


Figure 20.11 Frequency-dependent selection.

Figure 20.12 Positive frequency-dependent selection. In some cases, rare individuals stand out from the rest and draw the attention of predators; thus, in these cases, common phenotypes have the advantage (positive frequency-dependent selection).

In oscillating selection, the favored phenotype changes as the environment changes

In some cases, selection favors one phenotype at one time and another phenotype at another time, a phenomenon called **oscillating selection.** If selection repeatedly oscillates in this fashion, the effect will be to maintain genetic variation in the population.

One example, discussed in chapter 21, concerns the medium ground finch of the Galápagos Islands. In times of drought, the supply of small, soft seeds is depleted, but there are still enough large seeds around. Consequently, birds with big bills are favored. However, when wet conditions return, the ensuing abundance of small seeds favors birds with smaller bills.

Oscillating selection and frequency-dependent selection are similar because in both cases the form of selection changes through time. But it is important to recognize that they are not the same: In oscillating selection, the fitness of a phenotype does not depend on its frequency; rather, environmental changes lead to the oscillation in selection. In contrast, in frequency-dependent selection, it is the change in frequencies themselves that leads to the changes in fitness of the different phenotypes.

In some cases, heterozygotes may exhibit greater fitness than homozygotes

If heterozygotes are favored over homozygotes, then natural selection actually tends to maintain variation in the population. This **heterozygote advantage** favors individuals with copies of both alleles, and thus works to maintain both alleles in the population. Some evolutionary biologists believe that heterozygote advantage is pervasive and can explain the high levels of polymorphism observed in natural populations. Others, however, believe that it is relatively rare.

The best documented example of heterozygote advantage is sickle cell anemia, a hereditary disease affecting hemoglobin in humans. Individuals with sickle cell anemia exhibit symptoms of severe anemia and abnormal red blood cells that are irregular

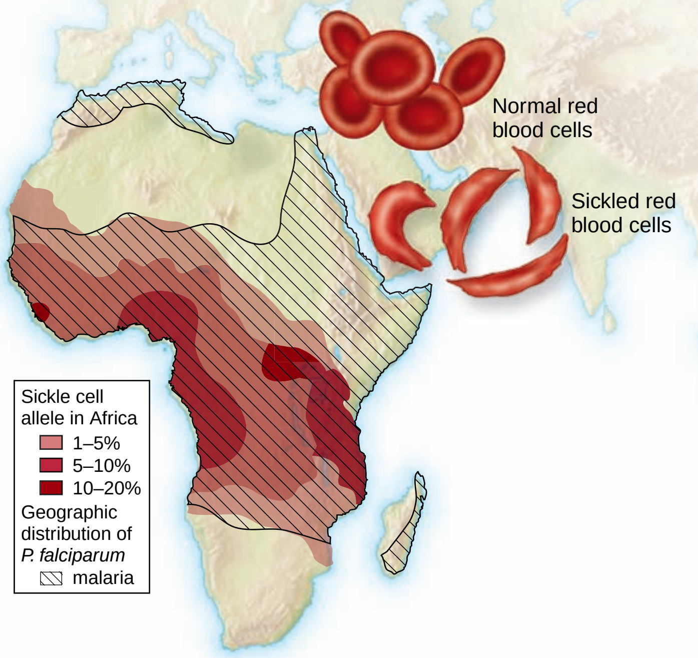


Figure 20.13 Frequency of sickle cell allele and distribution of *Plasmodium falciparum* malaria. The red blood cells of people homozygous for the sickle cell allele collapse into sickled shapes when the oxygen level in the blood is low. The distribution of the sickle cell allele in Africa coincides closely with that of *P. falciparum* malaria.

in shape, with a great number of long, sickle-shaped cells (figure 20.13). Chapter 13 discusses why the sickle cell mutation (*S*) causes red blood cells to sickle.

The average incidence of the *S* allele in central African populations is about 0.12, far higher than that found among African Americans. From the Hardy–Weinberg principle, you can calculate that 1 in 5 central African individuals is heterozygous at the *S* allele, and 1 in 100 is homozygous and develops the fatal form of the disorder. People who are homozygous for the sickle cell allele almost never reproduce because they usually die before they reach reproductive age.

Why, then, is the *S* allele not eliminated from the central African population by selection rather than being maintained at such high levels? As it turns out, one of the leading causes of illness and death in central Africa, especially among young children, is malaria. People who are heterozygous for the sickle cell allele (and thus do not suffer from sickle cell anemia) are much less susceptible to malaria. The reason is that when the parasite that causes malaria, *Plasmodium falciparum*, enters a red blood cell, it causes extremely low oxygen tension in the cell, which leads to sickling in cells of individuals either homozygous or heterozygous for the sickle cell allele (but not in individuals that do not have the sickle cell allele). Such cells are quickly filtered out of the bloodstream by the spleen, thus eliminating the parasite. (The spleen's filtering effect is what leads to anemia in persons homozygous for the sickle cell allele because large numbers of red blood cells become sickle-shaped and are removed; in the case of heterozygotes, only those cells containing the *Plasmodium* parasite sickle, whereas the remaining cells are not affected, and thus anemia does not occur.)

Consequently, even though most homozygous recessive individuals die at a young age, the sickle cell allele is maintained at high levels in these populations because it is associated with resistance to malaria in heterozygotes and also, for reasons not yet fully understood, with increased fertility in female heterozygotes. Figure 20.13 shows the overlap between regions where sickle cell anemia is found and where malaria is prevalent.

For people living in areas where malaria is common, having the sickle cell allele in the heterozygous condition has adaptive value (see figure 20.13). Among African Americans, however, many of whose ancestors have lived for many generations in a country where malaria is now essentially absent, the environment does not place a premium on resistance to malaria. Consequently, no adaptive value counterbalances the ill effects of the disease; in this nonmalarial environment, selection is acting to eliminate the *S* allele. Only 1 in 375 African Americans develops sickle cell anemia, far fewer than in central Africa.

Learning Outcomes Review 20.6

Selection can maintain variation within populations in a number of ways. Negative frequency-dependent selection tends to favor rare phenotypes. Oscillating selection favors different phenotypes at different times. In some cases, heterozygotes have a selective advantage that may act to retain deleterious alleles.

- ***How would genetic variation in a population change if heterozygotes had the lowest fitness?***

20.7 *Selection Acting on Traits Affected by Multiple Genes*

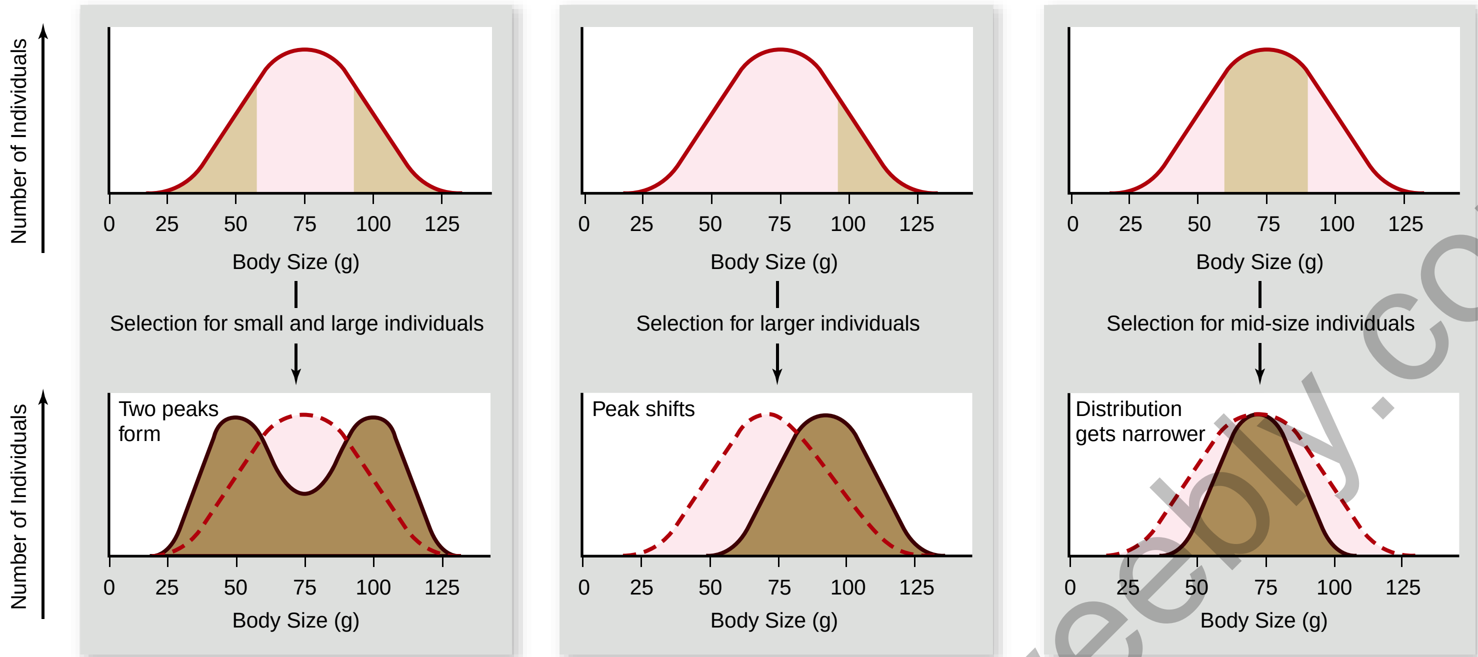
Learning Outcomes

1. ***Define and contrast disruptive, stabilizing, and directional selection.***
2. ***Explain the evolutionary outcome of each of these types of selection.***

In nature, many traits—perhaps most—are affected by more than one gene. The interactions between genes are typically complex, as you saw in chapter 12. For example, alleles of many different genes play a role in determining human height (see figure 12.11). In such cases, selection operates on all the genes, influencing most strongly those that make the greatest contribution to the phenotype. How selection changes the population depends on which genotypes are favored.

Disruptive selection removes intermediates

In some situations, selection acts to eliminate intermediate types, a phenomenon called **disruptive selection** (figure 20.14*a*). A clear example is the different beak sizes of the African black-bellied



a. Disruptive selection ***b.*** Directional selection ***c.*** Stabilizing selection

Figure 20.14 Three kinds of selection. The top panels show the populations before selection has occurred (under the solid red line). Within the population, those favored by selection are shown in light brown. The bottom panels indicate what the populations would look like in the next generation. The dashed red lines are the distribution of the original population and the solid, dark brown lines are the true distribution of the population in the next generation. ***a.*** In disruptive selection, individuals in the middle of the range of phenotypes of a certain trait are selected against, and the extreme forms of the trait are favored. ***b.*** In directional selection, individuals concentrated toward one extreme of the array of phenotypes are favored. ***c.*** In stabilizing selection, individuals with midrange phenotypes are favored, with selection acting against both ends of the range of phenotypes.

seedcracker finch *Pyrenestes ostrinus* (figure 20.15). Populations of these birds contain individuals with large and small beaks, but very few individuals with intermediate-sized beaks.

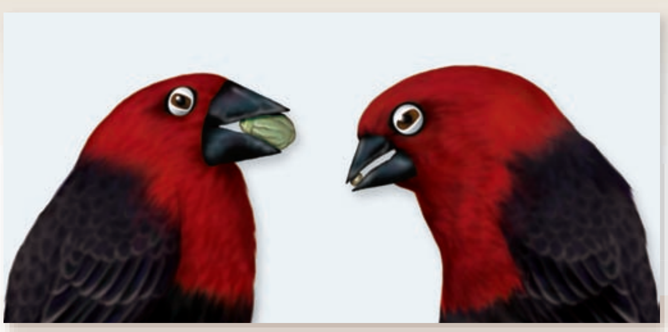
As their name implies, these birds feed on seeds, and the available seeds fall into two size categories: large and small. Only large-beaked birds can open the tough shells of large seeds, whereas birds with the smaller beaks are more adept at handling small seeds. Birds with intermediate-sized beaks are at a disadvantage with both seed types—they are unable to open large seeds and too clumsy to efficiently process small seeds. Consequently, selection acts to eliminate the intermediate phenotypes, in effect partitioning (or "disrupting") the population into two phenotypically distinct groups.

Directional selection eliminates phenotypes on one end of a range

When selection acts to eliminate one extreme from an array of phenotypes, the genes promoting this extreme become less frequent in the population and may eventually disappear. This form of selection is called **directional selection** (see figure 20.14*b*). Thus, in the *Drosophila* population illustrated in figure 20.16, eliminating flies that move toward light causes the population over time to contain fewer individuals with alleles promoting such behavior. If you were to pick an individual at random from a later generation of flies, there is a smaller chance that the fly

SCIENTIFIC THINKING

Question: *Does disruptive selection promote differences in beak size in the African Black-bellied Seedcracker Finches* (Pyrenestes ostrinus)*?*



Field Study: *Capture, measure, and release birds in a population. Follow the birds through time to determine how long each lives.*

Result: *Large- and small-beaked birds have higher survival rates than birds with intermediate-sized beaks.*

Interpretation: *What would happen if the distribution of seed size and hardness in the environment changed?*

Figure 20.15 Disruptive selection for large and small beaks. Differences in beak size in the black-bellied seedcracker finch of west Africa are the result of disruptive selection.

would spontaneously move toward light than if you had selected a fly from the original population. Artificial selection has changed the population in the direction of being less attracted to light. Directional selection often occurs in nature when the environment changes; one example is the widespread evolution of pesticide resistance discussed earlier in this chapter.

Stabilizing selection favors individuals with intermediate phenotypes

When selection acts to eliminate both extremes from an array of phenotypes, the result is to increase the frequency of the already common intermediate type. This form of selection is called **stabilizing selection** (see figure 20.14*c*). In effect, selection is operating to prevent change away from this middle range of values. Selection does not change the most common phenotype of the population, but rather makes it even more common by eliminating extremes. Many examples are known. In humans, infants with intermediate weight at birth have the highest survival rate (figure 20.17). In ducks and chickens, eggs of intermediate weight have the highest hatching success.

Learning Outcomes Review 20.7

In disruptive selection, intermediate forms of a trait diminish; in stabilizing selection, intermediates increase, whereas in disruptive selection they decrease. Directional selection shifts frequencies toward one end or the other and may eventually eliminate alleles entirely.

- ***How does directional selection differ from frequency-dependent selection?***

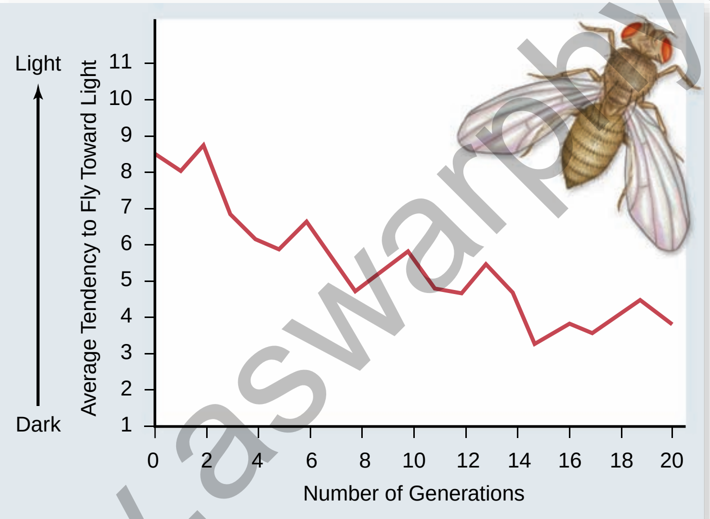


Figure 20.16 Directional selection for negative phototropism in *Drosophila*. Flies that moved toward light were discarded, and only flies that moved away from light were used as parents for the next generation. This procedure was repeated for 20 generations, producing substantial evolutionary change.

Inquiry question

What would happen if after 20 generations, experimenters started keeping flies that moved toward the light and discarded the others?

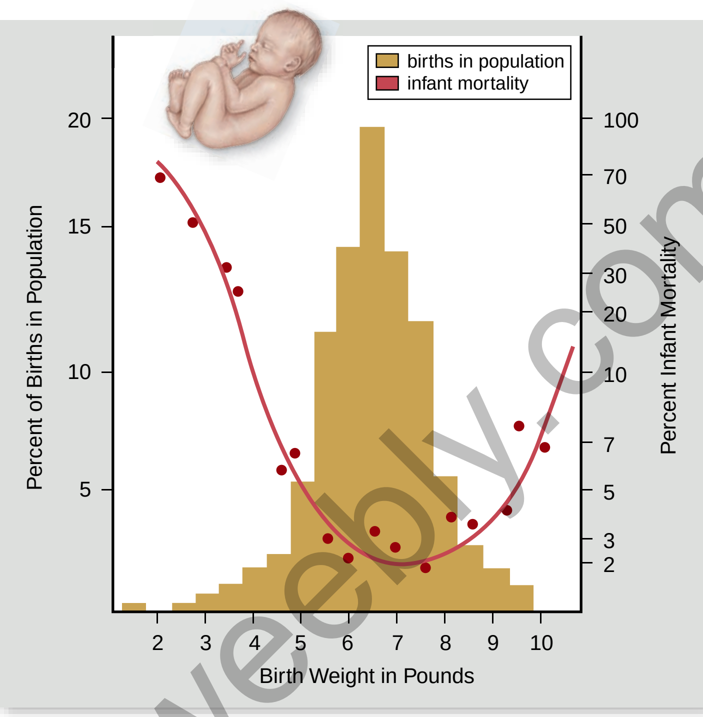


Figure 20.17 Stabilizing selection for birth weight in humans. The death rate among babies (red curve; right y-axis) is lowest at an intermediate birth weight; both smaller and larger babies have a greater tendency to die than those around the most frequent weight (tan area; left y-axis) of between 7 and 8 pounds. Recent medical advances have reduced mortality rates for small and large babies.

Inquiry question

As improved medical technology leads to decreased infant mortality rates, how would you expect the distribution of birth weights in the population to change?

20.8 *Experimental Studies of Natural Selection*

Learning Outcome

1. ***Explain how experiments can be used to test evolutionary hypotheses.***

To study evolution, biologists have traditionally investigated what has happened in the past, sometimes many millions of years ago. To learn about dinosaurs, a paleontologist looks at dinosaur fossils. To study human evolution, an anthropologist looks at human fossils and, increasingly, examines the "family tree" of mutations that have accumulated in human DNA over millions of years. In this traditional approach, evolutionary biology is similar to astronomy and history, relying on observation rather than experimentation to examine ideas about past events.

Nonetheless, evolutionary biology is not entirely an observational science. Darwin was right about many things, but one area in which he was mistaken concerns the pace at which evolution occurs. Darwin thought that evolution occurred at a very slow, almost imperceptible pace. But in recent years many case studies have demonstrated that in some circumstances, evolutionary change can occur rapidly. Consequently, experimental studies can be devised to test evolutionary hypotheses.

Although laboratory studies on fruit flies and other organisms have been common for more than 50 years, scientists have only recently started conducting experimental studies of evolution in nature. One excellent example of how observations of the natural world can be combined with rigorous experiments in the lab and in the field concerns research on the guppy, *Poecilia reticulata.*

Guppy color variation in different environments suggests natural selection at work

The guppy is a popular aquarium fish because of its bright coloration and prolific reproduction. In nature, guppies are found in small streams in northeastern South America and in many mountain streams on the nearby island of Trinidad. One interesting feature of several of the streams is that they have waterfalls. Amazingly, guppies and some other fish are capable of colonizing portions of the stream above the waterfall.

The killifish is a particularly good colonizer; apparently on rainy nights, it will wriggle out of the stream and move through the damp leaf litter. Guppies are not so proficient, but they are good at swimming upstream. During flood seasons, rivers sometimes overflow their banks, creating secondary channels that move through the forest. On these occasions, guppies may be able to swim upstream in the secondary channels and invade the pools above waterfalls.

By contrast, some species are not capable of such dispersal and thus are only found in streams below the first waterfall. One species whose distribution is restricted by waterfalls is the pike cichlid a voracious predator that feeds on other fish, including guppies.

Because of these barriers to dispersal, guppies can be found in two very different environments. In pools just below the waterfalls, predation by the pike cichlid is a substantial risk, and rates of survival are relatively low. But in similar pools just above the waterfall, the only predator present is the killifish, which rarely preys on guppies.

Guppy populations above and below waterfalls exhibit many differences. In the high-predation pools, guppies exhibit drab coloration. Moreover, they tend to reproduce at a younger age and attain relatively smaller adult sizes. Male fish above the waterfall, in contrast, are colorful (figure 20.18), mature later, and grow to larger sizes.

These differences suggest the operation of natural selection. In the low-predation environment, males display gaudy colors and spots that they use to court females. Moreover, larger males are most successful at holding territories and mating with females, and larger females lay more eggs. Thus, in the absence of predators, larger and more colorful fish may have produced more offspring, leading to the evolution of those traits.

In pools below the waterfall, natural selection would favor different traits. Colorful males are likely to attract the attention of the pike cichlid, and high predation rates mean that most fish live short lives. Individuals that are more drab and shunt energy into early reproduction, rather than growth to a larger size, are therefore likely to be favored by natural selection.

Experimentation reveals the agent of selection

Although the differences between guppies living above and below the waterfalls suggest evolutionary responses to differences in the strength of predation, alternative explanations are possible. Perhaps, for example, only very large fish are capable of crawling past the waterfall to colonize pools. If this were the case, then a founder effect would occur in which the new population was established solely by individuals with genes for large size. The only way to rule out such alternative possibilities is to conduct a controlled experiment.

The laboratory experiment

The first experiments were conducted in large pools in laboratory greenhouses. At the start of the experiment, a group of

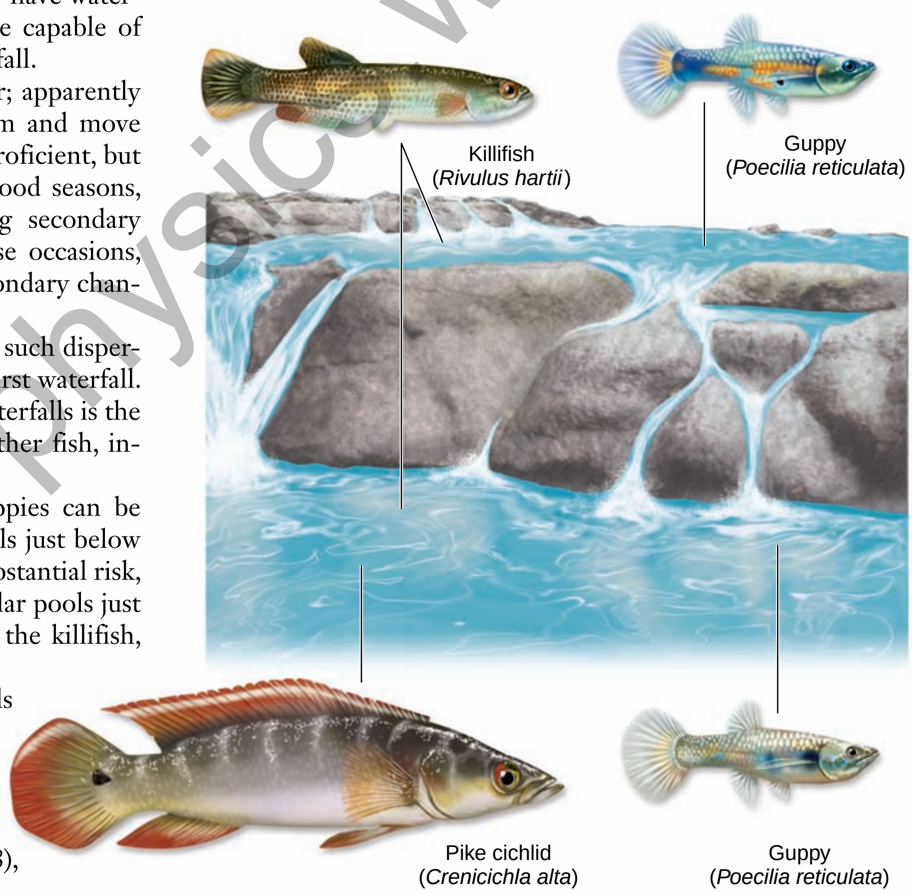


Figure 20.18 The evolution of protective coloration in guppies. In pools below waterfalls where predation is high, male guppies are drab in color. In the absence of the highly predatory pike cichlid *(Crenicichla alta)* in pools above waterfalls, male guppies are much more colorful and attractive to females. The killifish is also a predator, but it only rarely eats guppies. The evolution of these differences in guppies can be experimentally tested.

2000 guppies was divided equally among 10 large pools. Six months later, pike cichlids were added to four of the pools and killifish to another four, with the remaining two pools left to serve as "no-predation" controls.

Fourteen months later (which corresponds to 10 guppy generations), the scientists compared the populations. The guppies in the killifish and control pools were indistinguishable—brightly colored and large. In contrast, the guppies in the pike cichlid pools were smaller and drab in coloration (figure 20.19).

These results established that predation can lead to rapid evolutionary change, but do these laboratory experiments reflect what occurs in nature?

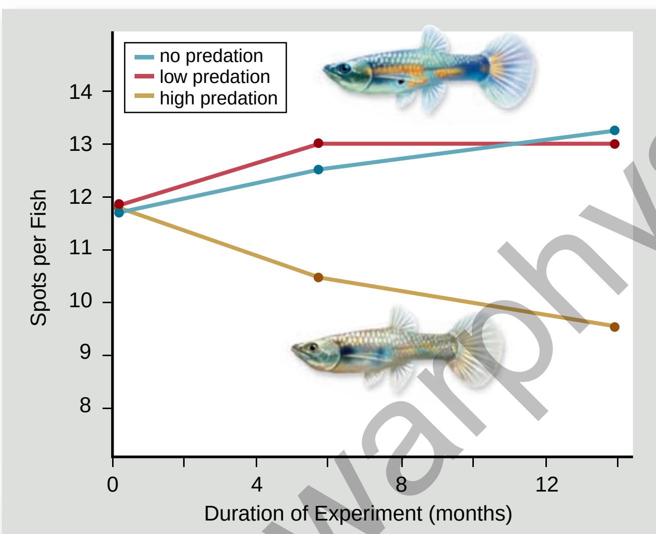
SCIENTIFIC THINKING

Question: *Does the presence of predators affect the evolution of guppy color?*

Hypothesis: *Predation on the most colorful individuals will cause a population to become increasingly dull through time. Conversely, in populations with few or no predators, increased color will evolve.*

Experiment: *Establish laboratory populations of guppies in large pools with or without predators.*

Result: *The populations with predators evolved to have fewer spots, while the populations in pools without predators evolved more spots.*



Interpretation: *Why does color increase in the absence of predators? How would you test your hypothesis?*

Figure 20.19 Evolutionary change in spot number. Guppy populations raised for 10 generations in low-predation or no-predation environments in laboratory greenhouses evolved a greater number of spots, whereas selection in more dangerous environments, such as the pools with the highly predatory pike cichlid, led to less conspicuous fish. The same results are seen in field experiments conducted in pools above and below waterfalls.

Inquiry question

? **How do these results depend on the manner by which the guppy predators locate their prey?**

The field experiment

To find out whether the laboratory results were an accurate reflection of natural processes, the scientists located two streams that had guppies in pools below a waterfall, but not above it. As in other Trinidadian streams, the pike cichlid was present in the lower pools, but only the killifish was found above the waterfalls.

The scientists then transplanted guppies to the upper pools and returned at several-year intervals to monitor the populations. Despite originating from populations in which predation levels were high, the transplanted populations rapidly evolved the traits characteristic of low-predation guppies: they matured late, attained greater size, and had brighter colors. The control populations in the lower pools, by contrast, continued to be drab and to mature early and at a smaller size. Laboratory analysis confirmed that the variations between the populations were the result of genetic differences.

These results demonstrate that substantial evolutionary change can occur in less than 12 years. More generally, these studies indicate how scientists can formulate hypotheses about how evolution occurs and then test these hypotheses in natural conditions. The results give strong support to the theory of evolution by natural selection.

Learning Outcome Review 20.8

Although much of evolutionary theory is derived from observation, experiments are sometimes possible in natural settings. Studies have revealed that traits can shift in populations in a relatively short time. The data obtained from evolutionary experiments can be used to refine theoretical assumptions.

- ***What experiments could you design to test other examples of natural selection, such as the evolution of pesticide resistance or background color matching?***

20.9 *The Limits of Selection*

Learning Outcomes

1. ***Define pleiotropy and epistasis.***
2. ***Explain how these phenomena may affect the evolutionary response to selective pressure.***

Although selection is the most powerful of the principal agents of genetic change, there are limits to what it can accomplish. These limits result from multiple phenotypic effects of alleles, lack of genetic variation upon which selection can act, and interactions between genes.

Genes have multiple effects

Alleles often affect multiple aspects of a phenotype (the phenomenon of *pleiotropy;* see chapter 12). These multiple effects tend to set limits on how much a phenotype can be altered.

For example, selecting for large clutch size in chickens eventually leads to eggs with thinner shells that break more easily. For this reason, we could never produce chickens that lay eggs twice as large as the best layers do now. Likewise, we cannot produce gigantic cattle that yield twice as much meat as our leading breeds, or corn with an ear at the base of every leaf, instead of just at the bases of a few leaves.

Evolution requires genetic variation

Over 80% of the gene pool of the thoroughbred horses racing today goes back to 31 ancestors from the late eighteenth century. Despite intense directional selection on thoroughbreds, their performance times have not improved for more than 50 years (figure 20.20). Decades of intense selection presumably have removed variation from the population at a rate greater than mutation can replenish it, such that little genetic variation now remains, and evolutionary change is not possible.

In some cases, phenotypic variation for a trait may never have had a genetic basis. The compound eyes of insects are made up of hundreds of visual units, termed ommatidia (described in chapter 34). In some individuals, the left eye contains more ommatidia than the right. In other individuals, the right eye contains more than the left (figure 20.21). However, despite intense selection experiments in the laboratory, scientists have never been able to produce a line of fruit flies that consistently has more ommatidia in the left eye than in the right.

The reason is that separate genes do not exist for the left and right eyes. Rather, the same genes affect both eyes, and differences in the number of ommatidia result from differences that occur as the eyes are formed in the development process. Thus, despite the existence of phenotypic variation, no underlying genetic variation is available for selection to favor.

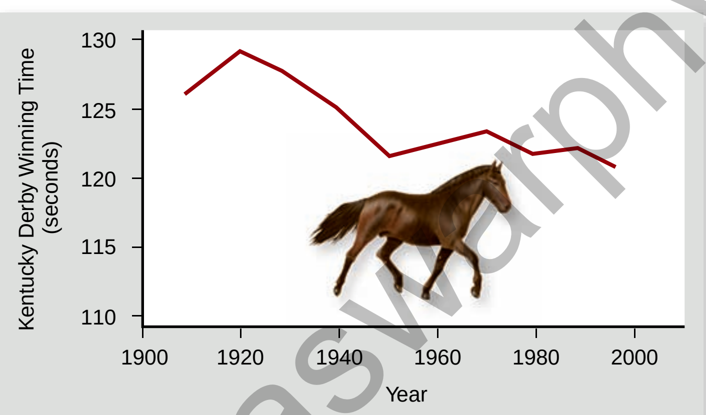


Figure 20.20 Selection for increased speed in racehorses is no longer effective. Kentucky Derby winning speeds have not improved significantly since 1950.

Inquiry question

? What might explain the lack of change in winning speeds?

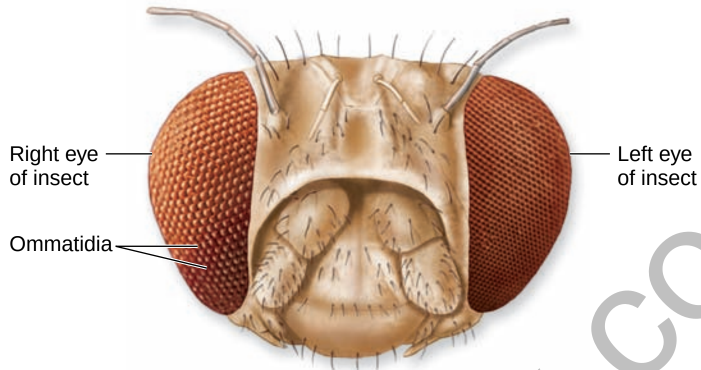


Figure 20.21 Phenotypic variation in insect ommatidia. In some individuals, the number of ommatidia in the left eye is greater than the number in the right.

Gene interactions affect fitness of alleles

As discussed in chapter 12, *epistasis* is the phenomenon in which an allele for one gene may have different effects, depending on alleles present at other genes. Because of epistasis, the selective advantage of an allele at one gene may vary from one genotype to another. If a population is polymorphic for a second gene, then selection on the first gene may be constrained because different alleles are favored in different individuals of the same population.

Studies on bacteria illustrate how selection on alleles for one gene can depend on which alleles are present at other genes. In *E. coli*, two biochemical pathways exist to break down gluconate, each using enzymes produced by different genes. One gene produces the enzyme 6-PGD, for which there are several alleles. When the common allele for the second gene, which codes for the other biochemical pathway, is present, selection does not favor one allele over another at the 6-PGD gene. In some *E. coli*, however, an alternative allele at the second gene occurs that is not functional. The bacteria with this alternative allele are forced to rely only on the 6-PGD pathway, and in this case, selection favors one 6-PGD allele over another. Thus, epistatic interactions exist between the two genes, and the outcome of natural selection on the 6-PGD gene depends on which alleles are present at the second gene.

Learning Outcomes Review 20.9

In pleiotropy, a single gene affects multiple traits; in epistasis, interaction between alleles of different genes affects a single trait. Both these conditions can constrain the effects of natural selection.

- ***How can epistasis and pleiotropy constrain the evolutionary response to natural selection?***

Chapter Review

20.1 Genetic Variation and Evolution

Many processes can lead to evolutionary change.

Darwin proposed that evolution of species occurs by the process of natural selection. Other processes can also lead to evolutionary change.

Populations contain ample genetic variation.

For a population to be able to evolve, it must contain genetic variation. DNA testing shows that natural populations generally have substantial variation.

20.2 Changes in Allele Frequency (figure 20.3)

The Hardy–Weinberg principle allows prediction of genotype frequencies.

Hardy–Weinberg equilibrium exists when observed genotype frequencies match the prediction from calculated frequencies. It occurs only when evolutionary processes are not acting to shift the distribution of alleles or genotypes in the population .

Hardy–Weinberg predictions can be applied to data to find evidence of evolutionary processes.

If genotype frequencies are not in Hardy–Weinberg equilibrium, then evolutionary processes must be at work.

20.3 Five Agents of Evolutionary Change (figure 20.4)

Mutation changes alleles.

Mutations are the ultimate source of genetic variation. Because mutation rates are low, mutation usually is not responsible for deviations from Hardy–Weinberg equilibrium.

Gene flow occurs when alleles move between populations.

Gene flow is the migration of new alleles into a population. It can introduce genetic variation and can homogenize allele frequencies between populations.

Nonrandom mating shifts genotype frequencies.

Assortative mating, in which similar individuals tend to mate, increases homozygosity; disassortative mating increases the frequency of heterozygotes.

Genetic drift may alter allele frequencies in small populations.

Genetic drift refers to random shifts in allele frequency. Its effects may be severe in small populations.

Selection favors some genotypes over others.

For natural selection to occur, genetic variation must exist, it must result in differential reproductive success, and it must be inheritable.

20.4 Fitness and Its Measurement

A phenotype with greater fitness usually increases in frequency.

Fitness is defined as the reproductive success of an individual. Relative fitness refers to the success of one genotype relative to others in a population. Usually, the genotype with highest relative fitness increases in frequency in the next generation.

Fitness may consist of many components.

Reproductive success is determined by how long an individual survives, how often it mates, and how many offspring it has per reproductive event.

20.5 Interactions Among Evolutionary Forces

Mutation and genetic drift may counter selection.

In theory, a high rate of mutation could oppose natural selection, but this rarely happens. Genetic drift also can work counter to natural selection.

Gene flow may promote or constrain evolutionary change.

Gene flow can spread a beneficial mutation to other populations, but it can also impede adaptation due to influx of alleles with low fitness in a population's environment.

20.6 Maintenance of Variation

Frequency-dependent selection may favor either rare or common phenotypes.

Negative frequency-dependent selection favors rare phenotypes and maintains variation within a population. Positive frequency-dependent selection favors the common phenotype and leads to decreased variation.

In oscillating selection, the favored phenotype changes as the environment changes.

If environmental change is cyclical, selection would favor first one phenotype, then another, maintaining variation.

In some cases, heterozygotes may exhibit greater fitness than homozygotes.

Heterozygote advantage favors individuals with both alleles.

20.7 Selection Acting on Traits Affected by Multiple Genes (figure 20.13)

Disruptive selection removes intermediates.

When intermediate phenotypes are at a disadvantage, a population may exhibit a bimodal trait distribution.

Directional selection eliminates phenotypes at one end of a range.

Directional selection tends to shift the mean value of the population toward the favored end of the distribution.

Stabilizing selection favors individuals with intermediate phenotypes.

Stabilizing selection eliminates both extremes and increases the frequency of an intermediate type. The population may have the same mean value, but with decreased variation.

20.8 Experimental Studies of Natural Selection

The hypothesis that natural selection leads to evolutionary change can be tested experimentally.

Guppy color variation in different environments suggests natural selection at work.

Experimentation reveals the agent of selection.

Guppies in natural populations subject to different predators were shown to undergo color change over generations.

20.9 The Limits of Selection

Genes have multiple effects.

Pleiotropic genes, which have multiple effects, set limits on how much a phenotype can be altered. Even if one affected trait is favored, other affected traits may not be.

Evolution requires genetic variation.

Intense selection pressure may remove genetic variation.

Gene interactions affect fitness of alleles.

In epistasis, fitness of one allele may vary depending on the genotype of a second gene.

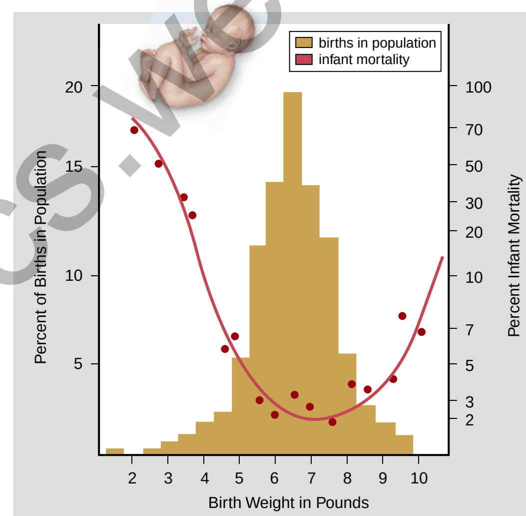
Review Questions

UNDERSTAND

1. Assortative mating
   a. affects genotype frequencies expected under Hardy–Weinberg equilibrium.
   b. affects allele frequencies expected under Hardy–Weinberg equilibrium.
   c. has no effect on the genotypic frequencies expected under Hardy–Weinberg equilibrium because it does not affect the relative proportion of alleles in a population.
   d. increases the frequency of heterozygous individuals above Hardy–Weinberg expectations.
2. When the environment changes from year to year and different phenotypes have different fitness in different environments
   a. natural selection will operate in a frequency-dependent manner.
   b. the effect of natural selection may oscillate from year to year, favoring alternative phenotypes in different years.
   c. genetic variation is not required to get evolutionary change by natural selection.
   d. none of the above.
3. Many factors can limit the ability of natural selection to cause evolutionary change, including
   a. a conflict between reproduction and survival as seen in Trinidadian guppies.
   b. lack of genetic variation.
   c. pleiotropy.
   d. all of the above.
4. Stabilizing selection differs from directional selection because
   a. in the former, phenotypic variation is reduced but the average phenotype stays the same, whereas in the latter both the variation and the mean phenotype change.
   b. the former requires genetic variation, but the latter does not.
   c. intermediate phenotypes are favored in directional selection.
   d. none of the above.
5. Founder effects and bottlenecks are
   a. expected only in large populations.
   b. mechanisms that increase genetic variation in a population.
   c. two different modes of natural selection.
   d. forms of genetic drift.
6. *Relative fitness*
   a. refers to the survival rate of one phenotype compared to that of another.
   b. is the physical condition of an individual's siblings and cousins.
   c. refers to the reproductive success of a phenotype.
   d. is none of the above.
7. For natural selection to result in evolutionary change
   a. variation must exist in a population.
   b. reproductive success of different phenotypes must differ.
   c. variation must be inherited from one generation to the next.
   d. all of the above.

APPLY

1. In a population of red (dominant allele) or white flowers in Hardy–Weinberg equilibrium, the frequency of red flowers is 91%. What is the frequency of the red allele?
   a. 9%   c. 91%
   b. 30%   d. 70%
2. Genetic drift and natural selection can both lead to rapid rates of evolution. However,
   a. genetic drift works fastest in large populations.
   b. only drift leads to adaptation.
   c. natural selection requires genetic drift to produce new variation in populations.
   d. both processes of evolution can be slowed by gene flow.
3. What would happen to average birth weight if over the next several years advances in medical technology reduced infant mortality rates of large babies to equal that for intermediate-sized babies (see the following figure, red line). Assume that differences in birth weight have a genetic basis.
   a. Over time, average birth weight would only increase.
   b. Over time, average birth weight would only decrease.
   c. Both a and b.
   d. None of the above.



SYNTHESIZE

1. In Trinidadian guppies a combination of elegant laboratory and field experiments builds a very compelling case for predator-induced evolutionary changes in color and life history traits. It is still possible, though not likely, that there are other differences between the sites above and below the falls aside from whether predators are present. What additional studies could strengthen the interpretation of the results?
2. On large, black lava flows in the deserts of the southwestern United States, populations of many types of animals are composed primarily of black individuals. By contrast, on small lava flows, populations often have a relatively high proportion of light-colored individuals. How can you explain this difference?
3. Based on a consideration of how strong artificial selection has helped eliminate genetic variation for speed in thoroughbred horses, we are left with the question of why, for many traits like speed (continuous traits), there is usually abundant genetic variation. This is true even for traits we know are under strong selection. Where does genetic variation ultimately come from, and how does the rate of production compare with the strength of natural selection? What other mechanisms can maintain and increase genetic variation in natural populations?

Chapter 21

The Evidence for Evolution

Chapter Outline

Introduction

As we discussed in chapter 1, when Darwin proposed his revolutionary theory of evolution by natural selection, little actual evidence existed to bolster his case. Instead, Darwin relied on observations of the natural world, logic, and results obtained by breeders working with domestic animals. Since his day, however, the evidence for Darwin's theory has become overwhelming.

The case is built upon two pillars: first, evidence that natural selection can produce evolutionary change, and second, evidence from the fossil record that evolution has occurred. In addition, information from many different areas of biology—fields as different as anatomy, molecular biology, and biogeography—is only interpretable scientifically as being the outcome of evolution.

21.1 *The Beaks of Darwin's Finches: Evidence of Natural Selection*

Learning Outcomes

1. ***Describe how the species of Darwin's finches have adapted to feed in different ways.***
2. ***Explain how climatic variation drives evolutionary change in the medium ground finch.***

As you learned in the preceding chapter, a variety of processes can produce evolutionary change. Most evolutionary biologists, however, agree with Darwin's thinking that natural selection is the primary process responsible for evolution. Although we cannot travel back through time, modern-day evidence allows us to test hypotheses about how evolution proceeds and confirms the power of natural selection as an agent of evolutionary change. This evidence comes from both the field and the laboratory and from both natural and human-altered situations.

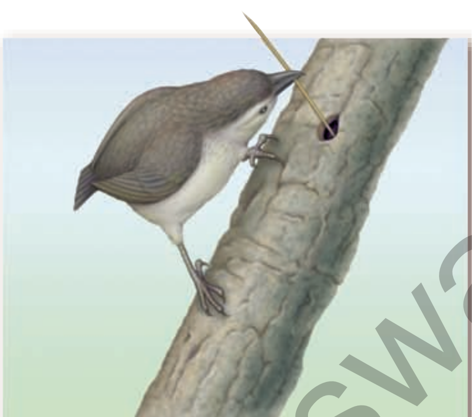
Darwin's finches are a classic example of evolution by natural selection. When he visited the Galápagos Islands off the coast of Ecuador in 1835, Darwin collected 31 specimens of finches from three islands. Darwin, not an expert on birds, had trouble identifying the specimens, believing by examining their bills that his collection contained wrens, "gross-beaks," and blackbirds.

Upon Darwin's return to England, ornithologist John Gould informed Darwin that his collection was in fact a closely related group of distinct species, all similar to one another except for their bills. In all, 14 species are now recognized.

Galápagos finches exhibit variation related to food gathering

The diversity of Darwin's finches is illustrated in figure 21.1. The ground finches feed on seeds that they crush in their powerful beaks; species with smaller and narrower bills such as the warbler finch eat insects. Other species include fruit and bud eaters, and species that feed on cactus fruits and the insects they attract; some populations of the sharp-beaked ground finch even include "vampires" that sometimes creep up on seabirds and use their sharp beaks to pierce the seabirds' skin and drink their blood. Perhaps most remarkable are the tool users, woodpecker finches that pick up a twig, cactus spine, or leaf stalk, trim it into shape with their bills, and then poke it into dead branches to pry out grubs.

The correspondence between the beaks of the finch species and their food source suggested to Darwin that natural selection had shaped them. In *The Voyage of the Beagle*, Darwin wrote, "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species has been taken and modified for different ends."

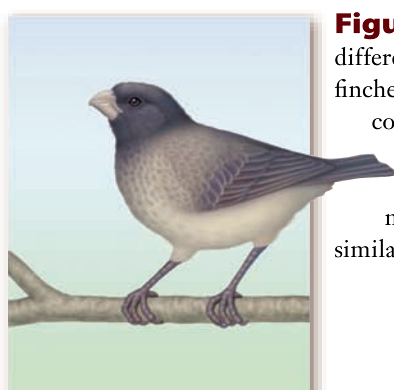


Woodpecker finch (*Cactospiza pallida*)

Large ground finch (*Geospiza magnirostris*)

Cactus finch (*Geospiza scandens*)

Warbler finch (*Certhidea olivacea*)



Vegetarian tree finch (*Platyspiza crassirostris*)

Figure 21.1 Darwin's finches. These species show differences in bills and feeding habits among Darwin's finches. This diversity arose when an ancestral finch colonized the islands and diversified into habitats lacking other types of small birds. The bills of several species resemble those of different families of birds on the mainland. For example, the warbler finch has a beak very similar to warblers, to which it is not closely related.

Modern research has verified Darwin's selection hypothesis

Darwin's observations suggest that differences among species in beak size and shape have evolved as the species adapted to use different food resources, but can this hypothesis be tested? In chapter 20, you read that the theory of evolution by natural selection requires that three conditions be met:

1. Variation must exist in the population.
2. This variation must lead to differences among individuals in lifetime reproductive success.
3. Variation among individuals must be genetically transmissible to the next generation.

The key to successfully testing Darwin's proposal proved to be patience. For more than 30 years, starting in 1973, Peter and Rosemary Grant of Princeton University and their students have studied the medium ground finch, *Geospiza fortis*, on a tiny island in the center of the Galápagos called Daphne Major. These finches feed preferentially on small, tender seeds, produced in abundance by plants in wet years. The birds resort to larger, drier seeds, which are harder to crush, only when small seeds become depleted during long periods of dry weather, when plants produce few seeds.

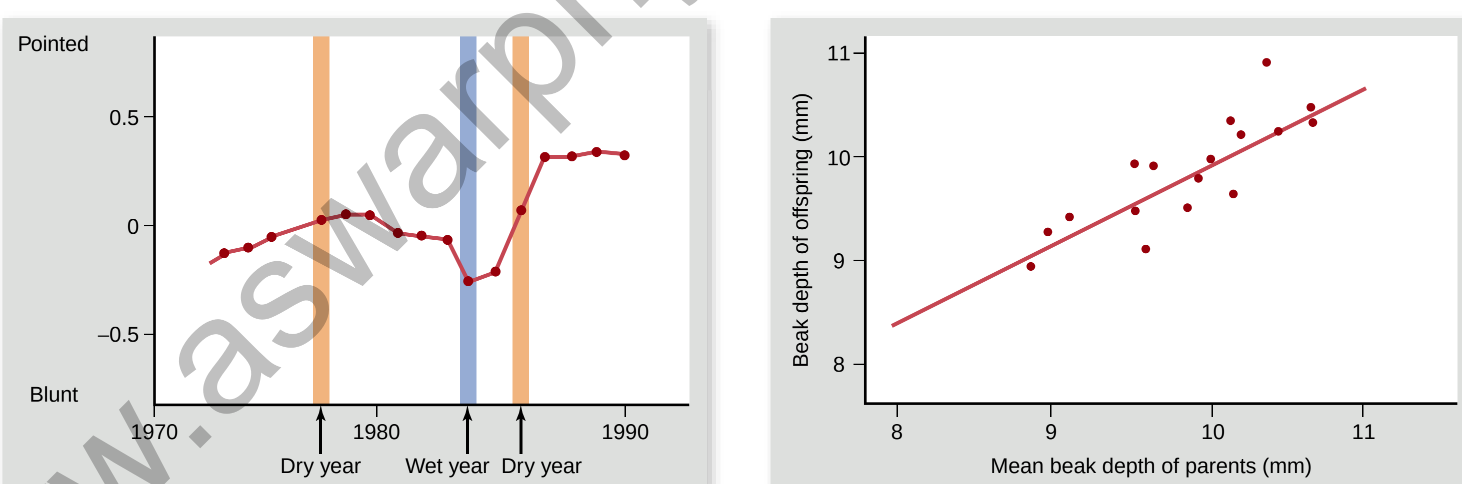
The Grants quantified beak shape among the medium ground finches of Daphne Major by carefully measuring beak depth (height of beak, from top to bottom, at its base) on individual birds. Measuring many birds every year, they were able to assemble for the first time a detailed portrait of evolution in action. The Grants found that not only did a great deal of variation in beak depth exist among members of the population, but the average beak depth changed from one year to the next in a predictable fashion.

During droughts, plants produced few seeds, and all available small seeds were quickly eaten, leaving large seeds as the major remaining source of food. As a result, birds with deeper, more powerful beaks survived better, because they were better able to break open these large seeds. Consequently, the average beak depth of birds in the population increased the next year. Then, when normal rains returned, average beak depth of the population decreased to its original size (figure 21.2*a*).

Conversely, in particularly wet years, plants flourished, producing an abundance of small seeds; as a result, small-beaked birds were favored, and beak depth decreased greatly.

Could these changes in beak dimension reflect the action of natural selection? An alternative possibility might be that the changes in beak depth do not reflect changes in gene frequencies, but rather are simply a response to diet—for example, perhaps crushing large seeds causes a growing bird to develop a larger beak.

To rule out this possibility, the Grants measured the relation of parent beak size to offspring beak size, examining many broods over several years. The depth of the beak was very similar between parents and offspring regardless of environmental conditions (figure 21.2*b*), suggesting that the differences among individuals in beak size reflect genetic differences, and therefore that the year-to-year changes in average beak depth represent evolutionary change resulting from natural selection.



a. ***b.***

Figure 21.2 Evidence that natural selection alters beak shape in the medium ground finch *(Geospiza fortis)*. ***a.*** In dry years, when only large, tough seeds are available, the mean beak depth increases. In wet years, when many small seeds are available, mean beak depth decreases. ***b.*** Beak depth is inherited from parents to offspring.

Inquiry question

? **Suppose a bird with a large bill mates with a bird with a small bill. Would the bills of the pair's offspring tend to be larger or smaller than the bills of offspring from a pair of birds with medium-sized bills?**

Learning Outcomes Review 21.1

Among Darwin's finches, natural selection has been responsible for changes in the shape of the beak corresponding to characteristics of the available food supply. Because beak morphology is a transmissible trait, a beak better suited to the distribution of available seed types would become more common in subsequent generations.

- ***Suppose that the act of eating hard seeds caused birds to develop bigger beaks. Would this lead to an evolutionary increase in beak size after a drought?***

21.2 *Peppered Moths and Industrial Melanism: More Evidence of Selection*

Learning Outcomes

1. ***Explain the relationship between pollution and color evolution in peppered moths.***
2. ***Distinguish between demonstrating that evolution has occurred and understanding the mechanism that caused it.***

When the environment changes, natural selection often may favor different traits in a species. One classic example concerns the peppered moth, *Biston betularia*. Adults come in a range of shades, from light gray with black speckling (hence the name "peppered" moth) to jet black (melanic).

Extensive genetic analysis has shown that the moth's body color is a genetic trait that reflects different alleles of a single gene. Black individuals have a dominant allele, one that was present but very rare in populations before 1850. From that time on, dark individuals increased in frequency in moth populations near industrialized centers until they made up almost 100% of these populations.

Biologists soon noticed that in industrialized regions where the dark moths were common, the tree trunks were darkened almost black by the soot of pollution, which also killed many of the light-colored lichens on tree trunks.

Light-colored moths decreased in polluted areas

Why did dark moths gain a survival advantage around 1850? In 1896, an amateur moth collector named J. W. Tutt proposed what became the most commonly accepted hypothesis explaining the decline of the light-colored moths. He suggested that peppered forms were more visible to predators on sooty trees that have lost their lichens. Consequently, birds ate the peppered moths resting on the trunks of trees during the day. The black forms, in contrast, had an advantage because they were camouflaged (figure 21.3).

Although Tutt initially had no evidence, British ecologist Bernard Kettlewell tested the hypothesis in the 1950s by releasing equal numbers of dark and light individuals into two sets of woods: one near heavily polluted Birmingham, and the other in unpolluted Dorset. Kettlewell then set up lights in the woods to attract moths to traps to see how many of both kinds of moths survived. To evaluate his results, he had marked the released moths with a dot of paint on the underside of their wings, where birds could not see it.

In the polluted area near Birmingham, Kettlewell recaptured only 19% of the light moths, but 40% of the dark ones. This indicated that dark moths had a far better chance of surviving in these polluted woods, where tree trunks were dark. In the relatively unpolluted Dorset woods, Kettlewell recovered 12.5% of the light moths but only 6% of the dark ones. This result indicated that where the tree trunks were still light-colored, light moths had a much better chance of survival.

Kettlewell later solidified his argument by placing moths on trees and filming birds looking for food. Sometimes the birds actually passed right over a moth that was the same color as its background.

Kettlewell's finding that birds more frequently detect moths whose color does not match their background has subsequently been confirmed in eight separate field studies, with a variety of experimental designs and corrections for deficiencies

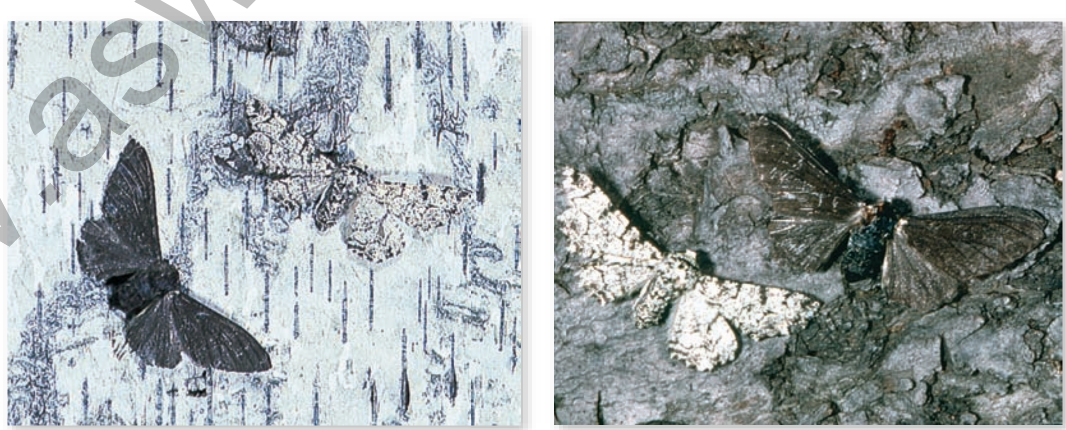


Figure 21.3 Tutt's hypothesis explaining industrial melanism. These photographs show preserved specimens of the peppered moth *(Biston betularia)* placed on trees. Tutt proposed that the dark melanic variant of the moth is more visible to predators on unpolluted trees *(left)*, while the light "peppered" moth is more visible to predators on bark blackened by industrial pollution *(right)*.

in Kettlewell's initial design. These results, combined with the recapture studies, provide strong evidence for the action of natural selection and implicate birds as the agent of selection in the case of the peppered moth.

When environmental conditions reverse, so does selection pressure

In industrialized areas throughout Eurasia and North America, dozens of other species of moths have evolved in the same way as the peppered moth. The term **industrial melanism** refers to the phenomenon in which darker individuals come to predominate over lighter ones. In the second half of the 20th century, with the widespread implementation of pollution controls, the trend toward melanism began reversing for many species of moths throughout the northern continents.

In England, the air pollution that promoted industrial melanism began to reverse following enactment of the Clean Air Act in 1956. Beginning in 1959, the *Biston* population at Caldy Common outside Liverpool has been sampled each year. The frequency of the melanic (dark) form has dropped from a high of 93% in 1959 to a low of 15% in 1995 (figure 21.4).

The drop correlates well with a significant drop in air pollution, particularly with a lowering of the levels of sulfur dioxide and suspended particulates, both of which act to darken trees. The drop is consistent with a 15% selective disadvantage acting against moths with the dominant melanic allele.

Interestingly, the same reversal of melanism occurred in the United States. Of 576 peppered moths collected at a field station near Detroit from 1959 to 1961, 515 were melanic, a frequency of 89%. The American Clean Air Act, passed in 1963, led to significant reductions in air pollution. Resampled in 1994, the Detroit field station peppered moth population had only 15% melanic moths (see figure 21.4). The moth populations in Liverpool and Detroit, both part of the same natural experiment, exhibit strong evidence for natural selection.

The agent of selection may be difficult to pin down

Although the evidence for natural selection in the case of the peppered moth is strong, Tutt's hypothesis about the agent of selection is currently being reevaluated. Researchers have noted that the recent selection against melanism does not appear to correlate with changes in tree lichens.

At Caldy Common, the light form of the peppered moth began to increase in frequency long before lichens began to reappear on the trees. At the Detroit field station, the lichens never changed significantly as the dark moths first became dominant and then declined over a 30-year period. In fact, investigators have not been able to find peppered moths on Detroit trees at all, whether covered with lichens or not. Some evidence suggests the moths rest on leaves in the treetops during the day, but no one is sure. Could poisoning by pollution rather than predation by birds be the agent of natural selection on the moths? Perhaps—but to date, only predation by birds is backed by experimental evidence.

Researchers supporting the bird predation hypothesis point out that a bird's ability to detect moths may depend less on the presence or absence of lichens, and more on other ways in which the environment is darkened by industrial pollution. Pollution tends to cover all objects in the environment with a fine layer of particulate dust, which tends to decrease how much light surfaces reflect. In addition, pollution has a particularly severe effect on birch trees, which are light in color. Both effects would tend to make the environment darker, and thus would favor darker moths by protecting them from predation by birds.

Despite this uncertainty over the agent of selection, the overall pattern is clear. Kettlewell's experiments established indisputably that selection favors dark moths in polluted habitats and light moths in pristine areas. The increase and subsequent decrease in the frequency of melanic moths, correlated with levels of pollution independently on two continents, demonstrates clearly that this selection drives evolutionary change.

The current reconsideration of the agent of natural selection illustrates well the way in which scientific progress is achieved: Hypotheses, such as Tutt's, are put forth and then tested. If rejected, new hypotheses are formulated, and the process begins anew.

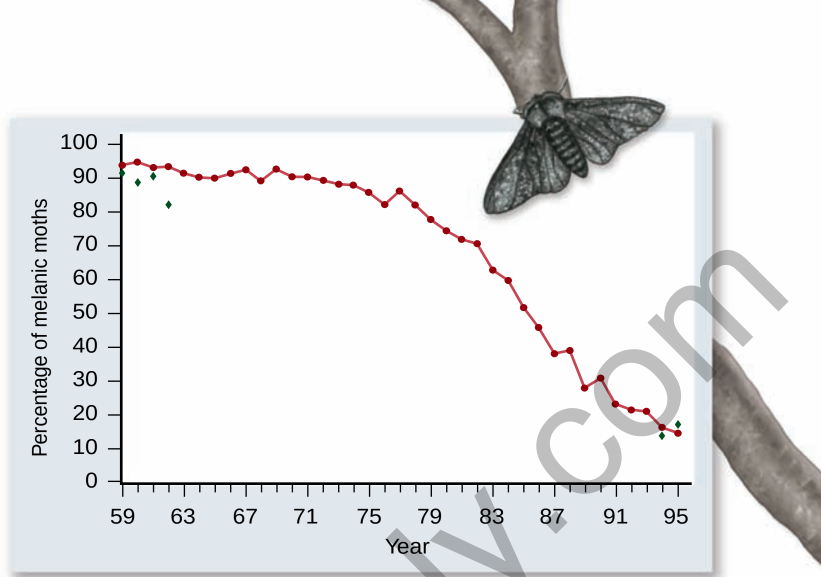


Figure 21.4 Selection against melanism. The red circles indicate the frequency of melanic *Biston betularia* moths at Caldy Common in England, sampled continuously from 1959 to 1995. Green diamonds indicate frequencies of melanic *B. betularia* in Michigan from 1959 to 1962 and from 1994 to 1995.

Inquiry question

? **What can you conclude from the fact that the frequency of melanic moths decreased to the same degree in the two locations?**

Learning Outcomes Review 21.2

Natural selection has favored the dark form of the peppered moth in areas subject to severe air pollution, perhaps because on darkened trees they are less easily seen by moth-eating birds. As pollution has abated, selection has in turn shifted to favor the light form. Although selection is clearly occurring, further research is required to understand whether predation by birds is the agent of selection.

- ***How would you test the idea that predation by birds is the agent of selection on moth coloration?***

21.3 Artificial Selection: Human-Initiated Change

Learning Outcomes

1. *Contrast the processes of artificial and natural selection.*
2. *Explain what artificial selection demonstrates about the power of natural selection.*

Humans have imposed selection upon plants and animals since the dawn of civilization. Just as in natural selection, artificial selection operates by favoring individuals with certain phenotypic traits, allowing them to reproduce and pass their genes on to the next generation. Assuming that phenotypic differences are genetically determined, this directional selection should lead to evolutionary change, and indeed it has.

Artificial selection, imposed in laboratory experiments, agriculture, and the domestication process, has produced substantial change in almost every case in which it has been applied. This success is strong proof that selection is an effective evolutionary process.

Experimental selection produces changes in populations

With the rise of genetics as a field of science in the 1920s and 1930s, researchers began conducting experiments to test the hypothesis that selection can produce evolutionary change. A favorite subject was the laboratory fruit fly, *Drosophila melanogaster*. Geneticists have imposed selection on just about every conceivable aspect of the fruit fly—including body size, eye color, growth rate, life span, and exploratory behavior—with a consistent result: Selection for a trait leads to strong and predictable evolutionary response.

In one classic experiment, scientists selected for fruit flies with many bristles (stiff, hairlike structures) on their abdomens. At the start of the experiment, the average number of bristles was 9.5. Each generation, scientists picked out the 20% of the population with the greatest number of bristles and allowed them to reproduce, thus establishing the next generation. After 86 generations of this directional selection, the average number of bristles had quadrupled, to nearly 40! In another experiment, fruit flies in one population were selected for high numbers of bristles, while fruit flies in the other cage were selected for low numbers of bristles. Within 35 generations, the populations did not overlap at all in range of variation (figure 21.5).

Similar experiments have been conducted on a wide variety of other laboratory organisms. For example, by selecting for rats that were resistant to tooth decay, in less than 20 generations scientists were able to increase the average time for onset of decay from barely over 100 days to greater than 500 days.

Agricultural selection has led to extensive modification of crops and livestock

Familiar livestock, such as cattle and pigs, and crops, such as corn and strawberries, are greatly different from their wild ancestors (figure 21.6). These differences have resulted from generations of human selection for desirable traits, such as greater milk production and larger corn ear size.

An experiment with corn demonstrates the ability of artificial selection to rapidly produce major change in crop plants. In 1896, agricultural scientists began selecting for the oil content of corn kernels, which initially was 4.5%. Just as in the fruit fly experiments, the top 20% of all individuals were allowed to reproduce. By 1986, at which time 90 generations had passed, average oil content of the corn kernels had increased approximately 450%.

Domesticated breeds have arisen from artificial selection

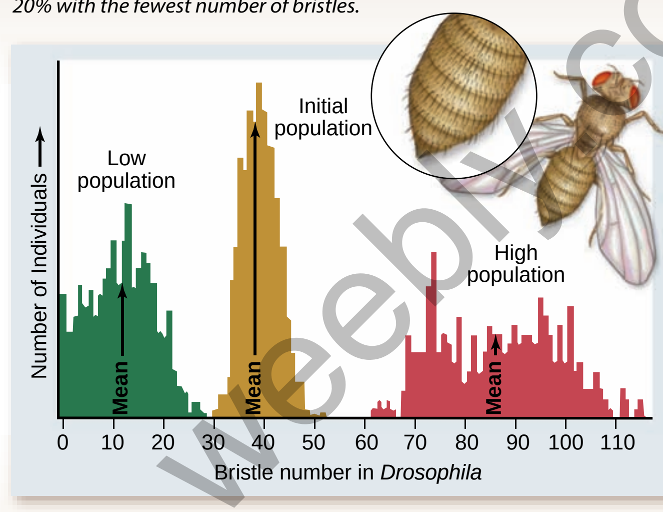
Human-imposed selection has produced a great variety of breeds of cats, dogs (figure 21.7), pigeons, and other domestic animals. In some cases, breeds have been developed for particular purposes. Greyhound dogs, for example, resulted from

SCIENTIFIC THINKING

Question: *Can artificial selection lead to substantial evolutionary change?*

Hypothesis: *Strong directional selection will quickly lead to a large shift in the mean value of the population.*

Experiment: *In one population, every generation pick out the 20% of the population with the most bristles and allow them to reproduce to form the next generation. In the other population, do the same with the 20% with the fewest number of bristles.*



Result: *After 35 generations, mean number of bristles has changed substantially in both populations.*

Interpretation: *Note that at the end of the experiment, the range of variation lies outside the range seen in the initial population. Selection can move a population beyond its original range because mutation and recombination continuously introduce new variation into populations.*

Figure 21.5 Artificial selection can lead to rapid and substantial evolutionary change.

Inquiry question

? **What would happen if, within a population, both small and large individuals were allowed to breed, but middle-sized ones were not?**

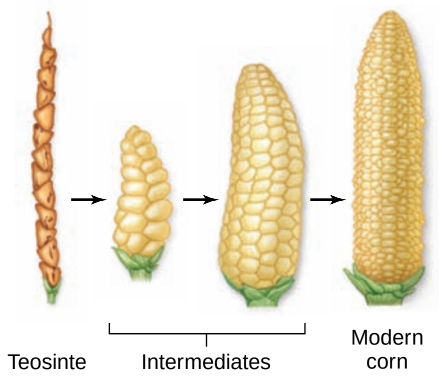


Figure 21.6 Corn looks very different from its ancestor. Teosinte, which can be found today in a remote part of Mexico, is very similar to the ancestor of modern corn. Artificial selection has transformed it into the form we know today.

selection for maximal running ability, resulting in an animal with long legs, a long tail for balance, an arched back to increase stride length, and great muscle mass. By contrast, the odd proportions of the ungainly dachshund resulted from selection for dogs that could enter narrow holes in pursuit of badgers. In other cases, varieties have been selected primarily for their appearance, such as the many colorful breeds of pigeons or cats.

Domestication also has led to unintentional selection for some traits. In recent years, as part of an attempt to domesticate the silver fox, Russian scientists have chosen the most docile animals in each generation and allowed them to reproduce. Within 40 years, most foxes were exceptionally tame, not only allowing themselves to be petted, but also whimpering to get attention and sniffing and licking their caretakers (figure 21.8). In many respects, they had become no different from domestic dogs.

It was not only their behavior that changed, however. These foxes also began to exhibit other traits seen in some dog breeds, such as different color patterns, floppy ears, curled tails, and shorter legs and tails. Presumably, the genes responsible for docile behavior either affect these traits as well or are closely linked to the genes for these other traits (the phenomena of pleiotropy and linkage, which are discussed in chapters 12 and 13).

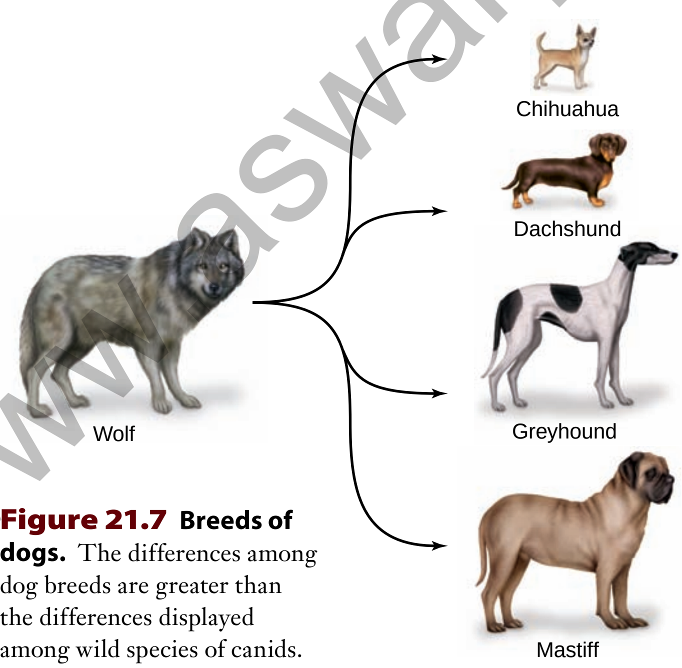


Figure 21.7 Breeds of dogs. The differences among dog breeds are greater than the differences displayed among wild species of canids.

Figure 21.8 Domesticated foxes. After 40 years of selectively breeding the tamest individuals, artificial selection has produced silver foxes that are not only as friendly as domestic dogs, but also exhibit many physical traits seen in dog breeds.

Can selection produce major evolutionary changes?

Given that we can observe the results of selection operating over a relatively short time, most scientists think that natural selection is the process responsible for the evolutionary changes documented in the fossil record. Some critics of evolution accept that selection can lead to changes within a species, but contend that such changes are relatively minor in scope and not equivalent to the substantial changes documented in the fossil record. In other words, it is one thing to change the number of bristles on a fruit fly or the size of an ear of corn, and quite another to produce an entirely new species.

This argument does not fully appreciate the extent of change produced by artificial selection. Consider, for example, the existing breeds of dogs, all of which have been produced since wolves were first domesticated, perhaps 10,000 years ago. If the various dog breeds did not exist and a paleontologist found fossils of animals similar to dachshunds, greyhounds, mastiffs, and chihuahuas, there is no question that they would be considered different species. Indeed, the differences in size and shape exhibited by these breeds are greater than those between members of different genera in the family Canidae—such as coyotes, jackals, foxes, and wolves—which have been evolving separately for 5 to 10 million years. Consequently, the claim that artificial selection produces only minor changes is clearly incorrect. If selection operating over a period of only 10,000 years can produce such substantial differences, it should be powerful enough, over the course of many millions of years, to produce the diversity of life we see around us today.

Learning Outcomes Review 21.3

In artificial selection, humans choose which plants or animals to mate in an attempt to conserve desirable traits. Rapid and substantial results can be obtained over a very short time, often in a few generations. From this we can see that natural selection is capable of producing major evolutionary change.

- ***In what circumstances might artificial selection fail to produce a desired change?***

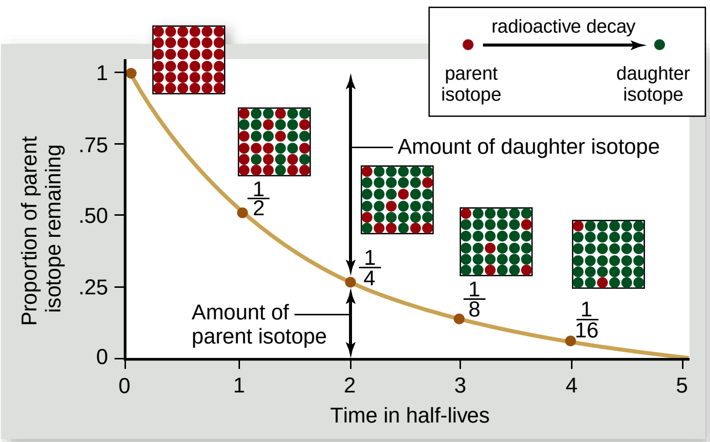


Figure 21.9 Radioactive decay. Radioactive elements decay at a known rate, called their half-life. After one half-life, one half of the original amount of parent isotope has transformed into a nonradioactive daughter isotope. After each successive half-life, one half of the remaining amount of parent isotope is transformed.

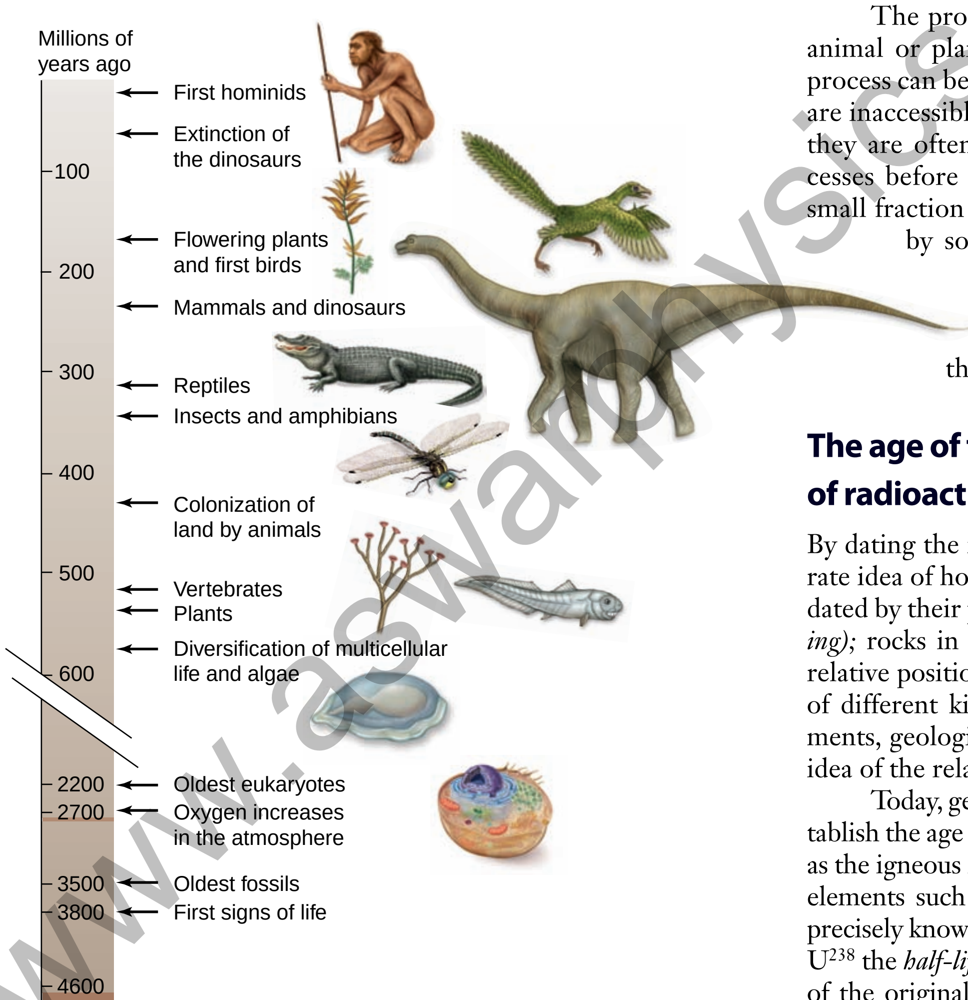


Figure 21.10 History of evolutionary change as revealed by the fossil record.

21.4 Fossil Evidence of Evolution

Learning Outcomes

1. *Describe how fossils are formed.*
2. *Explain the importance of the discovery of transitional fossils.*
3. *Name the evolutionary trends revealed by study of horse evolution.*

The most direct evidence that evolution has occurred is found in the fossil record. Today we have a far more complete understanding of this record than was available in Darwin's time.

Fossils are the preserved remains of once-living organisms. They include specimens preserved in amber, Siberian permafrost, and dry caves, as well as the more common fossils preserved as rocks.

Rock fossils are created when three events occur. First, the organism must become buried in sediment; then, the calcium in bone or other hard tissue must mineralize; and finally, the surrounding sediment must eventually harden to form rock.

The process of fossilization occurs only rarely. Usually, animal or plant remains decay or are scavenged before the process can begin. In addition, many fossils occur in rocks that are inaccessible to scientists. When they do become available, they are often destroyed by erosion and other natural processes before they can be collected. As a result, only a very small fraction of the species that have ever existed (estimated by some to be as many as 500 million) are known from fossils. Nonetheless, the fossils that have been discovered are sufficient to provide detailed information on the course of evolution through time.

The age of fossils is estimated by rates of radioactive decay

By dating the rocks in which fossils occur, we can get an accurate idea of how old the fossils are. In Darwin's day, rocks were dated by their position with respect to one another *(relative dating);* rocks in deeper strata are generally older. Knowing the relative positions of sedimentary rocks and the rates of erosion of different kinds of sedimentary rocks in different environments, geologists of the 19th century derived a fairly accurate idea of the relative ages of rocks.

Today, geologists take advantage of radioactive decay to establish the age of rocks *(absolute dating).* Many types of rock, such as the igneous rocks formed when lava cools, contain radioactive elements such as uranium-238. These isotopes transform at a precisely known rate into nonradioactive forms. For example, for U^{238} the *half-life* (that is, the amount of time needed for one-half of the original amount to be transformed) is 4.5 billion years. Once a rock is formed, no additional radioactive isotopes are added. Therefore, by measuring the ratio of the radioactive isotope to its derivative, "daughter" isotope (figure 21.9), geologists can determine the age of the rock. If a fossil is found between two layers of rock, each of which can be dated, then the age at which the fossil formed can be determined.

Fossils present a history of evolutionary change

When fossils are arrayed according to their age (figure 21.10), from oldest to youngest, they often provide evidence of successive evolutionary change. At the largest scale, the fossil record documents the course of life through time, from the origin of first prokaryotic and then eukaryotic organisms, through the evolution of fishes, the rise of land-dwelling organisms, the reign of the dinosaurs, and on to the origin of humans. In addition, the fossil record shows the waxing and waning of biological diversity through time, such as the periodic mass extinctions that have reduced the number of living species.

Fossils document evolutionary transition

Given the low likelihood of fossil preservation and recovery, it is not surprising that there are gaps in the fossil record. Nonetheless, intermediate forms are often available to illustrate how the major transitions in life occurred.

Undoubtedly the most famous of these is the oldest known bird, *Archaeopteryx* (meaning "ancient feather") which lived around 165 million years ago (figure 21.11). This specimen is clearly intermediate between birds and dinosaurs. Its feathers, similar in many respects to those of birds today, clearly reveal that it is a bird. Nonetheless, in many other respects—for example, possession of teeth, a bony tail, and other anatomical characteristics—it is indistinguishable from some carnivorous dinosaurs. Indeed, it is so similar to these dinosaurs that several specimens lacking preserved feathers were misidentified as dinosaurs and lay in the wrong natural history museum cabinet for several decades before the mistake was discovered!

Archaeopteryx reveals a pattern commonly seen in intermediate fossils—rather than being intermediate in every trait, such fossils usually exhibit some traits like their ancestors and others like their descendants. In other words, traits evolve at different rates and different times; expecting an intermediate form to be intermediate in every trait would not be correct.

The first *Archaeopteryx* fossil was discovered in 1859, the year Darwin published *On the Origin of Species*. Since then, paleontologists have continued to fill in the gaps in the fossil record. Today, the fossil record is far more complete, particularly among the vertebrates; fossils have been found linking all the major groups.

Recent years have seen spectacular discoveries, closing some of the major remaining gaps in our understanding of vertebrate evolution. For example, a four-legged aquatic mammal was discovered only recently that provides important insights concerning the evolution of whales and dolphins from land-dwelling, hoofed ancestors (figure 21.12). Similarly, a fossil snake with legs has shed light on the evolution of snakes, which are descended from lizards that gradually

Figure 21.11 Fossil of *Archaeopteryx,* the first bird. The remarkable preservation of this specimen reveals soft parts usually not preserved in fossils; the presence of feathers makes clear that *Archaeopteryx* was a bird, despite the presence of many dinosaurian traits.

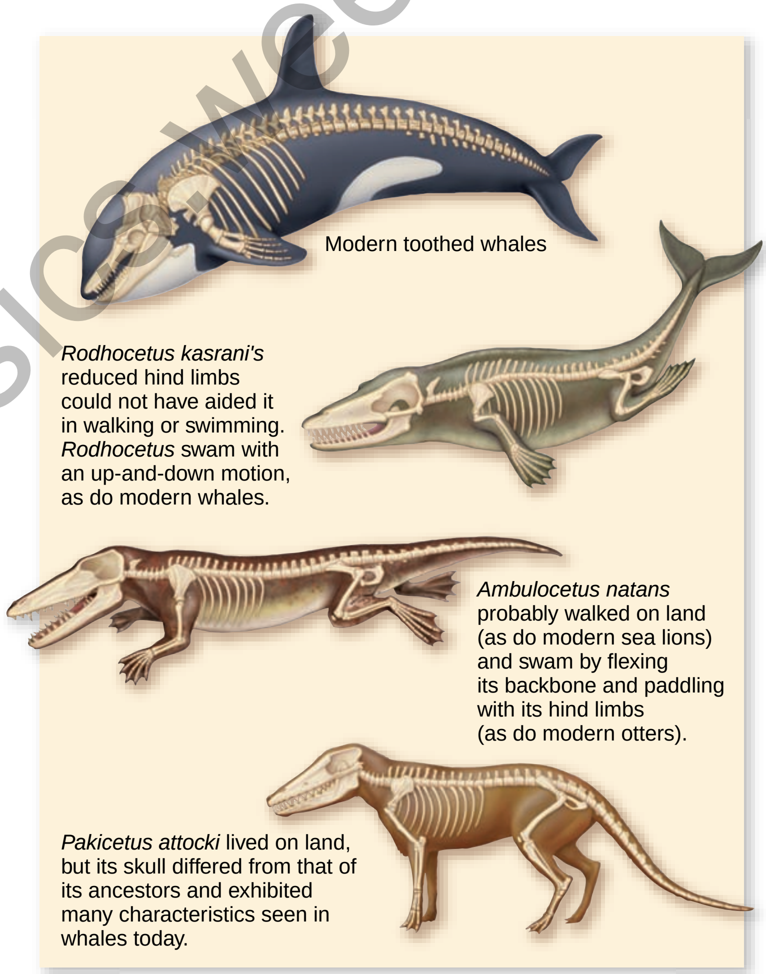


Figure 21.12 Whale "missing links." The recent discoveries of *Ambulocetus*, *Rodhocetus*, and *Pakicetus* have filled in the gaps between whales and their hoofed mammal ancestors. The features of *Pakicetus* illustrate that intermediate forms are not intermediate in all characteristics; rather, some traits evolve before others. In the case of the evolution of whales, changes occurred in the skull prior to evolutionary modification of the limbs. All three fossil forms occurred in the Eocene period, 45–55 MYA.

became more and more elongated with the simultaneous reduction and eventual disappearance of the limbs. In chapter 35, we discuss the most recent such discovery, *Tiktaalik*, a species that bridged the gap between fish and the first amphibians.

On a finer scale, evolutionary change within some types of animals is known in exceptional detail. For example, about 200 million years ago (MYA), oysters underwent a change from small, curved shells to larger, flatter ones, with progressively flatter fossils seen in the fossil record over a period of 12 million years. A host of other examples illustrate similar records of successive change. The demonstration of this successive change is one of the strongest lines of evidence that evolution has occurred.

The evolution of horses is a prime example of evidence from fossils

One of the most studied cases in the fossil record concerns the evolution of horses. Modern-day members of the family Equidae include horses, zebras, donkeys, and asses, all of which are large, long-legged, fast-running animals adapted to living on open grasslands. These species, all classified in the genus *Equus*, are the last living descendants of a long lineage that has produced 34 genera since its origin in the Eocene period, approximately 55 MYA. Examination of these fossils has provided a particularly well-documented case of how evolution has proceeded through adaptation to changing environments.

The first horse

The earliest known members of the horse family, species in the genus *Hyracotherium*, didn't look much like modern-day horses at all. Small, with short legs and broad feet, these species occurred in wooded habitats, where they probably browsed on leaves and herbs and escaped predators by dodging through openings in the forest vegetation. The evolutionary path from these diminutive creatures to the workhorses of today has involved changes in a variety of traits, including size, toe reduction, and tooth size and shape (figure 21.13).

Changes in size

The first species of horses were as big as a large house cat or a medium-sized dog. By contrast, modern equids can weigh more than 500 kg. Examination of the fossil record reveals that horses changed little in size for their first 30 million years, but since then, a number of different lineages have exhibited rapid and substantial increases. However, trends toward decreased size were also exhibited in some branches of the equid evolutionary tree.

Toe reduction

The feet of modern horses have a single toe enclosed in a tough, bony hoof. By contrast, *Hyracotherium* had four toes on its front feet and three on its hind feet. Rather than hooves, these toes were encased in fleshy pads like those of dogs and cats.

Examination of fossils clearly shows the transition through time: a general increase in length of the central toe, development of the bony hoof, and reduction and loss of the other toes (see figure 21.13). As with body size, these trends occurred concurrently on several different branches of the horse evolutionary tree and were not exhibited by all lineages.

At the same time as toe reduction was occurring, these horse lineages were evolving changes in the length and skeletal structure of their limbs, leading to animals capable of running long distances at high speeds.

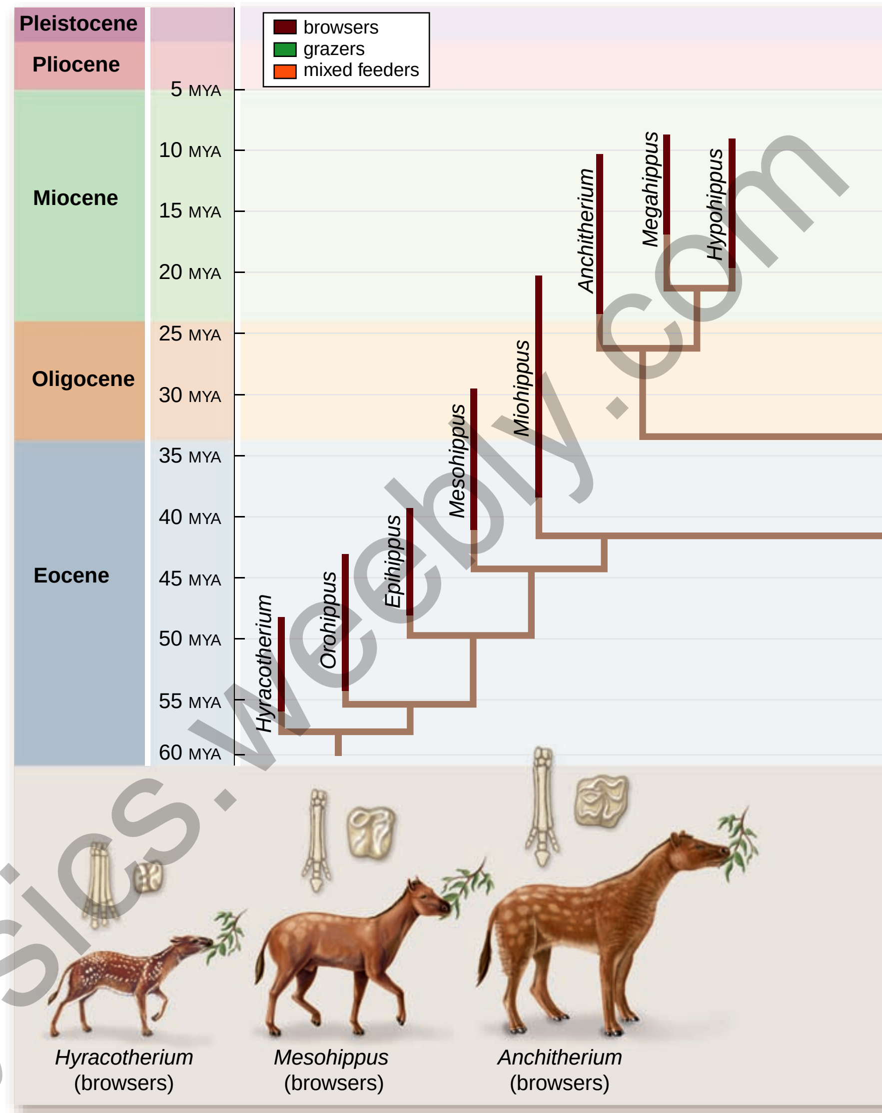
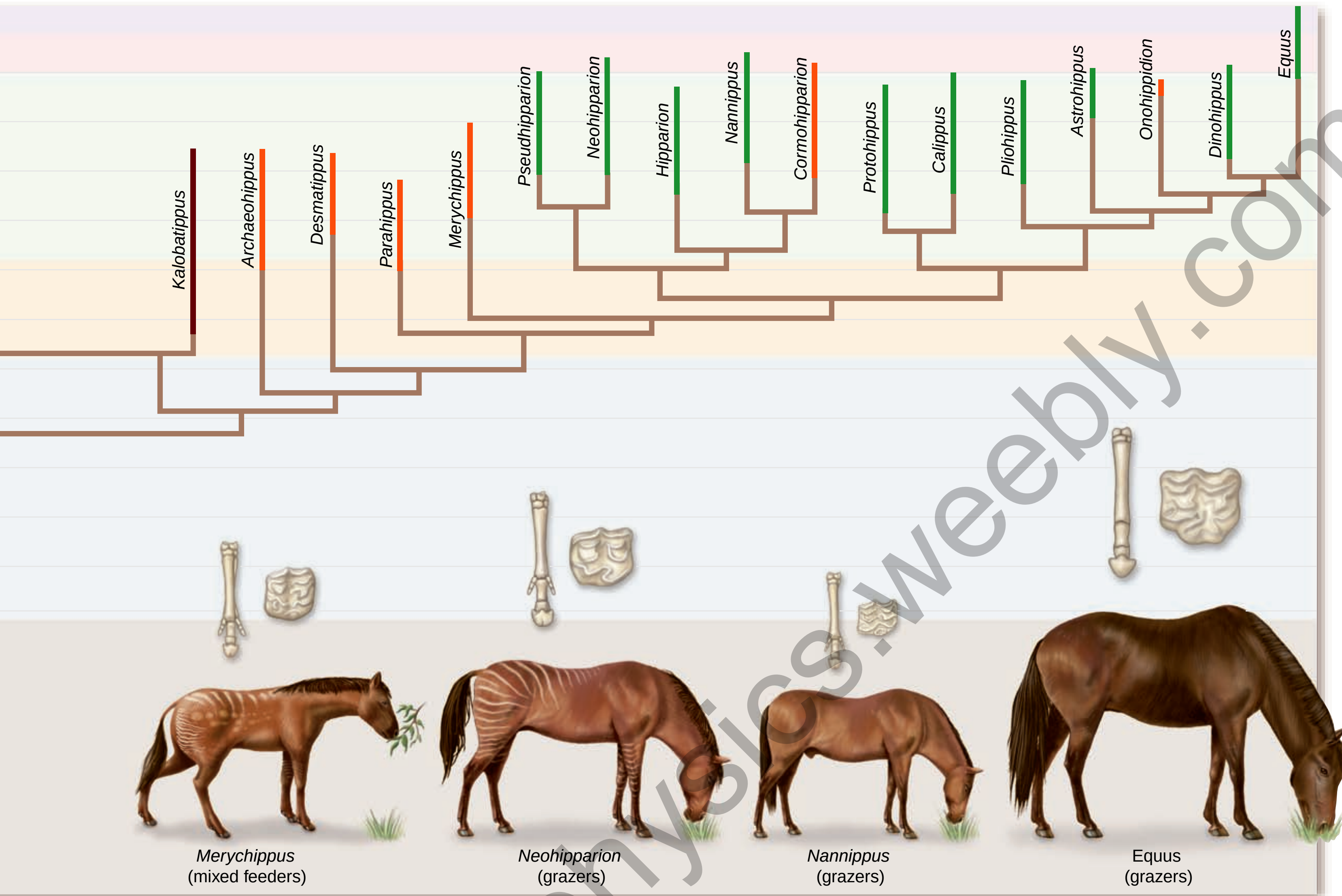


Figure 21.13 Evolutionary change in body size of horses. Lines indicate evolutionary relationships of the horse family. Horse evolution is more like a bush than a single-trunk tree; diversity was much greater in the past than it is today. In general, there has been a trend toward larger size, more complex molar teeth, and fewer toes, but this trend has exceptions. For example, a relatively recent form, *Nannippus*, evolved in the opposite direction, toward decreased size.

Inquiry question

? **Why might the evolutionary line leading to *Nannippus* have experienced an evolutionary decrease in body size?**



Tooth size and shape

The teeth of *Hyracotherium* were small and relatively simple in shape. Through time, horse teeth have increased greatly in length and have developed a complex pattern of ridges on their molars and premolars. The effect of these changes is to produce teeth better capable of chewing tough and gritty vegetation, such as grass, which tends to wear teeth down.

Accompanying these changes have been alterations in the shape of the skull that strengthened the skull to withstand the stresses imposed by continual chewing. As with body size, evolutionary change has not been constant through time. Rather, much of the change in tooth shape has occurred within the past 20 million years, and changes have not been constant among all horse lineages.

All of these changes may be understood as adaptations to changing global climates. In particular, during the late Miocene and early Oligocene epochs (approximately 20 to 25 MYA), grasslands became widespread in North America, where much of horse evolution occurred. As horses adapted to these habitats, high-speed locomotion probably became more important to escape predators. By contrast, the greater flexibility provided by multiple toes and shorter limbs, which was advantageous for ducking through complex forest vegetation, was no longer beneficial. At the same time, horses were eating grasses and other vegetation that contained more grit and other hard substances, thus favoring teeth and skulls better suited for withstanding such materials.

Evolutionary trends

For many years, horse evolution was held up as an example of constant evolutionary change through time. Some even saw in the record of horse evolution evidence for a progressive, guiding force, consistently pushing evolution in a single direction. We now know that such views are misguided, and that the course of evolutionary change over millions of years is rarely so simple.

Rather, the fossils demonstrate that even though overall trends have been evident in a variety of characteristics, evolutionary change has been far from constant and uniform through time. Instead, rates of evolution have varied widely, with long periods of little observable change and some periods of great change. Moreover, when changes happen, they often occur simultaneously in different lineages of the horse evolutionary tree.

Finally, even when a trend exists, exceptions, such as the evolutionary decrease in body size exhibited by some lineages, are not uncommon. These patterns are usually discovered for any group of plants and animals for which we have an extensive fossil record, as you will see when we discuss human evolution in chapter 35.

Horse diversity

One reason that horse evolution was originally conceived of as linear through time may be that modern horse diversity is relatively limited. For this reason it is easy to mentally picture a straight line from *Hyracotherium* to modern-day *Equus.* But today's limited horse diversity—only one surviving genus—is unusual. In fact, at the peak of horse diversity in the Miocene epoch, 13 genera of horses could be found in North America alone. These species differed in body size and in a wide variety of other characteristics. Presumably, they lived in different habitats and exhibited different dietary preferences. Had this diversity existed to modern times, early evolutionary biologists would likely have had a different outlook on horse evolution.

Learning Outcomes Review 21.4

Fossils form when an organism is preserved in a matrix such as amber, permafrost, or rock. They can be used to construct a record of major evolutionary transitions over long periods of time. The extensive fossil record for horses provides a detailed view of evolutionary diversification of this group, although trends are not constant and uniform and may include exceptions.

- ***Why might rates and direction of evolutionary change vary through time?***

21.5 *Anatomical Evidence for Evolution*

Learning Outcomes

1. ***Explain the evolutionary significance of homologous and vestigial structures.***
2. ***Describe how patterns of early development provide evidence for evolution.***

Much of the power of the theory of evolution is its ability to provide a sensible framework for understanding the diversity of life. Many observations from throughout biology simply cannot be understood in any meaningful way except as a result of evolution.

Homologous structures suggest common derivation

As vertebrates have evolved, the same bones have sometimes been put to different uses. Yet the bones are still recognizable, their presence betraying their evolutionary past. For example, the forelimbs of vertebrates are all **homologous structures**—structures with different appearances and functions that all derived from the same body part in a common ancestor.

You can see in figure 21.14 how the bones of the forelimb have been modified in different ways for different mammals. Why should these very different structures be composed of the same bones—a single upper forearm bone, a pair of lower forearm bones, several small carpals, and one or more digits? If evolution had not occurred, this would indeed be a riddle. But when we consider that all of these animals are descended from a common ancestor, it is easy to understand that natural selection has modified the same initial starting blocks to serve very different purposes.

Early embryonic development shows similarities in some groups

Some of the strongest anatomical evidence supporting evolution comes from comparisons of how organisms develop. Embryos of different types of vertebrates, for example, often are similar early on, but become more different as they develop. Early in their development vertebrate embryos possess pharyngeal pouches, which develop into different structures. In humans, for example, they become various glands and ducts; in fish, they turn into gill slits. At a later stage, every human embryo has a long tail, the vestige of which we carry to adulthood as the coccyx at the end of our spine. Human fetuses

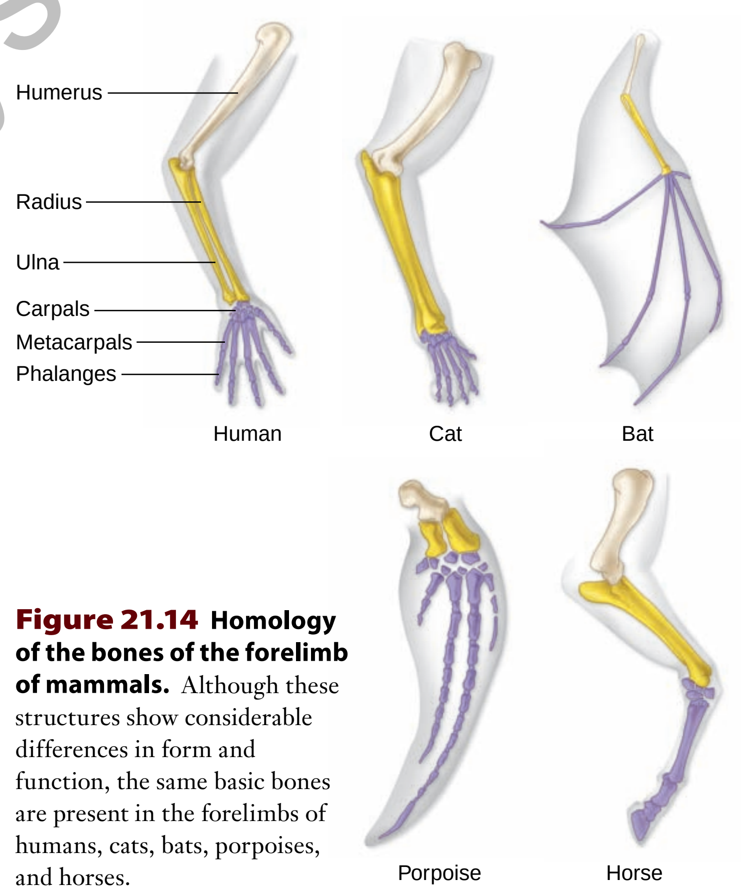


Figure 21.14 Homology of the bones of the forelimb of mammals. Although these structures show considerable differences in form and function, the same basic bones are present in the forelimbs of humans, cats, bats, porpoises, and horses.

Figure 21.15 Developmental features reflect evolutionary ancestry. Some species of frogs have lost the tadpole stage. Nonetheless, tadpole features first appear and then disappear during development in the egg.

even possess a fine fur (called *lanugo*) during the fifth month of development.

Similarly, although most frogs go through a tadpole stage, some species develop directly and hatch out as little, fully-formed frogs. However, the embryos of these species still exhibit tadpole features, such as the presence of a tail, which disappear before the froglet hatches (figure 21.15).

These relict developmental forms suggest strongly that our development has evolved, with new instructions modifying ancestral developmental patterns. We will return to the topic of embryonic development and evolution in chapter 25.

Some structures are imperfectly suited to their use

Because natural selection can only work on the variation present in a population, it should not be surprising that some organisms do not appear perfectly adapted to their environments. For example, most animals with long necks have many neck vertebrae for enhanced flexibility: Geese have up to 25, and plesiosaurs, the long-necked reptiles that patrolled the seas during the age of dinosaurs, had as many as 76. By contrast, almost all mammals have only 7 neck vertebrae, even the giraffe. In the absence of variation in vertebrae number, selection led to an evolutionary increase in vertebra size to produce the long neck of the giraffe.

An excellent example of an imperfect design is the eye of vertebrate animals, in which the photoreceptors face backward, toward the wall of the eye (figure 21.16*a*). As a result, the nerve fibers extend not backward, toward the brain, but forward into the eye chamber, where they slightly obstruct light. Moreover, these fibers bundle together to form the optic nerve, which exits through a hole at the back of the eye, creating a blind spot.

By contrast, the eye of mollusks—such as squid and octopuses—are more optimally designed: The photoreceptors face forward, and the nerve fibers exit at the back, neither obstructing light nor creating a blind spot (figure 21.16*b*).

Such examples illustrate that natural selection is like a tinkerer, working with whatever material is available to craft a workable solution, rather than like an engineer, who can design

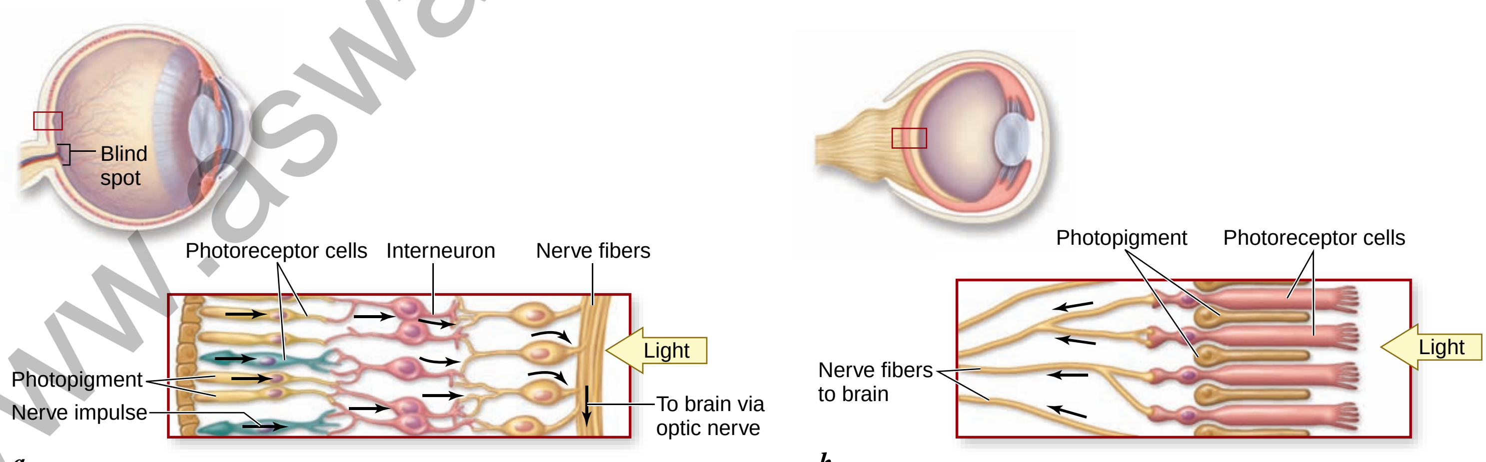


Figure 21.16 The eyes of vertebrates and mollusks. *a.* Photoreceptors of vertebrates point backward, whereas *(b)* those of mollusks face forward. As a result, vertebrate nerve fibers pass in front of the photoreceptor; and where they bundle together and exit the eye, a blind spot is created. Mollusks' eyes have neither of these problems.

and build the best possible structure for a given task. Workable, but imperfect, structures such as the vertebrate eye are an expected outcome of evolution by natural selection.

Vestigial structures can be explained as holdovers from the past

Many organisms possess **vestigial structures** that have no apparent function, but resemble structures their ancestors possessed. Humans, for example, possess a complete set of muscles for wiggling their ears, just like many other mammals do. Although these muscles allow other mammals to move their ears to pinpoint sounds such as the movements or growl of a predator, they have little purpose in humans other than amusement.

As other examples, boa constrictors have hip bones and rudimentary hind legs. Manatees (a type of aquatic mammal often referred to as "sea cows") have fingernails on their fins, which evolved from legs. Blind cave fish, which never see the light of day, have small, nonfunctional eyes. Figure 21.17 illustrates the skeleton of a baleen whale, which contains pelvic bones, as other mammal skeletons do, even though such bones serve no known function in the whale.

The human vermiform appendix is apparently vestigial; it represents the degenerate terminal part of the cecum, the blind pouch or sac in which the large intestine begins. In other mammals, such as mice, the cecum is the largest part of the large intestine and functions in storage—usually of bulk cellulose in herbivores. Although some functions have been suggested, it is difficult to assign any current function to the human vermiform appendix. In many respects, it can be a dangerous organ: appendicitis, which results from infection of the appendix, can be fatal.

It is difficult to understand vestigial structures such as these as anything other than evolutionary relicts, holdovers from the past. However, the existence of vestigial structures argues strongly for the common ancestry of the members of the groups that share them, regardless of how different those groups have subsequently become.

All of these anatomical lines of evidence—homology, development, and imperfect and vestigial structures—are readily understandable as a result of descent with modification, that is, evolution.

Learning Outcomes Review 21.5

Comparisons of the anatomy of different living animals often reveal evidence of shared ancestry. In cases of homology, the same organ has evolved to carry out different functions. In other cases, an organ is still present, usually in diminished form, even though it has lost its function altogether; such an organ or structure is termed vestigial.

- *How might homologous and vestigial structures be explained other than as a result of evolutionary descent with modification?*

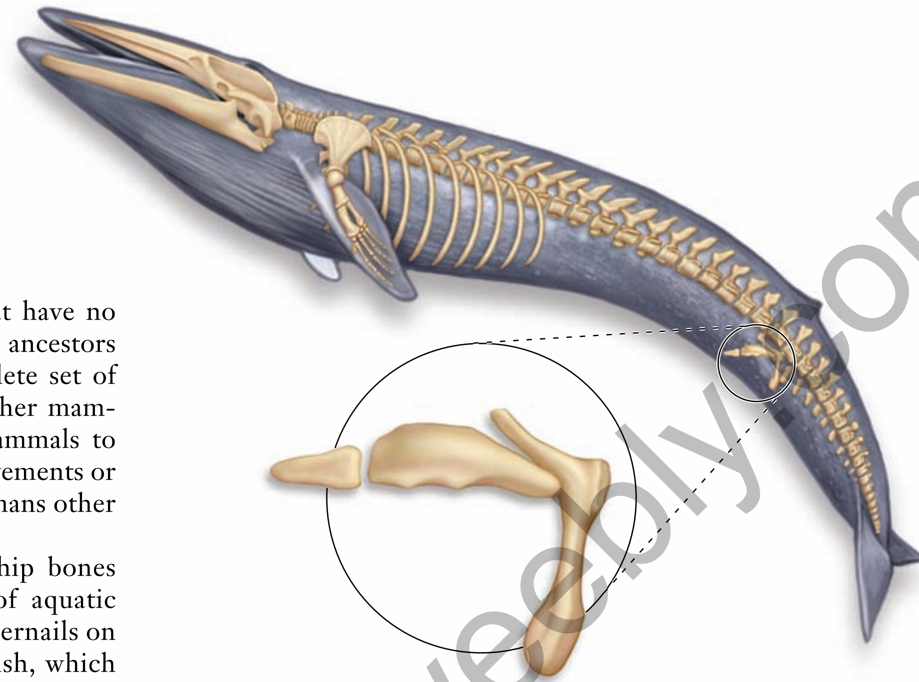


Figure 21.17 Vestigial structures. The skeleton of a whale reveals the presence of pelvic bones. These bones resemble those of other mammals, but are only weakly developed in the whale and have no apparent function.

21.6 Convergent Evolution and the Biogeographical Record

Learning Outcomes

1. *Explain the principle of convergent evolution.*
2. *Demonstrate how the biogeographical distribution of plant and animal species on islands provides evidence of evolutionary diversification.*

Biogeography, the study of the geographic distribution of species, reveals that different geographical areas sometimes exhibit groups of plants and animals of strikingly similar appearance, even though the organisms may be only distantly related.

It is difficult to explain so many similarities as the result of coincidence. Instead, natural selection appears to have favored parallel evolutionary adaptations in similar environments. Because selection in these instances has tended to favor changes that made the two groups more alike, their phenotypes have converged. This form of evolutionary change is referred to as **convergent evolution.**

Marsupials and placentals demonstrate convergence

In the best known case of convergent evolution, two major groups of mammals—marsupials and placentals—have evolved in very similar ways in different parts of the world. Marsupials

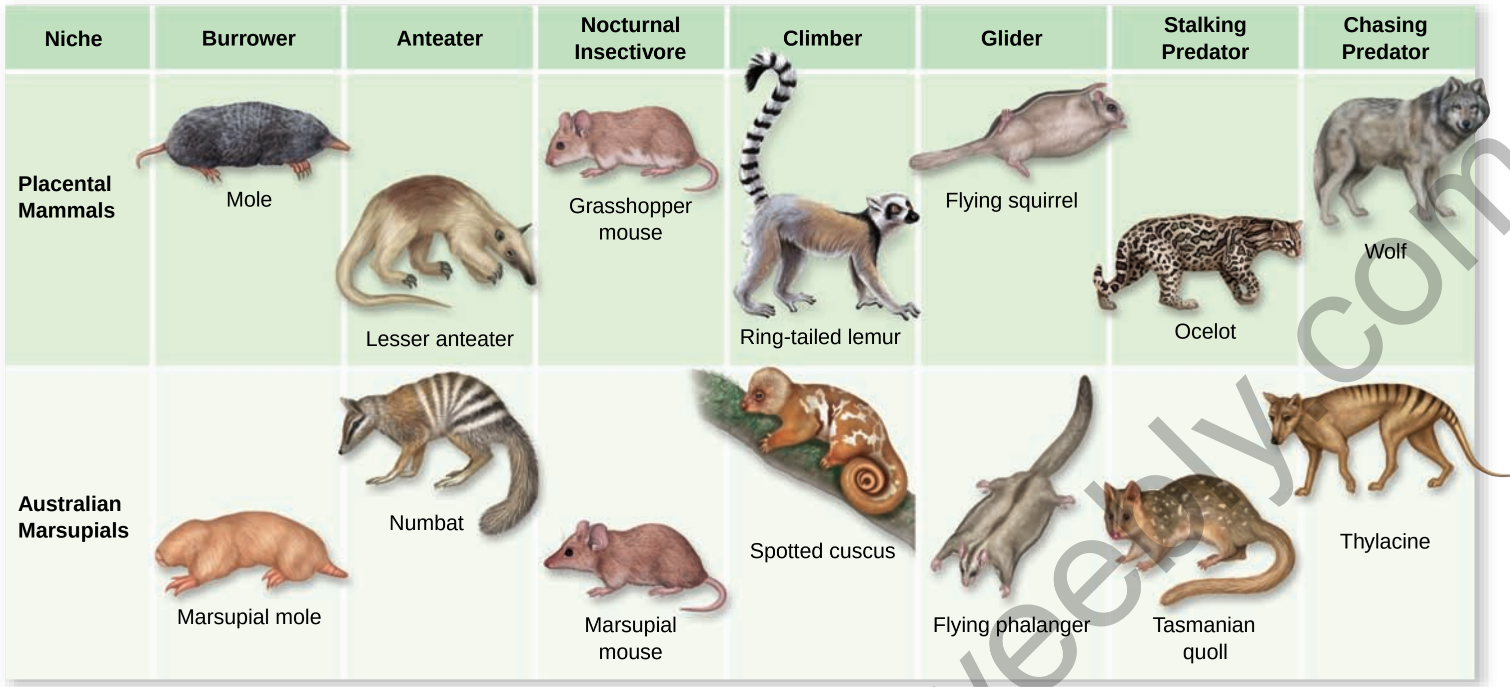


Figure 21.18 Convergent evolution. Many marsupial species in Australia resemble placental mammals occupying similar ecological niches elsewhere in the rest of the world. Marsupials evolved in isolation after Australia separated from other continents.

are a group in which the young are born in a very immature condition and held in a pouch until they are ready to emerge into the outside world. In placentals, by contrast, offspring are not born until they can safely survive in the external environment (with varying degrees of parental care).

Australia separated from the other continents more than 70 million years ago; at that time, both marsupials and placental mammals had evolved, but in different places. In particular, only marsupials occurred in Australia. As a result of this continental separation, the only placental mammals in Australia today are bats and a few colonizing rodents (which arrived relatively recently), and Australia is dominated by marsupials.

What are the Australian marsupials like? To an astonishing degree, they resemble the placental mammals living today on the other continents (figure 21.18). The similarity between some individual members of these two sets of mammals argues strongly that they are the result of convergent evolution, similar forms having evolved in different, isolated areas because of similar selective pressures in similar environments.

Convergent evolution is a widespread phenomenon

When species interact with the environment in similar ways, they often are exposed to similar selective pressures, and they therefore frequently develop the same evolutionary adaptations. Consider, for example, fast-moving marine predators (figure 21.19). The hydrodynamics of moving through water require a streamlined body shape to minimize friction. It is no coincidence that dolphins, sharks, and tuna—among the fastest of marine species—have all evolved to have the same basic shape. We can infer as well that ichthyosaurs—marine reptiles that lived during the Age of the Dinosaurs—exhibited a similar lifestyle.

Island trees exhibit a similar phenomenon. Most islands are covered by trees (or were until the arrival of humans). Careful inspection of these trees, however, reveals that they are not closely related to the trees with which we are familiar. Although they have all the characteristics of trees, such as being tall and having a tough outer covering, in many cases island trees are members of plant families that elsewhere exist only as flowers,

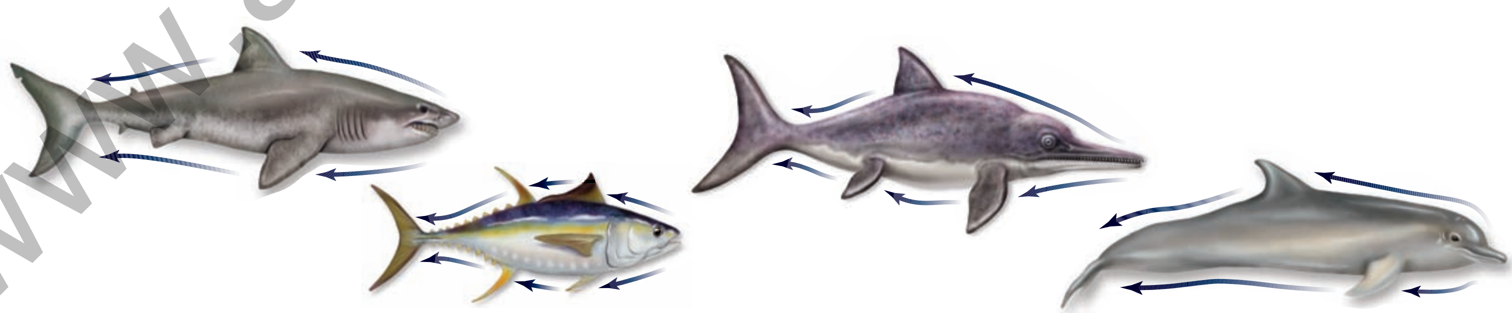


Figure 21.19 Convergence among fast-swimming predators. Fast movement through water requires a streamlined body form, which has evolved numerous times.

shrubs, or other small bushes. For example, on many islands, the native trees are members of the sunflower family.

Why do these plants evolve into trees on islands? Probably because seeds from trees rarely make it to isolated islands. As a result, those species that do manage to colonize distant islands face an empty ecological landscape upon arrival. In the absence of other treelike plants, natural selection often would favor individual plants that could capture the most sunlight for photosynthesis, and the result is the evolution of similar treelike forms on islands throughout the world.

Convergent evolution is even seen in humans. People in most populations stop producing lactase, the enzyme that digests milk, some time in childhood. However, individuals in African and European populations that raise cattle produce lactase throughout their lives. DNA analysis indicates that this has been accomplished by the incorporation of different mutations in Africa and Europe, which indicates that the populations have independently acquired this adaptation.

Biogeographical studies provide further evidence of evolution

Darwin made several important observations during his voyage around the world. He noted that islands often are missing plants and animals common on continents, such as frogs and land mammals. Accidental human introductions have proved that these species can survive if they are released on islands, so lack of suitable habitat is not the cause. In addition, those species that are present on islands often have diverged from their continental relatives and sometimes—as with Darwin's finches and the island trees just discussed—occupy ecological niches used by other species on continents. Lastly, island species usually are more closely related to species on nearby continents, even though the environment there is often not very similar to that on island.

Darwin deduced the explanation for these phenomena. Many islands have never been connected to continental areas. The species that occur there arrived by dispersing across the water; dispersal from nearby areas is more likely than from more distant sources, though long-distance colonization does occur occasionally. Some species, those that can fly, float, or swim are more likely to get to the island than others. Some, like frogs, are particularly vulnerable to dehydration in saltwater and have almost no chance of island colonization.

The absence of some types of plants and animals provides opportunity to those that do arrive; as a result, colonizers often evolve into many species exhibiting great ecological and morphological diversity.

Geographic proximity is not always a good predictor of evolutionary relationships, however. Earth's continents have not always been where they are today; rather, continents are constantly moving because of the process known as *continental drift*. Although the pace is slow, on the order of several centimeters per year, the configuration of the continents can, and has, changed considerably over geologic time. As a result, closely related species that at one time occurred near each other may now be separated by thousands of miles. Many examples occur on the southern continents, which were last united as the supercontinent Gondwana more than 100 million years ago. One such example is the southern beech tree, which is found in Chile, and also in Australia and New Zealand. In cases such as this, Earth's history and evolutionary history must be considered jointly to make sense of geographical distributions.

Learning Outcomes Review 21.6

Convergence is the evolution of similar forms in different lineages when exposed to similar selective pressures. The biogeographical distribution of species often reflects the outcome of evolutionary diversification with closely related species in nearby areas.

- ***Why does convergent evolution occur and why might species occupying similar environments in different localities sometimes not exhibit it?***

21.7 *Darwin's Critics*

Learning Outcomes

1. ***Characterize the criticisms of evolutionary theory and list counterarguments that can be made.***
2. ***Distinguish between hypothesis and theory in scientific usage.***

In the century and a half since he proposed it, Darwin's theory of evolution by natural selection has become nearly universally accepted by biologists, but has been a source of controversy among some members of the general public. Here we discuss seven principle objections that critics raise to the teaching of evolution as biological fact, along with some answers that scientists present in response.

1. **Evolution is not solidly demonstrated.** "Evolution is just a theory," Darwin's critics point out, as though *theory* meant a lack of knowledge, or some kind of guess.

   Scientists, however, use the word *theory* in a very different sense than the general public does. Theories are the solid ground of science—that about which we are most certain. Few of us doubt the theory of gravity because it is "just a theory."
2. **There are no fossil intermediates.** "No one ever saw a fin on the way to becoming a leg," critics claim, pointing to the many gaps in the fossil record in Darwin's day.

   Since that time, however, many fossil intermediates in vertebrate evolution have indeed been found. A clear line of fossils now traces the transition between hoofed mammals and whales, between reptiles and mammals, between dinosaurs and birds, and between apes and humans. The fossil evidence of evolution between major forms is compelling.
3. **The intelligent design argument.** "The organs of living creatures are too complex for a random process to have produced—the existence of a clock is evidence of the existence of a clockmaker."

Evolution by natural selection is not a random process. Quite the contrary, by favoring those variations that lead to the highest reproductive fitness, natural selection is a nonrandom process that can construct highly complex organs by incrementally improving them from one generation to the next.

For example, the intermediates in the evolution of the mammalian ear can be seen in fossils, and many intermediate "eyes" are known in various invertebrates. These intermediate forms arose because they have value—being able to detect light slightly is better than not being able to detect it at all. Complex structures such as eyes evolved as a progression of slight improvements. Moreover, inefficiencies of certain designs, such as the vertebrate eye and the existence of vestigial structures, do not support the idea of an intelligent designer.

4. **Evolution violates the Second Law of Thermodynamics.** "A jumble of soda cans doesn't by itself jump neatly into a stack—things become more disorganized due to random events, not more organized."

   Biologists point out that this argument ignores what the second law really says: Disorder increases in a closed system, which the Earth most certainly is not. Energy continually enters the biosphere from the Sun, fueling life and all the processes that organize it.

5. **Proteins are too improbable.** "Hemoglobin has 141 amino acids. The probability that the first one would be leucine is 1/20, and that all 141 would be the ones they are by chance is $(1/20)^{141}$, an impossibly rare event."

   This argument illustrates a lack of understanding of probability and statistics—probability cannot be used to argue backwards. The probability that a student in a classroom has a particular birthdate is 1/365; arguing this way, the probability that everyone in a class of 50 would have the birthdates that they do is $(1/365)^{50}$, and yet there the class sits, all with their actual birthdates.

6. **Natural selection does not imply evolution.** "No scientist has come up with an experiment in which fish evolve into frogs and leap away from predators."

   Can we extrapolate from our understanding that natural selection produces relatively small changes that are observable in populations *within* species to explain the major differences observed *between* species? Most biologists who have studied the problem think so. The differences between breeds produced by artificial selection—such as chihuahuas, mastiffs, and greyhounds—are more distinctive than the differences between some wild species, and laboratory selection experiments sometimes create forms that cannot interbreed and thus would in nature be considered different species. Thus, production of radically different forms has indeed been observed, repeatedly. To object that evolution still does not explain really major differences, such as those between fish and amphibians, simply takes us back to point number 2. These changes take millions of years, and they are seen clearly in the fossil record.

7. **The irreducible complexity argument.** Because each part of a complex cellular mechanism such as blood clotting is essential to the overall process, the intricate machinery of the cell cannot be explained by evolution from simpler stages.

   What's wrong with this argument is that each part of a complex molecular machine evolves as part of the whole system. Natural selection can act on a complex system because at every stage of its evolution, the system functions. Parts that improved function are added. Subsequently, other parts may be modified or even lost, so that parts that were not essential when they first evolved become essential. In this way, an "irreducible complex" structure can evolve by natural selection. The same process works at the molecular level.

   For example, snake venom initially evolved as enzymes to increase the ability of snakes to digest large prey items, which were captured by biting the prey and then constricting them with coils. Subsequently, the digestive enzymes evolved to become increasingly lethal. Rattlesnakes kill large prey by injecting them with venom, letting them go, and then tracking them down and eating them after they die. To do so, they have evolved extremely toxic venom, highly modified syringelike front teeth, and many other characteristics. Take away the fangs or the venom and the rattlesnakes can't feed—what initially evolved as nonessential parts are now indispensable; irreducible complexity has evolved by natural selection.

   The mammalian blood clotting system similarly has evolved from much simpler systems. The core clotting system evolved at the dawn of the vertebrates more than 500 million years ago, and it is found today in primitive fishes such as lampreys. One hundred million years later, as vertebrates continued to evolve, proteins were added to the clotting system, making it sensitive to substances released from damaged tissues. Fifty million years later, a third component was added, triggering clotting by contact with the jagged surfaces produced by injury. At each stage, as the clotting system evolved to become more complex, its overall performance came to depend on the added elements. Thus, blood clotting has become "irreducibly complex" as the result of Darwinian evolution.

Statements that various structures could not have been built by natural selection have repeatedly been made over the past 150 years. In many cases, after detailed scientific study, the likely path by which such structures have evolved has been discovered.

Learning Outcomes Review 21.7

Darwin's theory of evolution is controversial to some in the general public. Objections are often based on a misunderstanding of the theory. In scientific usage, a hypothesis is an educated guess, whereas a theory is an explanation that fits available evidence and has withstood rigorous testing.

- ***Suppose someone suggests that humans originally came from Mars. Would this be a hypothesis or a theory, and how could it be tested?***

Chapter Review

21.1 The Beaks of Darwin's Finches: Evidence of Natural Selection

Galápagos finches exhibit variation related to food gathering.

The correspondence between beak shape and its use in obtaining food suggested to Darwin that finch species had diversified and adapted to eat different foods.

Modern research has verified Darwin's selection hypothesis.

Natural selection acts on variation in beak morphology, favoring larger-beaked birds during extended droughts and smaller-beaked birds during long periods of heavy rains.

Because this variation is heritable, evolutionary change occurs in the frequencies of beak sizes in subsequent generations.

21.2 Peppered Moths and Industrial Melanism: More Evidence of Selection

Light-colored moths decreased in polluted areas.

In polluted areas where soot built up on tree trunks, the dark-colored form of the peppered moth became more common. In unpolluted areas, light-colored forms remained predominant.

Experiments suggested that predation by birds was the cause; light-colored moths stand out on dark trunks, and vice-versa.

When environmental conditions reverse, so does selection pressure.

In the last 40 years, pollution has decreased in many areas and the frequency of light-colored moths has rebounded.

The agent of selection may be difficult to pin down.

Recent research has questioned whether bird predation is the agent of selection. Regardless, the observation that the dark-colored form has increased during times of pollution and then declined as pollution abates indicates that natural selection has acted on moth coloration.

21.3 Artificial Selection: Human-Initiated Change

(see figure 21.5)

Experimental selection produces changes in populations.

Laboratory experiments in directional selection have shown that substantial evolutionary change can occur in these controlled populations.

Agricultural selection has led to extensive modification of crops and livestock.

Domesticated breeds have arisen from artificial selection.

Crop plants and domesticated animal breeds are often substantially different from their wild ancestors.

If artificial selection can rapidly create substantial change, then it is reasonable to assume that natural selection could have created the Earth's diversity of life over millions of years.

21.4 Fossil Evidence of Evolution

The age of fossils is estimated by rates of radioactive decay.

Specimens become fossilized in different ways. Fossils in rock can be dated by calculating the extent of radioactive decay based on half-lives of known isotopes.

Fossils present a history of evolutionary change.

Fossils document evolutionary transition.

The history of life on Earth can be traced through the fossil record. In recent years, new fossil discoveries have provided more detailed understanding of major evolutionary transitions.

The evolution of horses is a prime example of evidence from fossils.

The fossil record indicates that horses have evolved from small, forest-dwelling animals to the large and fast plains-dwelling species alive today.

Over the course of 50 million years, evolution has not been constant and uniform. Rather, change has been rapid at some times, slow at others. Although a general trend toward increase in size is evident, some species evolved to smaller sizes.

21.5 Anatomical Evidence for Evolution

Homologous structures suggest common derivation.

Homologous structures may have different appearances and functions even though derived from the same common ancestral body part.

Early embryonic development shows similarities in some groups.

Embryonic development shows similarity in developmental patterns among species whose adult phenotypes are very different.

Species that have lost a feature that was present in an ancestral form often develop and then lose that feature during embryological development.

Some structures are imperfectly suited to their use.

Natural selection can influence only the variation present in a population; because of this, evolution often results in workable, but imperfect structures, such as the vertebrate eye.

Vestigial structures can be explained as holdovers from the past.

The existence of vestigial structures supports the concept of common ancestry among organisms that share them.

21.6 Convergent Evolution and the Biogeographical Record

Marsupials and placentals demonstrate convergence.

Convergent evolution may occur in species or populations exposed to similar selective pressures. Marsupial mammals in Australia have converged upon features of their placental counterparts elsewhere.

Convergent evolution is a widespread phenomenon.

Examples include hydrodynamic streamlining in marine species and the evolution of tree species on islands from ancestral forms that were not treelike.

Biogeographical studies provide further evidence of evolution.

Island species usually are closely related to species on nearby continents even if the environments are different. Early island colonizers often evolve into diverse species because other, competing species are scarce.

21.7 Darwin's Critics

Darwin's theory of evolution by natural selection is almost universally accepted by biologists. Many criticisms have been made both historically and recently, but most stem from a lack of understanding of scientific principles, the theory's actual content, or the time spans involved in evolution.

Review Questions

UNDERSTAND

1. Artificial selection is different from natural selection because
   a. artificial selection is not capable of producing large changes.
   b. artificial selection does not require genetic variation.
   c. natural selection cannot produce new species.
   d. breeders (people) choose which individuals reproduce based on desirability of traits.
2. Gaps in the fossil record
   a. demonstrate our inability to date geological sediments.
   b. are expected since the probability that any organism will fossilize is extremely low.
   c. have not been filled in as new fossils have been discovered.
   d. weaken the theory of evolution.
3. The evolution of modern horses *(Equus)* is best described as
   a. the constant change and replacement of one species by another over time.
   b. a complex history of lineages that changed over time, with many going extinct.
   c. a simple history of lineages that have always resembled extant horses.
   d. none of these.
4. Homologous structures
   a. are structures in two or more species that originate as the same structure in a common ancestor.
   b. are structures that look the same in different species.
   c. cannot serve different functions in different species.
   d. must serve different functions in different species.
5. Convergent evolution
   a. is an example of stabilizing selection.
   b. depends on natural selection to independently produce similar phenotypic responses in different species or populations.
   c. occurs only on islands.
   d. is expected when different lineages are exposed to vastly different selective environments.
6. Darwin's finches are a noteworthy case study of evolution by natural selection because evidence suggests
   a. they are descendants of many different species that colonized the Galápagos.
   b. they radiated from a single species that colonized the Galápagos.
   c. they are more closely related to mainland species than to one another.
   d. none of the above.
7. The possession of fine fur in 5-month human embryos indicates
   a. that the womb is cold at that point in pregnancy.
   b. humans evolved from a hairy ancestor.
   c. hair is a defining feature of mammals.
   d. some parts of the embryo grow faster than others.

APPLY

1. In Darwin's finches,
   a. occurrence of wet and dry years preserves genetic variation for beak size.
   b. increasing beak size over time proves that beak size is inherited.
   c. large beak size is always favored.
   d. all of the above.
2. Artificial selection experiments in the laboratory such as in figure 21.5 are an example of
   a. stabilizing selection.
   b. negative frequency-dependent selection.
   c. directional selection.
   d. disruptive selection.
3. Convergent evolution is often seen among species on different islands because
   a. island populations are usually smaller and more affected by genetic drift.
   b. disruptive selection occurs commonly on islands.
   c. island species are usually most closely related to species in similar habitats elsewhere.
   d. when islands are first colonized, many ecological resources are unused, allowing descendants of a colonizing species to diversify and adapt to many different parts of the environment.

SYNTHESIZE

1. What conditions are necessary for evolution by natural selection?

Refer to figure 21.2 for the following two questions.

2. Explain how data shown in figure 21.2*a* and *b* relate to the conditions identified by you in question 1.
3. On figure 21.2*b*, draw the relationship between offspring beak depth and parent beak depth, assuming that there is no genetic basis to beak depth in the medium ground finch.
4. Refer to figure 21.5, artificial selection in the laboratory. In this experiment, one population of *Drosophila* was selected for low numbers of bristles and the other for high numbers. Note that not only did the means of the populations change greatly in 35 generations, but also all individuals in both experimental populations lie outside the range of the initial population. What would the result of this experiment have been if only flies with high numbers of bristles were allowed to breed?
5. The ancestor of horses was a small, many-toed animal that lived in forests, whereas today's horses are large animals with a single hoof that live on open plains. A series of intermediate fossils illustrate how this transition has occurred, and for this reason, many old treatments of horse evolution portrayed it as a steady increase through time in body size accompanied by a steady decrease in toe number. Why is this interpretation incorrect?

Chapter 22

The Origin of Species

Chapter Outline

Introduction

Although Darwin titled his book On the Origin of Species, *he never actually discussed what he referred to as that "mystery of mysteries"—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 an important mechanism of evolutionary change, the process of adaptation does not explain how one species becomes another, a process we call* speciation. *As we shall see, adaptation may be involved in the speciation process, but it does not have to be.*

Before we can discuss how one species gives rise to another, we need to understand exactly what a species is. Even though the definition of 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.

22.1 The Nature of Species and the Biological Species Concept

Learning Outcomes

1. *Distinguish between the biological species concept and the ecological species concept.*
2. *Define the two kinds of reproductive isolating mechanisms.*
3. *Describe the relationship of reproductive isolating mechanisms to the biological species concept.*

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 different populations belonging to the same species.

Sympatric species inhabit the same locale but remain distinct

Put out birdfeeders on your balcony or in your back yard, and you will attract a wide variety of birds (especially if you include 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.

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**) are distinctive entities that are phenotypically different, utilize different parts of the habitat, and behave differently. This observation is generally true not only for birds, but also for most other types of organisms.

Occasionally, two species occur together that appear to be nearly identical. In such cases, we need to go beyond visual similarities. When other aspects of the phenotype are examined, such as the mating calls or the chemicals exuded by each species, they usually reveal great differences. In other words, even though we might have trouble distinguishing them, the organisms themselves have no such difficulties.

Populations of a species exhibit geographic variation

Within a single species, individuals in populations that occur in different areas may be distinct from one another. Such groups of distinctive individuals may be classified as **subspecies** (the vague term *race* has a similar connotation, but is no longer commonly used). In areas where these populations occur close to one another, individuals often exhibit combinations of features characteristic of both populations (figure 22.1). In other words, even though geographically distant populations may appear distinct, they are usually connected by intervening populations that are intermediate in their characteristics.

The biological species concept focuses on the ability to exchange genes

What can account for both the distinctiveness of sympatric species and the connectedness of geographically separate 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 exchanged genes, which they generally do not, we might expect such species to rapidly lose their distinctions, as the gene pools (that is, all of the alleles present in a species) of the different species became homogenized. Conversely, the ability of geographically distant populations of a single species to share genes through the process of gene flow may keep these populations integrated as members of the same species.

Based on these ideas, in 1942 the evolutionary biologist Ernst Mayr set forth 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 composed of populations whose members mate with each other and produce fertile offspring—or would do so if they came into contact. Conversely, populations whose members do not mate with each other or who cannot produce fertile offspring are said to be **reproductively isolated** and, therefore, are members of different species.

What causes reproductive isolation? If organisms cannot interbreed or cannot produce fertile offspring, they clearly belong to different species. However, some populations that are considered separate species can interbreed and produce fertile offspring,

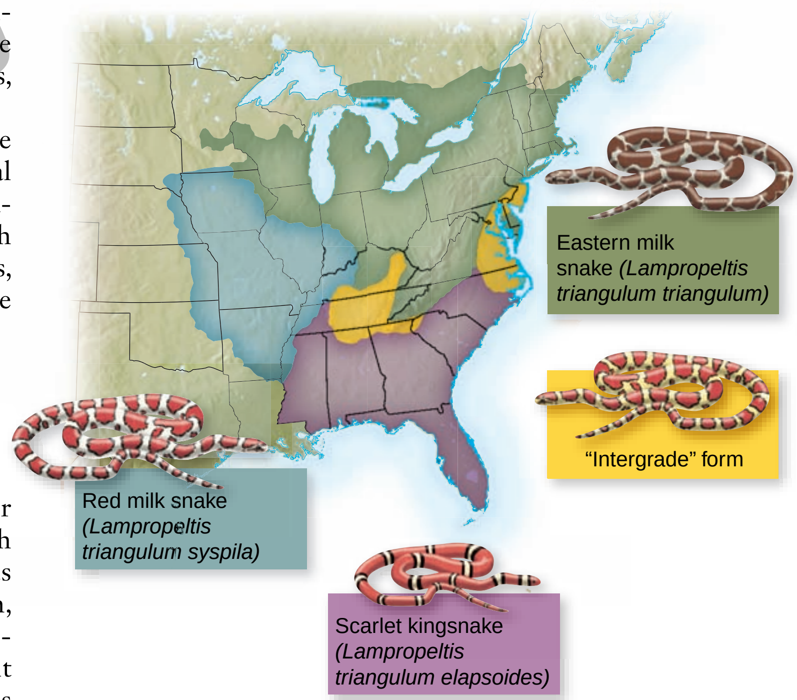
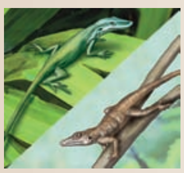
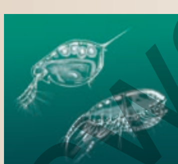
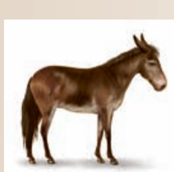


Figure 22.1 Geographic variation in the milk snake, *Lampropeltis triangulum*. Although subspecies appear phenotypically quite distinctive from one another, they are connected by populations that are phenotypically intermediate.

but they ordinarily do not do so under natural conditions. They are still considered reproductively isolated in that genes from one species generally will not enter the gene pool of the other.

Table 22.1 summarizes the steps at which barriers to successful reproduction may occur. Such barriers are termed **reproductive isolating mechanisms** because they prevent genetic exchange between species. We will discuss examples of these next, beginning with those that prevent the formation of zygotes, which are called **prezygotic isolating mechanisms.** Mechanisms that prevent the proper functioning of zygotes after they form are called **postzygotic isolating mechanisms.**

TABLE 22.1 Reproductive Isolating Mechanisms

Mechanism		Description
PREZYGOTIC ISOLATING MECHANISMS		
Geographic isolation		Species occur in different areas, which are often separated by a physical barrier, such as a river or mountain range.
Ecological isolation		Species occur in the same area, but they occupy different habitats and rarely encounter each other.
Behavioral isolation		Species differ in their mating rituals.
Temporal isolation		Species reproduce in different seasons or at different times of the day.
Mechanical isolation		Structural differences between species prevent mating.
Prevention of gamete fusion		Gametes of one species function poorly with the gametes of another species or within the reproductive tract of another species.
POSTZYGOTIC ISOLATING MECHANISMS		
Hybrid inviability or infertility		Hybrid embryos do not develop properly, hybrid adults do not survive in nature, or hybrid adults are sterile or have reduced fertility.

Prezygotic isolating mechanisms prevent the formation of a zygote

Mechanisms that prevent formation of a zygote include ecological or environmental isolation, behavioral isolation, temporal isolation, mechanical isolation, and prevention of gamete fusion.

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 so, 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 22.2). 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. *B. woodhousei* prefers to breed in streams, and *B. americanus* breeds in rainwater puddles.

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 m, 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 m 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 little intermediate habitat where the hybrids might flourish.

Figure 22.2 Lions and tigers are ecologically isolated. The ranges of lions and tigers overlap in India. However, lions and tigers do not hybridize in the wild because they utilize different portions of the habitat. Lions live in open grassland, whereas tigers are solitary animals that live in the forest. Hybrids, such as this tiglon, have been successfully produced in captivity, but hybridization does not occur in the wild.

Figure 22.3 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 the two other species of boobies that occur in the Galápagos is very different, as is the color of their feet.

Behavioral isolation

Chapter 54 describes 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 22.3). For example, mallard and pintail ducks are perhaps the two most common freshwater ducks in North America. In captivity, they produce completely fertile hybrid offspring, but in nature they nest side by side and only rarely hybridize.

Sympatric species avoid mating with members of the wrong species in a variety of ways; every mode of communication imaginable appears to be used by some species. Differences in visual signals, as just discussed, are common; however, other types of animals rely more on other sensory modes for communication. Many species, such as frogs, birds, and a variety of insects, use sound to attract mates. Predictably, sympatric species of these animals produce different calls. Similarly, the "songs" of lacewings are produced when they vibrate their abdomens against the surface on which they are sitting, and sympatric species produce different vibration patterns (figure 22.4).

Other species rely on the detection of chemical signals, called **pheromones.** The use of pheromones in moths has been particularly well studied. When female moths are ready to mate, they emit a pheromone that males can detect at great distances. Sympatric species differ in the pheromone they produce: Either they use different chemical compounds, or, if using the same compounds the proportions used are different. Laboratory studies indicate that males are remarkably adept at distinguishing the pheromones of their own species from those of other species or even from synthetic compounds similar, but not identical, to that of their own species.

Some species even use electroreception. African and South Asian electric fish independently have evolved specialized organs in their tails that produce electrical discharges and electroreceptors on their skins to detect them. These discharges are used to communicate in social interactions; field experiments indicate that males can distinguish between signals produced by their own and other species, probably on the basis of differences in the timing of the electrical pulses.

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 these hybrids are rare in nature because *L. graminifolia* flowers in early spring and *L. canadensis* flowers in summer. When their blooming periods overlap, as happens 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. 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.

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 distinguishing species.

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 carry the pollen of one species on a certain place on their bodies; if this area does not come into

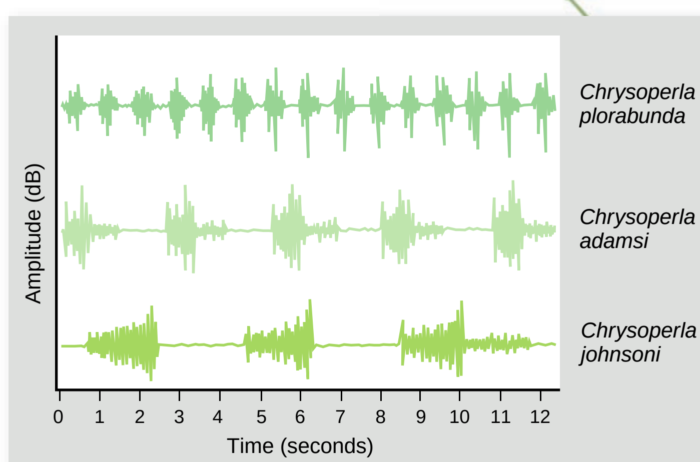


Figure 22.4 Differences in courtship song of sympatric species of lacewings. Lacewings are small insects that rely on auditory signals produced by moving their abdomens to vibrate the surface on which they are sitting to attract mates. As these recordings indicate, the vibration patterns produced by sympatric species differ greatly. Females, which detect the calls as they are transmitted through solid surfaces such as branches, are able to distinguish calls of different species and only respond to individuals producing their own species' call.

Figure 22.5 Postzygotic isolation in leopard frogs. These four species resemble one another closely in their external features. Their status as separate species first was suspected when hybrids between some pairs of these species were found to produce defective embryos in the laboratory. Subsequent research revealed that the mating calls of the four species differ substantially, indicating that the species have both pre- and postzygotic isolating mechanisms.

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 gametes directly into water, the eggs and sperm derived from different species may not attract or fuse with one another. Many land animals may not hybridize successfully because the sperm of one species functions 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, isolating mechanisms such as these prevent the union of gametes, even following successful mating.

Postzygotic isolating mechanisms prevent normal development into reproducing adults

All of the factors we have discussed so far 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.

As you saw in chapter 19, development 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.

The 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 22.5). Careful examination, however, 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 experiments, are common in plants. Sometimes the hybrid plant 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 when hybrids survive the embryo stage, they may still not develop normally. If the hybrids are less physically fit than their parents, they will almost certainly be eliminated in nature. Even if a hybrid is vigorous and strong, as in the case of the mule, which is a hybrid between a female horse and a male donkey, it may still be sterile and thus incapable of contributing to succeeding generations.

Hybrids may be sterile because the development of sex organs is abnormal, because the chromosomes derived from the respective parents cannot pair properly during meiosis, or due to a variety of other causes.

The biological species concept does not explain all observations

The biological species concept has proved to be an effective way of understanding the existence of species in nature. Nonetheless, it fails to take into account all observations, leading some biologists to propose alternative species concepts.

One criticism of the biological species concept concerns the extent to which all species truly are reproductively isolated. By definition, under the biological species concept, species should not interbreed and produce fertile offspring. But in recent years, biologists have detected much greater amounts of interspecies hybridization than was previously thought to occur between populations that seem to coexist as distinct biological entities.

Botanists have always been aware that plant species often undergo substantial amounts of hybridization. More than 50% of California plant species included in one study, for example, were not well defined by genetic isolation. This coexistence without genetic isolation can be long-lasting: Fossil data show that balsam poplars and cottonwoods have been phenotypically distinct for 12 million years, but they also have routinely produced hybrids throughout this time. Consequently, many botanists have long felt that the biological species concept applies only to animals.

New evidence, however, increasingly indicates that hybridization is not all that uncommon in animals, either. In recent years, many cases of substantial hybridization between animal species have been documented. One recent survey indicated that almost 10% of the world's 9500 bird species are known to have hybridized in nature.

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 they occupy different ecological niches. 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 ground finches mated with other species every year. Furthermore, hybrid offspring appeared to be at no disadvantage in terms of survival or subsequent reproduction. This is not a trivial amount of genetic exchange, and one might expect to see the species coalesce into one genetically variable population—but the species are maintaining their distinctiveness.

Hybridization is not rampant throughout the animal world, however. Most bird species do not hybridize, and probably even fewer experience significant amounts of hybridization. Still, hybridization is common enough to cast doubt on whether reproductive isolation is the only force maintaining the integrity of species.

Natural selection and the ecological species concept

An alternative hypothesis proposes 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, described in chapter 20, then maintains the species' adaptations. Hybridization has little effect because alleles introduced into one species' gene pool from other species are quickly eliminated by natural selection.

You probably recall from 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, an ecological species concept is not likely to have any fewer exceptions than does the biological species concept, although it might prove to be a more successful description for certain types of organisms or habitats.

Other weaknesses of the biological species concept

The biological species concept has been criticized for other reasons as well. For example, it can be difficult to apply the concept to populations that are geographically separated in nature. 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. Many species that coexist without interbreeding in nature will readily hybridize in the artificial settings of the laboratory or zoo. Consequently, evaluating whether such 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 therefore has no meaning for such organisms.

For these reasons, 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 reality, there may be 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 would not be surprising to find that different processes are operating in different organisms.

In addition, some scientists have turned from emphasizing the processes that maintain species distinctions to examining the evolutionary history of populations. These genealogical species concepts are currently a topic of great debate and are discussed further in chapter 23.

Learning Outcomes Review 22.1

Species are populations of organisms that are distinct from other, co-occurring species, and are interconnected geographically. The biological species concept therefore defines species based on their ability to interbreed. Reproductive isolating mechanisms prevent successful interbreeding between species. The ecological species concept relies on adaptation and natural selection as a force for maintaining separation of species.

- ***How does the ability to exchange genes explain why sympatric species remain distinct and geographic populations of one species remain connected?***

22.2 Natural Selection and Reproductive Isolation

Learning Outcomes

1. ***Define reinforcement in the context of reproductive isolation.***
2. ***Explain the possible outcomes when two populations that are partially reproductively isolated become sympatric.***

One of the oldest questions in the field of evolution is: How does one ancestral species become divided into two descendant species (a process termed cladogenesis)? If species are defined by the existence of reproductive isolation, then the process of speciation is identical to the evolution of reproductive isolating mechanisms.

Selection may reinforce isolating mechanisms

The formation of species is a continuous process, and as a result, two populations may only be partially reproductively isolated. For example, because of behavioral or ecological differences, individuals of two populations may be more likely to mate with members of their own population, and yet between-population matings may still occur. If mating occurs and fertilization produces a zygote, postzygotic barriers may also be incomplete: developmental problems may result in lower embryo survival or reduced fertility, but some individuals may survive and reproduce.

What happens when two populations come into contact thus depends on the extent to which isolating mechanisms have already evolved. If isolating mechanisms have not evolved at all,

Figure 22.6 Reinforcement in European flycatchers. The pied flycatcher *(Ficedula hypoleuca)* and the collared flycatcher *(F. albicollis)* appear very similar when they occur alone. However, in places where the two species occur sympatrically (indicated by the yellow color on the map), they have evolved differences in color and pattern, which allow individuals to choose mates from their own species and thus avoid hybridizing.

then the two populations will interbreed freely, and whatever other differences have evolved between them should disappear over the course of time, as genetic exchange homogenizes the populations. Conversely, if the populations are completely reproductively isolated, then no genetic exchange will occur, and the two populations will remain different species.

How reinforcement can complete the speciation process

The intermediate state, in which reproductive isolation has partially evolved but is not complete, is perhaps the most interesting situation. If the hybrids are partly sterile, or not as well adapted to the existing habitats as their parents, they will be at a disadvantage. Selection would favor any alleles in the parental populations that prevented hybridization, because individuals that did not engage in hybridization would produce more successful offspring.

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.

An example of reinforcement is provided by pied and collared flycatchers. Throughout much of eastern and central Europe, these two bird species are geographically separated **(allopatric)** and are very similar in color (figure 22.6). However, in the Czech Republic and Slovakia, the two species occur together and occasionally hybridize, producing offspring that usually have very low fertility. At those sites, the species have evolved to look very different from each other, and birds prefer to mate with individuals with their own species' coloration. In contrast, birds from the allopatric populations prefer the allopatric color pattern. As a consequence of the color differences where the species are sympatric the rate of hybridization is extremely low. These results indicate that when populations of the two species came into contact, natural selection led to the evolution of differences in color patterns, resulting in the evolution of behavioral, prezygotic isolation.

How gene flow may counter speciation

Reinforcement is not inevitable, however. When incompletely isolated populations come together, gene flow immediately begins to occur between them. Although hybrids may be inferior, they are not completely inviable or infertile—if they were, the species would already be completely reproductively isolated. When these surviving hybrids reproduce with members of either population, they will serve as a conduit of genetic exchange from one population to the other, and the two populations will tend to lose their genetic distinctiveness. Thus, a race ensues: Can complete reproductive isolation evolve before gene flow erases the differences between the populations? Experts disagree on the likely outcome, but many consider reinforcement to be the much less common outcome.

Learning Outcomes Review 22.2

Natural selection may favor the evolution of increased prezygotic reproductive isolation between sympatric populations. This phenomenon is termed reinforcement, and it may lead to populations becoming completely reproductively isolated. In contrast, however, genetic exchange between populations may decrease genetic differences among populations, thus preventing speciation from occurring.

- ***How might the initial degree of reproductive isolation affect the probability that reinforcement will occur when two populations come into sympatry?***

22.3 *The Role of Genetic Drift and Natural Selection in Speciation*

Learning Outcomes

1. ***Describe the effects of genetic drift on a population.***
2. ***Explain how genetic drift and natural selection can lead to speciation.***

What role does natural selection play in the speciation process? Certainly, the process of reinforcement is driven by natural selection, favoring the evolution of complete reproductive isolation. But reinforcement may not be common. In situations other than reinforcement, does natural selection play a role in the evolution of reproductive isolating mechanisms?

Random changes may cause reproductive isolation

As mentioned 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 involved a founder effect, in which one or a few flies—perhaps only a single pregnant female—was blown by strong winds to the new island. Changes in courtship behavior between ancestor and descendant populations may be the result of such founder events.

Given enough time, any two isolated populations will diverge because of genetic drift (remember that even large populations experience drift, but at a lower rate than in small populations). In some cases, this random divergence may affect traits responsible for reproductive isolation, and speciation may occur.

Adaptation can lead to speciation

Although random processes may sometimes be responsible, in many cases natural selection probably plays a role in the speciation process. As populations of a species adapt to different circumstances, they likely accumulate many differences that may lead to reproductive isolation. For example, if one population of flies adapts to wet conditions and another to dry ones, then natural selection will favor a variety of corresponding differences in physiological and sensory traits. These differences may promote ecological and behavioral isolation and may cause any hybrids the two populations 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*, located under their throats (figure 22.7). The ability of one lizard to see the dewlap of another lizard depends not only on the color of the dewlap, but on the environment in which the lizards occur. A light-colored dewlap, for example, 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 favors evolutionary change in dewlap color because males whose dewlaps cannot be seen will attract few mates. But the lizards also distinguish members of their own species from other species by the color of the dewlap. Adaptive change in mating signals in new environments could therefore have the incidental consequence of producing reproductive isolation from populations in the ancestral environment.

Laboratory scientists have conducted experiments on fruit flies and other fast-reproducing organisms in which they isolate populations 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). Although natural selection in the experiment does not directly favor traits because they lead to reproductive isolation, the incidental effect of adaptive divergence is that populations in different environments become reproductively isolated. 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—except reinforcement—is probably incorrect.

Learning Outcomes Review 22.3

Genetic drift refers to randomly generated changes in a population's genetic makeup. Isolated populations will eventually diverge because of genetic drift. Adaptation to different environments may also lead to populations becoming reproductively isolated from each other.

- ***How is the evolution of reproductive isolation in populations adapting to different environments different from the process of reinforcement?***

Figure 22.7 Dewlaps of 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. Darker-colored dewlaps, such as those of the two species on the left, are easier to see in open habitats, whereas lighter-colored dewlaps, like those of the two species on the right, are more visible in shaded environments.