16

How Populations Evolve

When your grandparents were young, infectious diseases, such as tuberculosis, pneumonia, and syphilis, killed thousands of people every year. Then in the 1940s, penicillin and other antibiotics were developed, and public health officials thought infectious diseases were a thing of the past. Today, however, many infections are back with a vengeance. Why? Because natural selection occurred. As with Staphylococcus aureus, *a few bacteria were resistant to penicillin. Therefore, they were selected over and over again to reproduce, until the entire population of bacteria became resistant to penicillin. A new antibiotic called methicillin became available in 1959 to treat penicillin-resistant bacterial strains, but by 1997, 40% of hospital staph infections were caused by* methicillin-resistant Staphylococcus aureus, *or MRSA. Now, community-acquired MRSA (CA-MRSA) can spread freely through the general populace, particularly when people are in close contact.*

This chapter gives the principles of evolution a genetic basis and shows how it is possible to genetically recognize when a population has undergone evolutionary changes. Evolutionary changes observed at the population level are termed microevolution.

MRSA can spread between members of a human social group.

concepts

16.1 POPULATION GENETICS

- Genetic diversity is a necessity for microevolution to occur, and today investigators are interested in DNA sequence differences between individuals. It might be possible to associate particular variations with illnesses. 284
- The Hardy-Weinberg principle provides a way to know if a population has evolved. Allele frequency changes in the next generation signify that microevolution has occurred. 285–86
- Microevolution will occur unless five conditions are met: no mutations, no gene flow, mating is random, no genetic drift, and no selection of a particular trait. 286–88

16.2 NATURAL SELECTION

- A change in phenotype frequencies occurs if a population has undergone stabilizing selection, directional selection, or disruptive selection. 289–90
- Sexual selection fostered by male competition and female choice is also a type of natural selection because it influences reproductive success. 291–92

16.3 MAINTENANCE OF DIVERSITY

- Genetic diversity is maintained within a population; for example, by the diploid genotype and also when the heterozygote is the most adaptive genotype. 294–95

16.1 Population Genetics

Darwin stressed that diversity exists among the members of a population. A **population** is all the members of a single species occupying a particular area at the same time. **Population genetics,** as its name implies, studies this diversity in terms of allele differences. Since Darwin was unaware of Mendel's work, he never had the opportunity to study the genetics of a population, as we will do in this chapter.

Genetic Diversity

When we consider that a population can have many subpopulations, such as those illustrated for a human population in Figure 16.1, we begin to realize that a population can have many phenotypic, and therefore genotypic, differences. Many traits in a population are controlled by polygenes, and if these multiple gene loci were to have multiple alleles, genetic diversity becomes plentiful, indeed.

Studies have been done to determine enzyme variations among members of a population. Extracted enzymes are subjected to electrophoresis, a process that separates proteins according to size and shape. The result in *Drosophila* suggests that a fly population has multiple alleles at no less than 30% of its gene loci. Similar results are the rule in all populations.

Increasingly today, instead of studying proteins, investigators go right to sequencing DNA to discover the amount of genetic diversity in a population. This has allowed them to discover various loci that exhibit **single nucleotide polymorphisms,** or **SNPs** (pronounced snips). These are DNA sequences in an organism's genome that differ by a single nucleotide. To take an example of an SNP, compare ACGTACGTA to ACGTACCTA and notice that there is only a single base difference between the two sequences. Investigators would say that the SNP has two alleles, in this case, G and C. SNPs generally have two alleles.

SNPs that occur within a protein-coding DNA sequence can result in a change sequence of amino acids, but not necessarily, due to redundancy of the genetic code (see page 221). SNPs that do not result in a changed amino acid sequence may still cause regulatory differences. Therefore, SNPs are now thought to be an important source of genetic diversity in the populations of all organisms, including humans (Fig. 16.1).

Another interesting finding is that humans inherit patterns of base-pair differences now called haplotypes (from the terms haploid and genotype). To take an example, if a chromosome has a G rather than a C at a particular location, this change is most likely accompanied by other particular base differences near the G. Researchers are in the process of discovering the most common haplotypes among African, Asian, and European populations. They want to link haplotypes to the risk of specific illnesses, in the hope it will lead to new methods of preventing, diagnosing, and treating disease. Also, certain haplotypes may respond better than others to particular medicines, vaccines, and other treatment strategies.

FIGURE 16.1 The HapMap project.

The HapMap project compares DNA base-pair sequences among African, Asian, and European populations to discover unique base pair differences.

Microevolution

It wasn't until the 1930s that population geneticists worked out a way to describe the diversity in a population in terms of alleles, and to, thereby, develop a way to recognize when evolution had occurred. **Microevolution** pertains to evolutionary changes within a population.

In population genetics, the various alleles at all the gene loci in all individuals make up the **gene pool** of the population. It is customary to describe the gene pool of a population in terms of genotype and allele frequencies. Let's take an example based on the peppered moths we discussed in Chapter 15 (page 275). Suppose you research the literature and find that the color of peppered moths is controlled by a single set of alleles, and you decide to use the following key:

D = dark color

d = light color

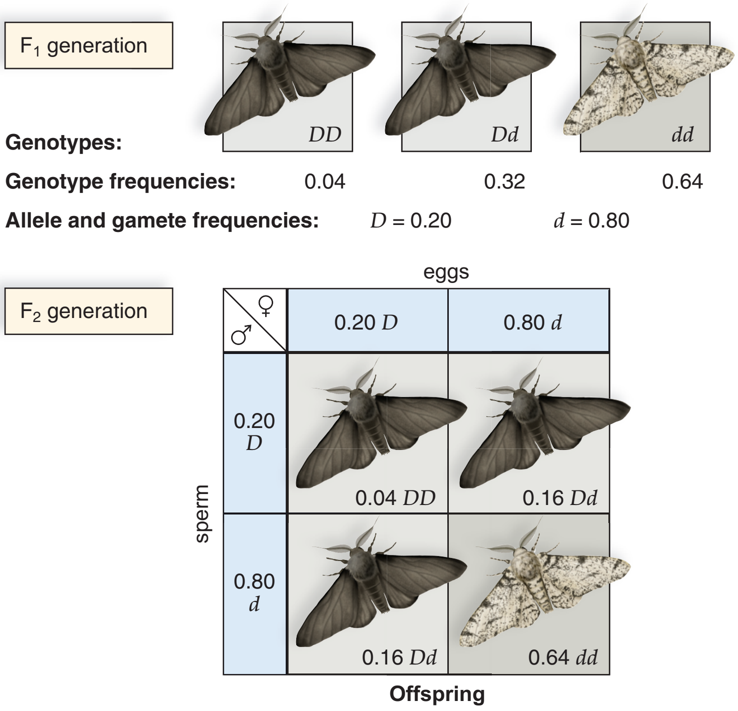
Further, in one Great Britain population before pollution fully darkened the trees, only 4% (0.04) of moths were homozygous dominant; 32% (0.32) were heterozygous, and 64% (0.64) were homozygous recessive. From these genotype frequencies, you can calculate the allele and gamete frequencies in the populations:

genotypes	*DD*	*Dd*	*dd*
frequency of genotypes in the population	0.04	0.32	0.64

frequency of alleles and gametes in the population: $\underbrace{0.04 + 0.16}_{0.20\ D}$ $\underbrace{0.16 + 0.64}_{0.80\ d}$

The frequency of the gametes (sperm and egg) produced by this population will necessarily be the same as the allele frequencies. Assuming random mating (all possible gametes have an equal chance to combine with any other), we can use these gamete frequencies to calculate the ratio of genotypes in the next generation by using a Punnett square (Fig. 16.2).

There is an important difference between a Punnett square used for a cross between individuals, as we have done previously, and the one shown in Figure 16.2. In Figure 16.2, we are using the gamete frequencies in the population to determine the genotype frequencies in the next generation. As you can see, the genotype frequencies (and therefore the allele frequencies) in the next generation are the same as they were in the previous generation. In other words, we will find that the homozygous dominant moths are still 0.04; the heterozygous moths are still 0.32; and the homozygous recessive moths are still 0.64. This is an amazing finding, and it tells us that: *Sexual reproduction alone cannot bring about a change in genotype and allele frequencies of a population.* By the way, what percentage of moths are dark-colored, and what percentage of moths are light-colored? Adding the homozygous dominant and the heterozygous moths = 36% are dark-colored, and 64% are light-colored.



Genotype frequencies: 0.04 *DD* + 0.32 *Dd* + 0.64 *dd* = 1

$p^2 + 2pq + q^2 = 1$

p^2 = frequency of *DD* genotype (dark-colored) = $(0.20)^2$ = 0.04

$2pq$ = frequency of *Dd* genotype (dark-colored) = 2(0.20)(0.80) = 0.32

q^2 = frequency of *dd* genotype (light-colored) = $(0.80)^2$ = $\underline{0.64}$

1.00

FIGURE 16.2 Hardy-Weinberg equilibrium.

Using the gamete frequencies in a population, it is possible to use a Punnett square to calculate the genotype frequencies of the next generation. When this is done, it can be shown that sexual reproduction alone does not alter the Hardy-Weinberg equilibrium: the genotype, and therefore allele frequencies, remain the same. Notice the binomial expression is used to calculate the genotype frequencies of a population.

Also, the dominant allele need not increase from one generation to the next. Dominance does not cause an allele to become a common allele. The potential constancy, or equilibrium state, of gene pool frequencies was independently recognized in 1908 by G. H. Hardy, an English mathematician, and W. Weinberg, a German physician. They used the binomial expression to calculate the genotype and allele frequencies of a population, as illustrated beneath the Punnett square in Figure 16.2.

In the Hardy-Weinberg equation: $(p^2 + 2pq + q^2)$
p^2 = frequency of the homozygous dominant
p = frequency of the dominant allele
$2pq$ = frequency of the heterozygous
q^2 = frequency of the homozygous recessive
q = frequency of the recessive allele

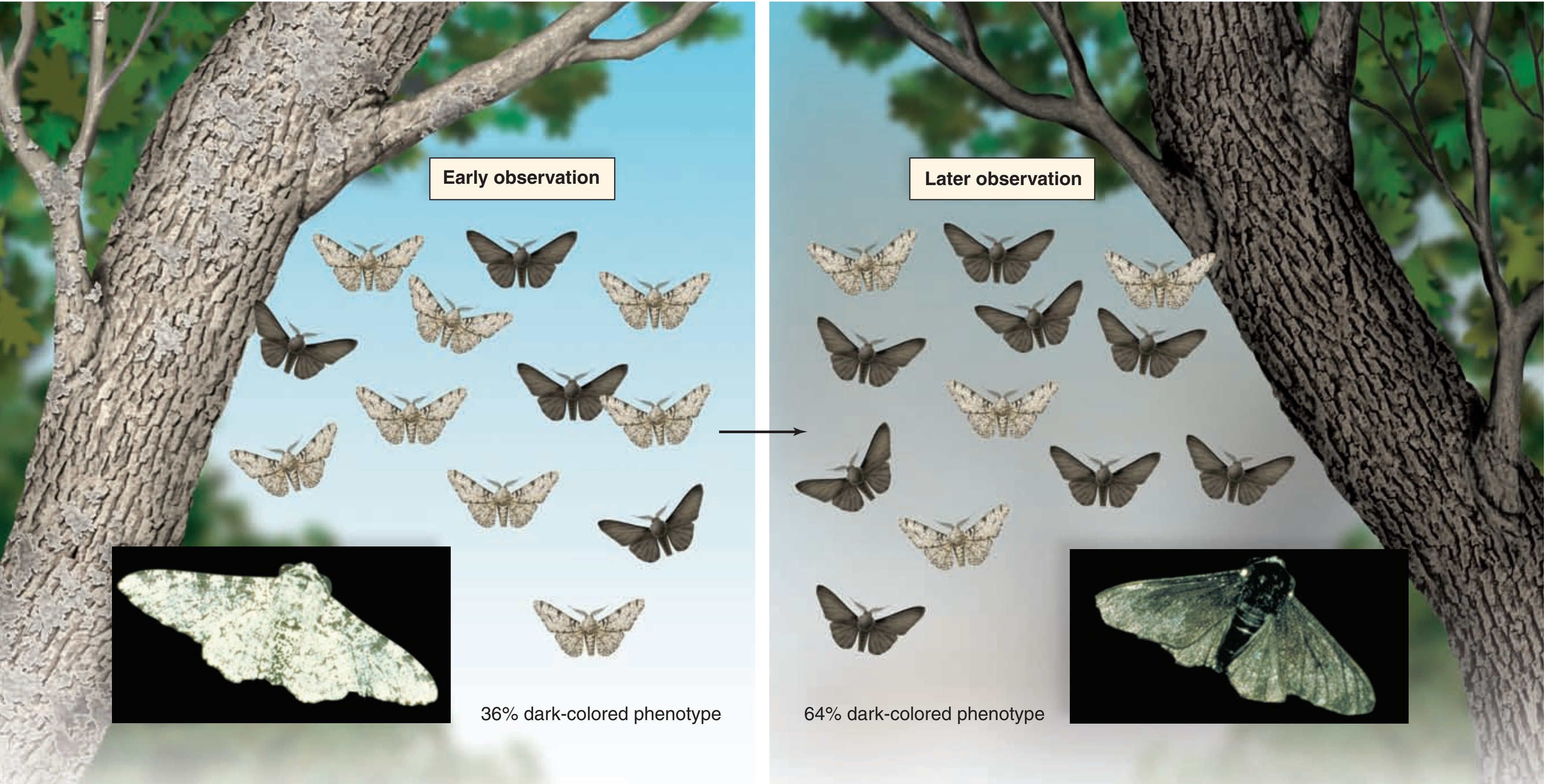


FIGURE 16.3 **Microevolution.**

Microevolution has occurred when there is a change in gene pool frequencies—in this case, due to natural selection. On the left, birds cannot see light-colored peppered moths, *Biston betularia*, against light-colored vegetation—and, therefore, light-colored moths are more frequent in the population. On the right, after vegetation has been darkened due to pollution, birds are less likely to see dark-colored moths against dark vegetation, and dark moths are more frequent in the population.

The **Hardy-Weinberg principle** states that an equilibrium of gene pool frequencies, calculated by using the binomial expression, will remain in effect in each succeeding generation of a sexually reproducing population, as long as five conditions are met:

1. No mutations: Allele changes do not occur, or changes in one direction are balanced by changes in the opposite direction.
2. No gene flow: Migration of alleles into or out of the population does not occur.
3. Random mating: Individuals pair by chance, not according to their genotypes or phenotypes.
4. No genetic drift: The population is very large, and changes in allele frequencies due to chance alone are insignificant.
5. No selection: Selective forces do not favor one genotype over another.

In real life, these conditions are rarely, if ever, met, and allele frequencies in the gene pool of a population do change from one generation to the next. Therefore, evolution has occurred. The significance of the Hardy-Weinberg principle is that it tells us what factors cause evolution—those that violate the conditions listed. Microevolution can be detected by noting any deviation from a Hardy-Weinberg equilibrium of allele frequencies in the gene pool of a population.

A change in allele frequencies may result in a change in phenotype frequencies. Our calculation of gene pool frequencies in Figure 16.3 assumes that industrial melanism may have started but was not fully in force yet. **Industrial melanism** refers to a darkening of moths once industrialization has begun in a country. Prior to the Industrial Revolution in Great Britain, light-colored peppered moths living on the light-colored, unpolluted vegetation, were more common than dark-colored peppered moths. When dark-colored moths landed on light vegetation, they were seen and eaten by predators. In Figure 16.3, *left*, we suppose that only 36% of the population were dark-colored, while 64% were light-colored. With the advent of industry and an increase in pollution, the vegetation was stained darker. Now, light-colored moths were easy prey for predators. Figure 16.3, *right*, assumes that the gene pool frequencies switched, and now the dark-colored moths are 64% of the population. Can you calculate the change in gene pool frequencies using Figure 16.2 as a guide?

Just before the Clean Air legislation in the mid-1950s, the numbers of dark-colored moths exceeded a frequency of 80% in some populations. After the legislation, a dramatic reversal in the ratio of light-colored moths to dark-colored moths occurred once again as light-colored moths became more and more frequent. Aside from showing that natural selection can occur within a short period of time, our example shows that a change in gene pool frequencies does occur as microevolution occurs. Recall that microevolution occurs below the species level.

Causes of Microevolution

The list of conditions for a Hardy-Weinberg equilibrium implies that the opposite conditions can cause evolutionary change. The conditions are mutation, nonrandom mating, gene flow, genetic drift, and natural selection. Only natural selection results in adaptation to the environment.

Mutations

The Hardy-Weinberg principle recognizes new mutations as a force that can cause the allele frequencies to change in a gene pool and cause microevolution to occur. **Mutations,** which are permanent genetic changes, are the raw material for evolutionary change because without mutations, there could be no inheritable phenotypic diversity among members of a population. The rate of mutations is generally very low—on the order of one per 100,000 cell divisions. Also, it is important to realize that evolution is not directed, meaning that no mutation arises because the organism "needs" one. For example, the mutation that causes bacteria to be resistant was already present before antibiotics appeared in the environment.

Mutations are the primary source of genetic differences among prokaryotes that reproduce asexually. Generation time is so short that many mutations can occur quickly, even though the rate is low, and since these organisms are haploid, any mutation that results in a phenotypic change is immediately tested by the environment. In diploid organisms, a recessive mutation can remain hidden and become significant only when a homozygous recessive genotype arises. The importance of recessive alleles increases if the environment is changing; it's possible that the homozygous recessive genotype could be helpful in a new environment, if not the present one. It's even possible that natural selection will maintain a recessive allele if the heterozygote has advantages. As noted on page 284, investigators now know that even SNPs can be a significant source of diversity in a population.

In sexually reproducing organisms, sexual recombination is just as important as mutation in generating phenotypic differences, because sexual recombination can bring together a new and different combination of alleles. This new combination might produce a more successful phenotype. Success, of course, is judged by the environment and counted by the relative number of healthy offspring an organism produces.

Nonrandom Mating and Gene Flow

Random mating occurs when individuals pair by chance. You make sure random mating occurs when you do a genetic cross on paper or in the lab, and cross all possible types of sperm with all possible types of eggs. **Nonrandom mating** occurs when certain genotypes or phenotypes mate with one another. **Assortative mating** is a type of nonrandom mating that occurs when individuals tend to mate with those having the *same* phenotype with respect to a certain characteristic. For example, flowers such as the garden pea usually self-pollinate—therefore, the same phenotype has mated with the same phenotype (Fig. 16.4). Assortative mating can also be observed in human society. Men and women tend to marry individuals with characteristics such as intelligence and height that are similar to their own. Assortative mating causes homozygotes for certain gene loci to increase in frequency and heterozygotes for these loci to decrease in frequency.

Gene flow, also called gene migration, is the movement of alleles between populations. When animals move between populations, or when pollen is distributed between species (Fig. 16.5), gene flow has occurred. When gene flow brings a new or rare allele into the population, the allele frequency in the next generation changes. When gene flow between adjacent populations is constant, allele frequencies continue to change until an equilibrium is reached. Therefore, continued gene flow tends to make the gene pools similar and reduce the possibility of allele frequency differences between populations.

Genetic Drift

Genetic drift refers to changes in the allele frequencies of a gene pool due to chance rather than selection by the environment. Therefore, genetic drift does not necessarily result in

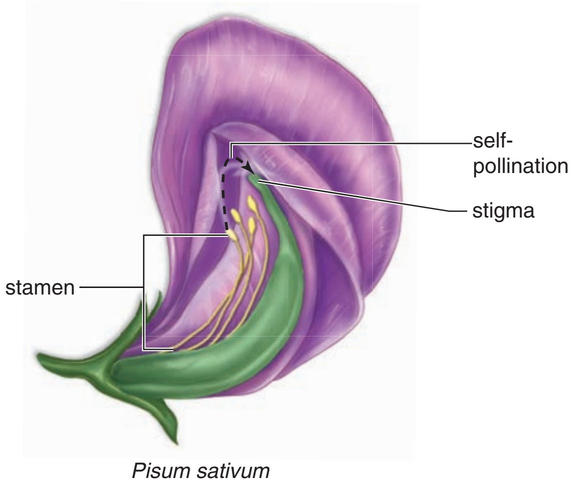


FIGURE 16.4 **Anatomy of the garden pea.**

The anatomy of the garden pea, *Pisum sativum,* ensures self-pollination, an example of nonrandom mating.

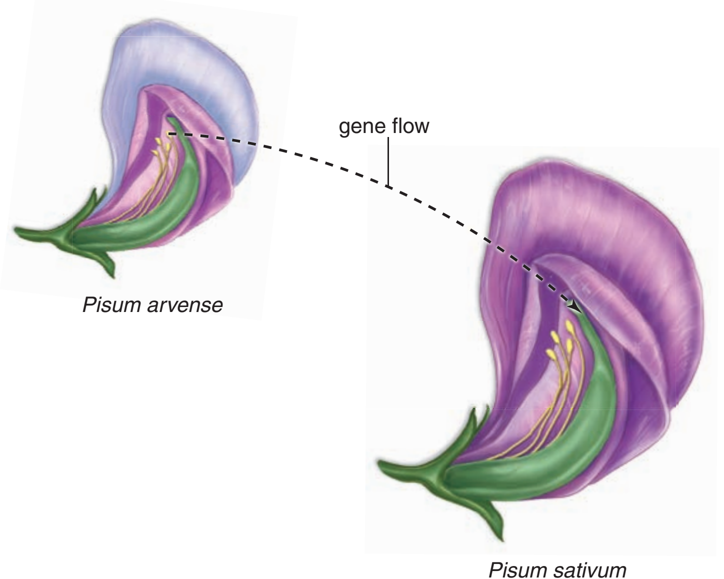


FIGURE 16.5 **Gene flow.**

Occasional cross-pollination between a population of *Pisum sativum* and a population of *Pisum arvense* is an example of gene flow.

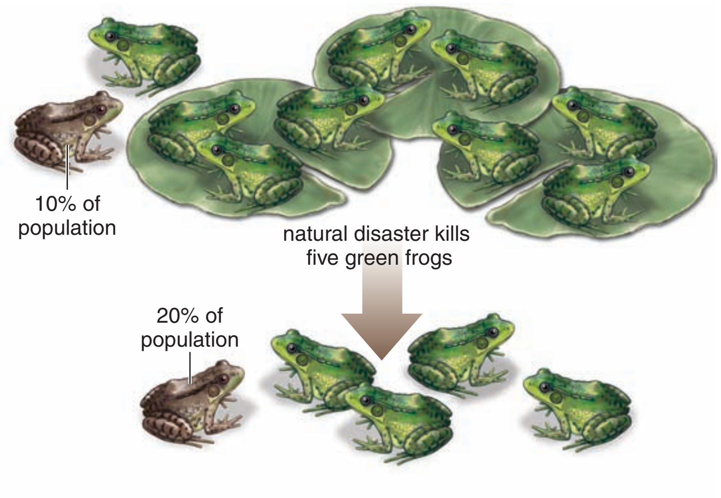


FIGURE 16.6 **Genetic drift.**

Genetic drift occurs when, by chance, only certain members of a population (in this case, green frogs) reproduce and pass on their alleles to the next generation. A natural disaster can cause the allele frequencies of the next generation's gene pool to be markedly different from those of the previous generation.

adaptation to the environment, as does natural selection. For example, in California, there are a number of cypress groves, each a separate population. The phenotypes within each grove are more similar to one another than they are to the phenotypes in the other groves. Some groves have conical-shaped trees, and others have pyramidally-shaped trees. The bark is rough in some colonies and smooth in others. The leaves are gray to bright green or bluish, and the cones are small or large. The environmental conditions are similar for all the groves, and no correlation has been found between phenotype and the environment across groves. Therefore, scientists hypothesize that diversity among the groves are due to genetic drift.

Although genetic drift occurs in populations of all sizes, a smaller population is more likely to show the effects of drift. Suppose the allele *B* (for brown) occurs in 10% of the members in a population of frogs. In a population of 50,000 frogs, 5,000 will have the allele *B*. If a hurricane kills off half the frogs, the frequency of allele *B* may very well remain the same among the survivors. On the other hand, 10% of a population with ten frogs means that only one frog has the allele *B*. Under these circumstances, a natural disaster could very well do away with that one frog, should half the population perish. Or, let's suppose that only five green frogs out of a ten-member population die. Now, the frequency of allele *B* will increase from 10% to 20% (Fig. 16.6).

Bottleneck and Founder Effects. When a species is subjected to near extinction because of a natural disaster (e.g., hurricane, earthquake, or fire) or because of overhunting, overharvesting, and habitat loss, it is as if most of the population has stayed behind and only a few survivors have passed through the neck of a bottle. This so-called **bottleneck effect** prevents the majority of genotypes from participating in the production of the next generation. The extreme genetic similarity found in cheetahs is believed to be due to a bottleneck effect. In a study of 47 different enzymes, each of which can come in several different forms, the sequence of amino acids in the enzymes was exactly the same in all the cheetahs. What caused the cheetah bottleneck is not known, but today they suffer from relative infertility because of the intense inbreeding that occurred after the bottleneck. Even if humans were to intervene and the population were to increase in size, without genetic variation, the cheetah could still become extinct. Other organisms pushed to the brink of extinction suffer a similar plight as the cheetah.

The **founder effect** is an example of genetic drift in which rare alleles, or combinations of alleles, occur at a higher frequency in a population isolated from the general population. Founding individuals could contain only a fraction of the total genetic diversity of the original gene pool. Which alleles the founders carry is dictated by chance alone. The Amish of Lancaster County, Pennsylvania, are an isolated group that was begun by German founders. Today, as many as 1 in 14 individuals carries a recessive allele that causes an unusual form of dwarfism (affecting only the lower arms and legs) and polydactylism (extra fingers) (Fig. 16.7). In the general population, only 1 in 1,000 individuals has this allele.

Check Your Progress 16.1

1. If two genetically different subpopulations of the same species come into contact and gene flow begins, in general, how will the genetic makeup of the merged populations change?
2. Many zoological parks send the offspring of a single breeding pair of animals to zoos around the country. How is this an example of the founder effect?

FIGURE 16.7 **Founder effect.**

A member of the founding population of Amish in Pennsylvania had a recessive allele for a rare kind of dwarfism linked with polydactylism. The percentage of the Amish population with this phenotype is much higher compared to that of the general population.

16.2 Natural Selection

In this chapter, we wish to consider natural selection in a genetic context. Many traits are polygenic (controlled by many genes), and the continuous variation in phenotypes results in a bell-shaped curve. When a range of phenotypes is exposed to the environment, natural selection favors the one that is most adaptive under the present environmental circumstances. Natural selection acts much the same way as a governing board that decides which applying students will be admitted to a college. Some students will be favored and allowed to enter, while others will be rejected and not allowed to enter. Of course, in the case of natural selection, the chance to reproduce is the prize awarded. In this context, natural selection can be stabilizing, directional, or disruptive (Fig. 16.8).

Stabilizing selection occurs when an intermediate phenotype can improve the adaptation of the population to those aspects of the environment that remain constant. With stabilizing selection, extreme phenotypes are selected against, and the intermediate phenotype is favored. As an example, consider that when Swiss starlings lay four to five eggs, more young survive than when the female lays more or less than this number. Genes determining physiological characteristics, such as the production of yolk, and behavioral characteristics, such as how long the female will mate, are involved in determining clutch size.

Human birth weight is another example of stabilizing selection. Through the years, hospital data have shown that human infants born with an intermediate birth weight (3–4 kg) have a better chance of survival than those at either extreme (either much less or much greater than usual). When a baby is small, its systems may not be fully functional, and when a baby is large, it may have experienced a difficult delivery. Stabilizing selection reduces the variability in birth weight in human populations (Fig. 16.9).

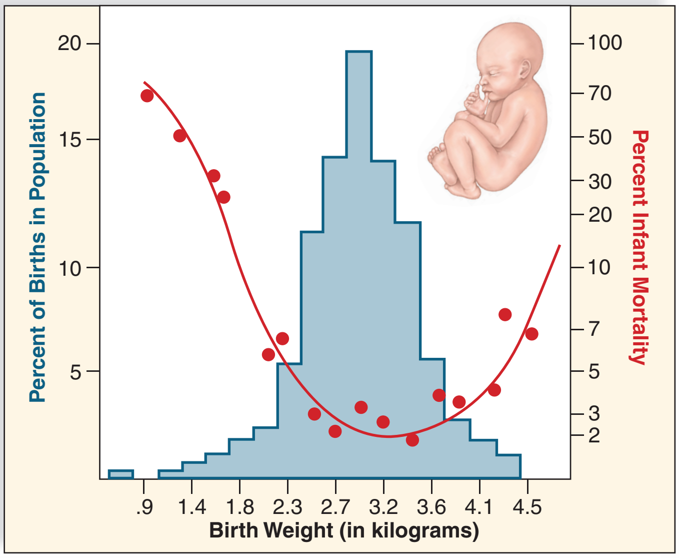


FIGURE 16.9 **Human birth weight.**

Due to stabilizing selection, the average human birth weight stays steady.

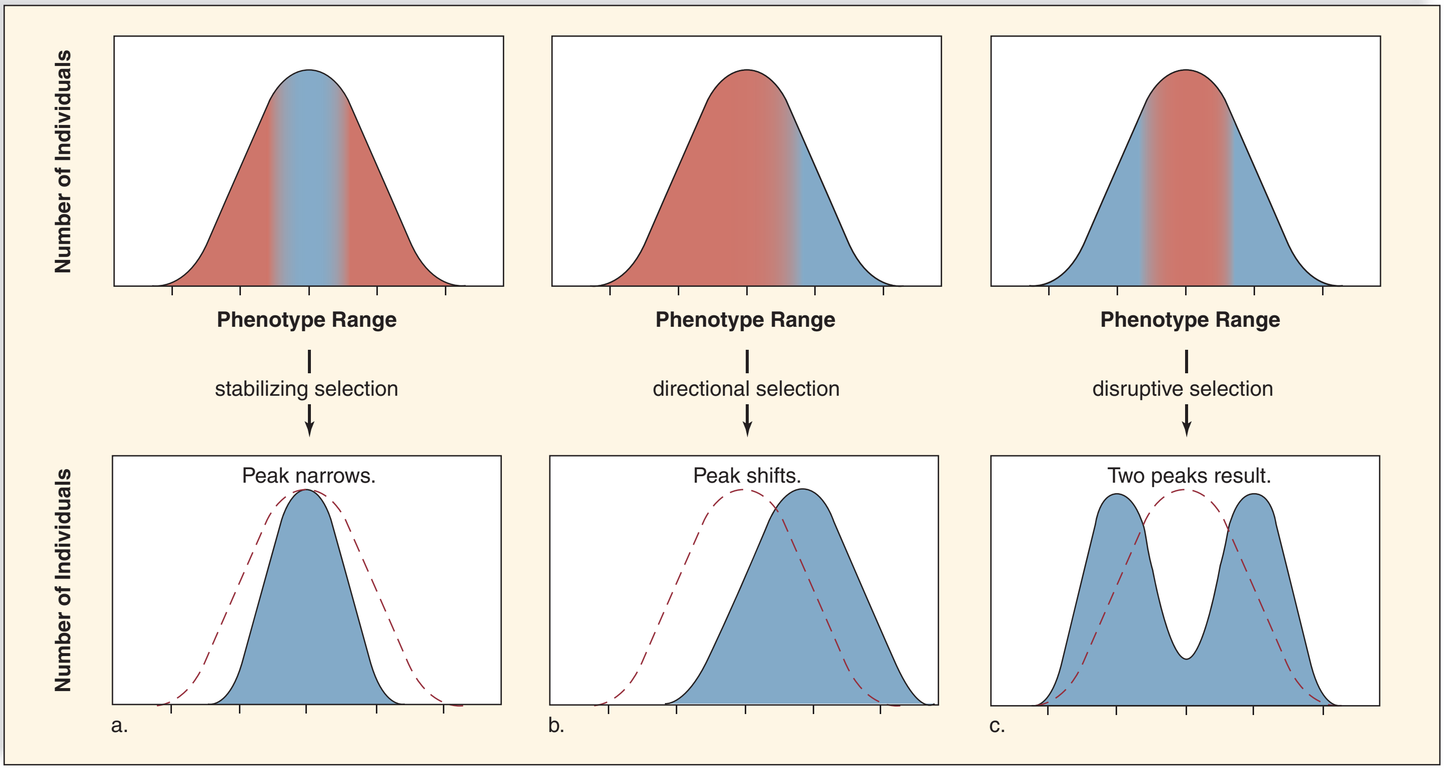
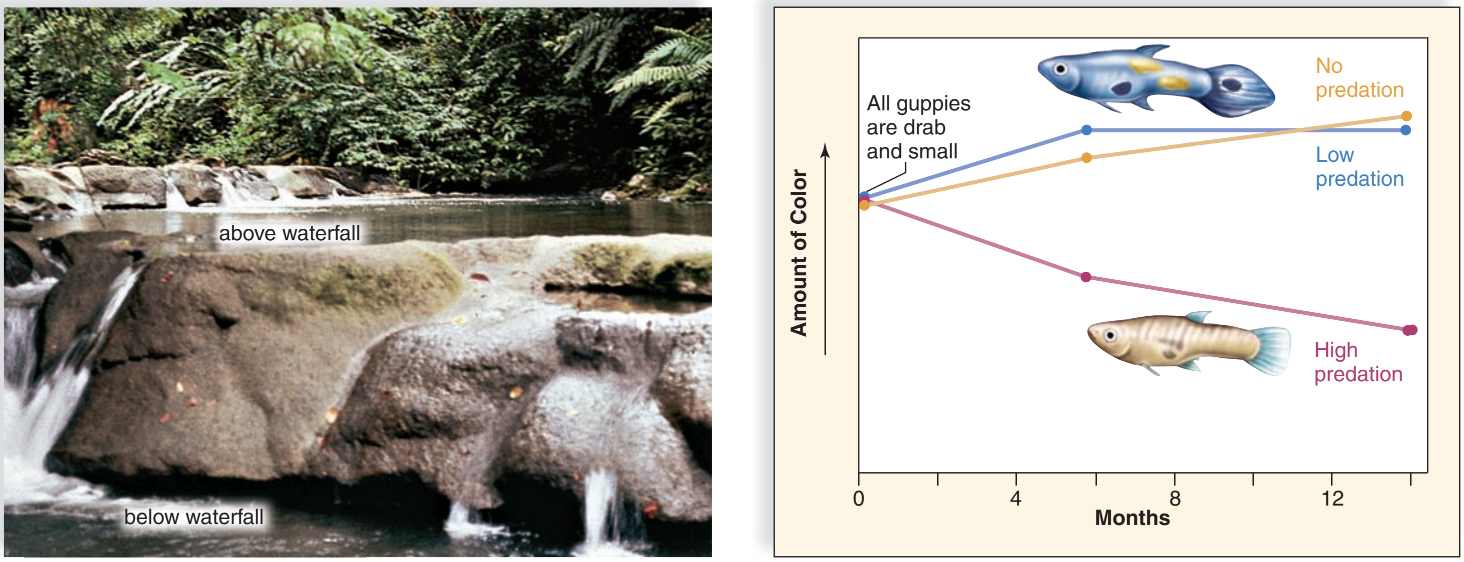


FIGURE 16.8 **Three types of natural selection.**

a. During stabilizing selection, the intermediate phenotype is favored; **(b)** during directional selection, an extreme phenotype is favored; and **(c)** during disruptive selection, two extreme phenotypes are favored.



Experimental site

Result

FIGURE 16.10 **Directional selection.**

Guppies, *Poecilia reticulata*, become more colorful in the absence of predation and less colorful when in the face of predation.

Directional selection occurs when an extreme phenotype is favored, and the distribution curve shifts in that direction. Such a shift can occur when a population is adapting to a changing environment.

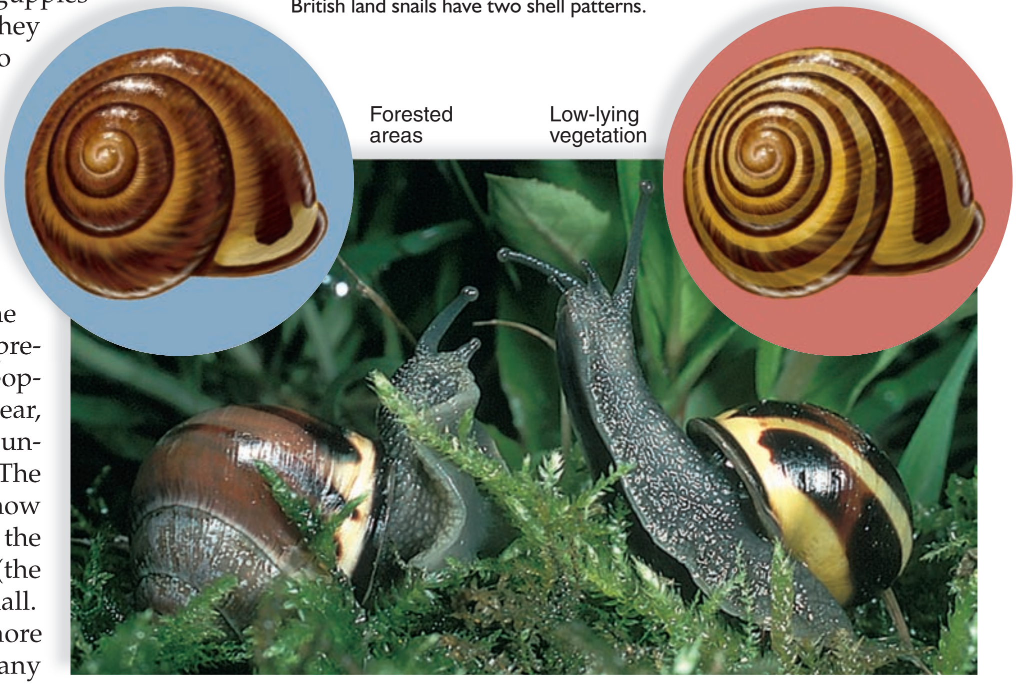
Two investigators, John Endler and David Reznick, both at the University of California, conducted a study of guppies, which are known for their bright colors and reproductive potential. These investigators noted that on the island of Trinidad, when male guppies are subjected to high predation by other fish, they tend to be drab in color and to mature early and at a smaller size. The drab color and small size are most likely protective against being found and eaten. On the other hand, when male guppies are exposed to minimal or no predation, they tend to be colorful, to mature later, and to attain a larger size.

Endler and Reznick performed many experiments, and one set is of particular interest. They took a supply of guppies from a high-predation area (below a waterfall) and placed them in a low-predation area (above a waterfall) (Fig. 16.10). The waterfall prevented the predator fish (pike) from entering the low-predation area. They monitored the guppy population for 12 months, and during that year, the guppy population above the waterfall underwent directional selection (Fig. 16.10). The male members of the population were now colorful and large in size. The members of the guppy population below the waterfall (the control population) were still drab and small.

In **disruptive selection,** two or more extreme phenotypes are favored over any intermediate phenotype. For example, British land snails have a wide habitat range that includes low-vegetation areas (grass fields and hedgerows) and forests. In forested areas, thrushes feed mainly on light-banded snails, and the snails with dark shells become more prevalent. In low-vegetation areas, thrushes feed mainly on snails with dark shells, and light-banded snails become more prevalent. Therefore, these two distinctly different phenotypes are found in the population (Fig. 16.11).

FIGURE 16.11 **Disruptive selection.**

Due to exposure to two different environments, British land snails have two shell patterns.



Sexual Selection

Sexual selection refers to adaptive changes in males and females that lead to an increased ability to secure a mate. Sexual selection in males may result in an increased ability to compete with other males for a mate, while females may select a male with the best **fitness** (ability to produce surviving offspring). In that way, the female increases her own fitness. Many consider sexual selection a form of natural selection because it affects fitness.

Female Choice

Females produce few eggs, so the choice of a mate becomes a serious consideration. In a study of satin bowerbirds, two opposing hypotheses regarding female choice were tested:

1. *Good genes hypothesis:* Females choose mates on the basis of traits that improve the chance of survival.
2. *Runaway hypothesis:* Females choose mates on the basis of traits that improve male appearance. The term *runaway* pertains to the possibility that the trait will be exaggerated in the male until its mating benefit is checked by the trait's unfavorable survival cost.

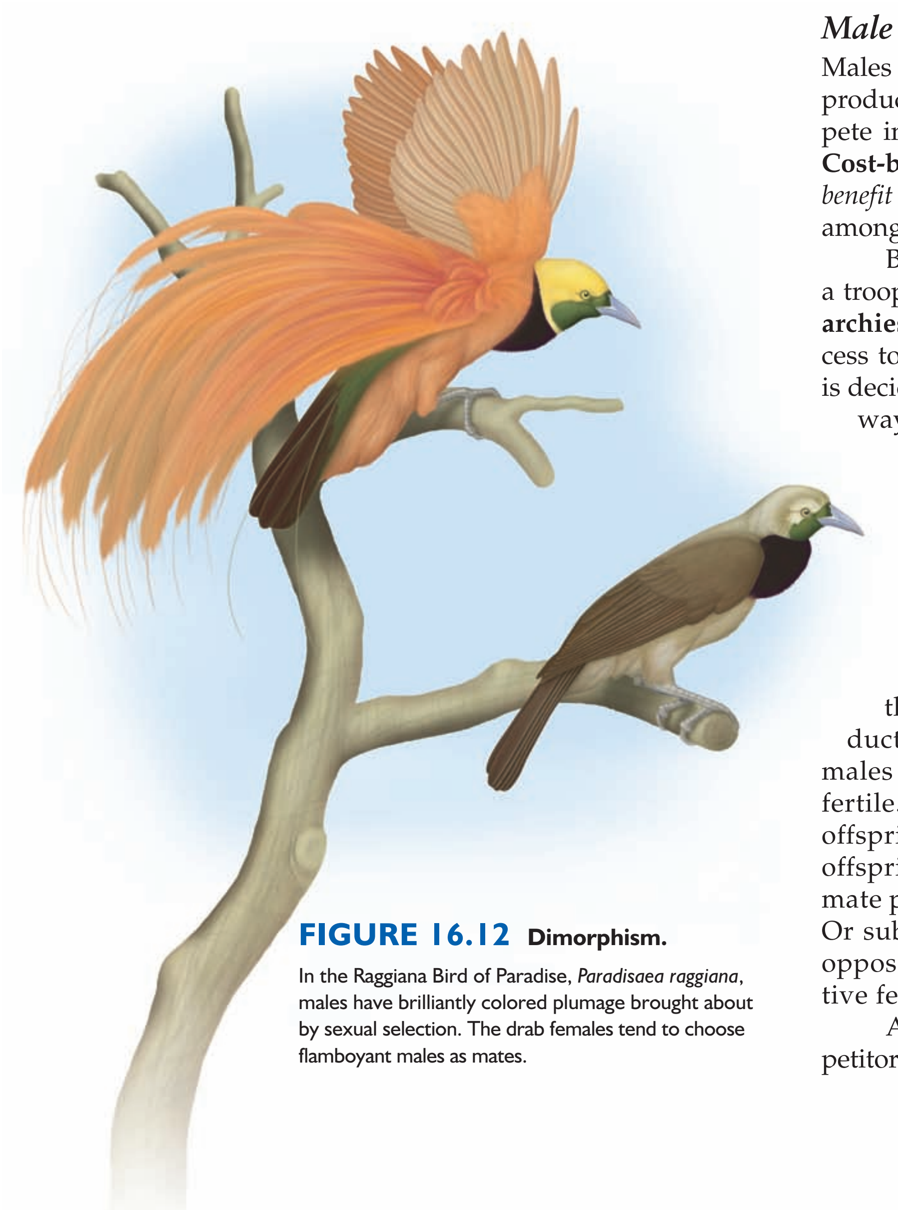


FIGURE 16.12 Dimorphism.

In the Raggiana Bird of Paradise, *Paradisaea raggiana*, males have brilliantly colored plumage brought about by sexual selection. The drab females tend to choose flamboyant males as mates.

As investigators observed the behavior of satin bowerbirds, they discovered that aggressive males were usually chosen as mates by females. It could be that inherited aggressiveness does improve the chance of survival, or it could be aggressive males are good at stealing blue feathers from other males. Females prefer blue feathers as bower decorations. Therefore, the data did not clearly support either hypothesis.

The Raggiana Bird of Paradise is remarkably *dimorphic*, meaning that males and females differ in size and other traits. The males are larger than the females and have beautiful orange flank plumes. In contrast, the females are drab (Fig. 16.12). Female choice can explain why male birds are more ornate than females. Consistent with the two hypotheses, it is possible that the remarkable plumes of the male signify health and vigor to the female. Or, it's possible that females choose the flamboyant males on the basis that their sons will have an increased chance of being selected by females. Some investigators have hypothesized that extravagant male features could indicate that they are relatively parasite-free. In barn swallows, females also choose those with the longest tails, and investigators have shown that males that are relatively free of parasites have longer tails than otherwise.

Male Competition

Males can father many offspring because they continuously produce sperm in great quantity. We expect males to compete in order to inseminate as many females as possible. **Cost-benefit analyses** have been done to determine if the *benefit* of access to mating is worth the *cost* of competition among males.

Baboons, a type of Old World monkey, live together in a troop. Males and females have separate **dominance hierarchies** in which a higher-ranking animal has greater access to resources than a lower-ranking animal. Dominance is decided by confrontations, resulting in one animal giving way to the other.

Baboons are dimorphic; the males are larger than the females, and they can threaten other members of the troop with their long, sharp canines (Fig. 16.13). One or more males become dominant by frightening the other males. However, the male baboon pays a cost for his dominant position. Being larger means that he needs more food, and being willing and able to fight predators means that he may get hurt, and so forth. Is there a reproductive benefit to his behavior? Yes, in that dominant males do indeed monopolize females when they are most fertile. Nevertheless, there may be other ways to father offspring. A male may act as a helper to a female and her offspring; then, the next time she is in estrus, she may mate preferentially with him instead of a dominant male. Or subordinate males may form a friendship group that opposes a dominant male, making him give up a receptive female.

A **territory** is an area that is defended against competitors. Scientists are able to track an animal in the wild in

FIGURE 16.13 **A male olive baboon displaying full threat.**

In olive baboons, *Papio anubis*, males are larger than females and have enlarged canines. Competition between males establishes a dominance hierarchy for the distribution of resources.

order to determine its home range or territory. **Territoriality** includes the type of defensive behavior needed to defend a territory. Baboons travel within a home range, foraging for food each day and sleeping in trees at night. Dominant males decide where and when the troop will move. If the troop is threatened, dominant males protect the troop as it retreats and attack intruders when necessary. Vocalization and displays, rather than outright fighting, may be sufficient to defend a territory. In songbirds, for example, males use singing to announce their willingness to defend a territory. Other males of the species become reluctant to make use of the same area.

Red deer stags (males) on the Scottish island of Rhum compete to be the harem master of a group of hinds (females) that mate only with them. The reproductive group occupies a territory that the harem master defends against other stags. Harem masters first attempt to repel challengers by roaring. If the challenger remains, the two lock antlers and push against one another (Fig. 16.14). If the challenger then withdraws, the master pursues him for a short distance, roaring the whole time. If the challenger wins, he becomes the harem master.

A harem master can father two dozen offspring at most, because he is at the peak of his fighting ability for only a short time. And there is a cost to being a harem master. Stags must be large and powerful in order to fight; therefore, they grow faster and have less body fat. During bad times, they are more likely to die of starvation, and in general, they have shorter lives. Harem master behavior will persist in the population only if its cost (reduction in the potential number of offspring because of a shorter life) is less than its benefit (increased number of offspring due to harem access).

Check Your Progress 16.2

1. The evolution of the horse from an animal adapted to living in a forest to one adapted to living on a plain is an example of what types of selection? Explain.
2. Why is sexual selection a form of natural selection?

FIGURE 16.14 **Competition between male red deer.**

Male red deer, *Cervus elaphus*, compete for a harem within a particular territory. **a.** Roaring alone may frighten off a challenger, but **(b)** outright fighting may be necessary, and the victor is most likely the stronger of the two animals.

science focus

Sexual Selection in Humans

A study of sexual selection among humans shows that the concepts of female choice and male competition apply to humans as well as to the animals we have been discussing. Increased fitness (ability to produce surviving offspring) again seems to be the result of sexual selection.

Human Males Compete

Consider that women, by nature, must invest more in having a child than men. After all, it takes nine months to have a child, and pregnancy is followed by lactation, when a woman may nurse her infant. Men, on the other hand, need only contribute sperm during a sex act that may require only a few minutes. The result is that men are generally more available for mating than are women. Because more men are available, they necessarily have to compete with others for the privilege of mating.

Like many other animals, humans are dimorphic. Males tend to be larger and more aggressive than females, perhaps as a result of past sexual selection by females. As in other animals, males pay a price for their physical attractiveness to females. Male humans live on the average seven years less than females do.

Females Choose

A study in modern Quebec sampled a large number of respondents on how often they had copulated with different sexual partners in the preceding year. Male mating success correlated best with income—those males who had both wealth and status were much more successful in acquiring mates than those who lacked these attributes. In this study, it would appear that females prefer to mate with a male who is wealthy and has a successful career because these men are more likely to be able to provide them with the resources they need to raise their children (Fig. 16A).

The desire of women for just certain types of men has led to the practice of polygamy in many primitive human societies and even in some modern societies. Women would rather share a husband who can provide resources than to have a one-on-one relationship with a poor man, because the resources provided by the wealthy man make it all the more certain that her children will live to reproduce. On the other hand, polygamy works for wealthy men because having more than one wife will undoubtedly increase their fitness as well. As an alternative to polygamy, modern societies stress monogamy in which the male plays a prominent role in helping to raise the children. This is another way males can raise their fitness.

Men Also Have a Choice

Just as women choose men who can provide resources, men prefer women who are most likely to present them with children. It has been shown that the "hourglass figure" so touted by men actually correlates with the best distribution of body fat for reproductive purposes! Men responding to questionnaires about their preferences in women list attributes that biologists associate with a strong immune system, good health, high estrogen levels, and especially with youthfulness. Young males prefer partners who are their own age, give or take five years, but as men age, they prefer women who are many years younger than themselves. Men can reproduce for many more years than women can. Therefore, by choosing younger women, older men increase their fitness as judged by the number of children they have (Fig. 16A).

Men, unlike women, do not have the same assurance that a child is their own. Therefore, men put a strong emphasis on having a wife who is faithful to them. Both men and women respondents to questionnaires view adultery in women as more offensive than adultery in men.

FIGURE 16A King Hussein and family.
The tendency of men to mate with fertile younger women is exemplified by King Hussein of Jordan, who was about 16 years older than his wife, Queen Noor. This photo shows some of their children, one of whom is now King Abdullah of Jordan.

Pantheropsis obsoleta obsoleta

Pantheropsis obsoleta quadrivittata

Pantheropsis obsoleta lindheimeri

Pantheropsis obsoleta rossalleni

Pantheropsis obsoleta spiloides

FIGURE 16.15 **Subspecies help maintain diversity.**

Each subspecies of rat snakes represents a separate population of snakes. Each subspecies has a reservoir of alleles different from another subspecies. Because the populations are adjacent to one another, there is interbreeding, and, therefore, gene flow among the populations. This introduces alleles that may keep each subspecies from fully adapting to their particular environment.

16.3 Maintenance of Diversity

Diversity is maintained in a population for any number of reasons. Mutations still create new alleles, and recombination still recombines these alleles during gametogenesis and fertilization. Genetic drift also occurs, particularly in small populations, and the end result may be contrary to adaptation to the environment.

Natural Selection

The process of natural selection itself causes imperfect adaptation to the environment. First, it is important to realize that evolution doesn't start from scratch. Just as you can only bake a cake with the ingredients available to you, evolution is constrained by the available diversity. Lightweight titanium bones might benefit birds, but their bones contain calcium and other minerals the same as the reptiles, their ancestors. When you mix the ingredients for a cake, you probably follow the same steps taught to you by your elders. Similarly, the processes of development prevent the emergence of novel features, and therefore the wing of a bird has the same bones as those of other vertebrate forelimbs.

Imperfections are common because of necessary compromises. The success of humans is attributable to their dexterous hands, but the spine is subject to injury because the vertebrate spine was not originally designed to stand erect. A feature that evolves has a benefit that is worth the cost. For example, the benefit of freeing the hands must have been worth the cost of spinal injuries from assuming an erect posture. We should also consider that sexual selection has a reproductive benefit but not necessarily an adaptive benefit.

Second, we want to realize that the environment plays a role in maintaining diversity. It's easy to see that disruptive selection, dependent on an environment that differs widely, promotes polymorphisms in a population (see Fig. 16.11). Then, too, if a population occupies a wide range, as shown in Figure 16.15, it may have several subpopulations designated as subspecies because of recognizable differences. (Subspecies are given a third name in addition to the usual binomial name.) Each subspecies is partially adapted to its own environment and can serve as a reservoir for a different combination of alleles that flow from one group to the next when adjacent subspecies interbreed.

The environment also includes specific selecting agents that help maintain diversity. We have already seen how predatory birds can help maintain the frequencies of both the light-colored and dark-colored moths, depending on the color of background vegetation. Some predators have a search image that causes them to select the most common phenotype among its prey. This promotes the survival of the rare form and helps maintain variation. Or, a herbivore can oscillate in its preference for food. In Figure 15.11, we observed that the medium ground finch on the Galápagos Islands had a different-sized beak dependent on the available food supply. In times of drought, when only large seeds were available, birds with larger beaks were favored. In this case, we can clearly see that maintenance of variation among a population has survival value for the species.

Heterozygote Advantage

Heterozygote advantage occurs when the heterozygote is favored over the two homozygotes. In this way, heterozygote advantage assists the maintenance of genetic, and therefore phenotypic, diversity in future generations.

Sickle-Cell Disease

Sickle-cell disease can be a devastating condition. Patients can have severe anemia, physical weakness, poor circulation, impaired mental function, pain and high fever, rheumatism, paralysis, spleen damage, low resistance to disease, and kidney and heart failure. In these individuals, the red blood cells are sickle-shaped and tend to pile up and block flow through tiny capillaries. The condition is due to an abnormal form of hemoglobin (*Hb*), the molecule that carries oxygen in red blood cells. People with sickle-cell disease (Hb^SHb^S) tend to die early and leave few offspring, due to hemorrhaging and organ destruction. Interestingly, however, geneticists studying the distribution of sickle-cell disease in Africa have found that the recessive allele (Hb^S) has a higher frequency in regions (blue color) where the disease malaria is also prevalent (Fig. 16.16). Malaria is caused by a protozoan parasite that lives in and destroys the red blood cells of the normal homozygote (Hb^AHb^A). Individuals with this genotype also have fewer offspring, due to an early death or to debilitation caused by malaria.

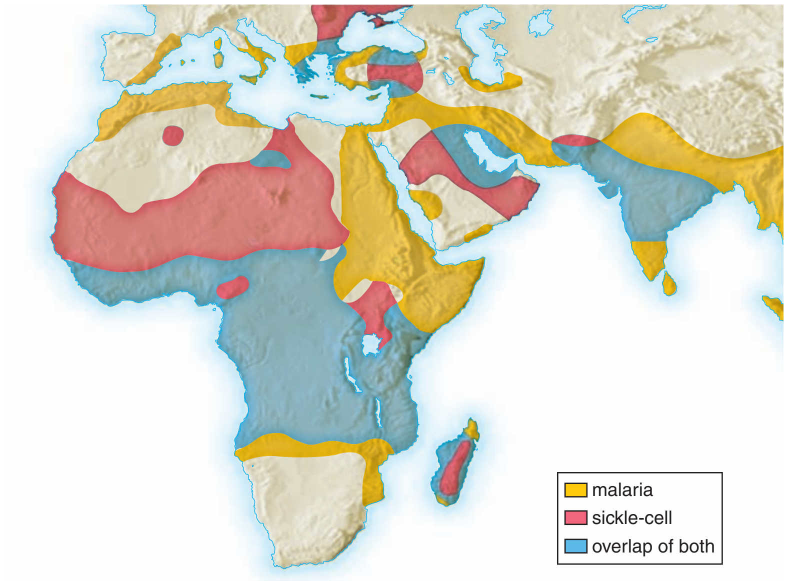


FIGURE 16.16 **Sickle-cell disease.**

Sickle-cell disease is more prevalent in areas of Africa where malaria is more common.

Heterozygous individuals (Hb^AHb^S) have an advantage because they don't die from sickle-cell disease, and they don't die from malaria. The parasite causes any red blood cell it infects to become sickle-shaped. Sickle-shaped red blood cells lose potassium, and this causes the parasite to die. Heterozygote advantage causes all three alleles to be maintained in the population. It's as if natural selection were a store owner balancing the advantages and disadvantages of maintaining the recessive allele Hb^S in the warehouse. As long as the protozoan that causes malaria is present in the environment, it is advantageous to maintain the recessive allele.

Heterozygote advantage is also an example of stabilizing selection because the genotype Hb^AHb^S is favored over the two extreme genotypes, Hb^AHb^A and Hb^SHb^S. In the parts of Africa where malaria is common, one in five individuals is heterozygous (has sickle-cell trait) and survives malaria, while only 1 in 100 is homozygous and dies of sickle-cell disease. What happens in the United States where malaria is not prevalent? As you would expect, the frequency of the Hb^S allele is declining among African Americans because the heterozygote has no particular advantage in this country.

Cystic Fibrosis

Stabilizing selection is also thought to have influenced the frequency of other alleles. Cystic fibrosis is a debilitating condition that leads to lung infections and digestive difficulties. In this instance, the recessive allele, common among individuals of northwestern European descent, causes the person to have a defective plasma membrane protein. The agent that causes typhoid fever can use the normal version of this protein, but not the defective one, to enter cells. Here again, heterozygote superiority caused the recessive allele to be maintained in the population.

Check Your Progress 16.3

1. Natural selection cannot do away with diversity in a population. Explain.
2. Use a Hardy-Weinberg equilibrium to explain why heterozygote advantage maintains diversity.

Connecting the Concepts

We have seen that there are variations among the individuals in any population, whether the population is tuberculosis-causing bacteria in a city, the dandelions on a hill, or the squirrels in your neighborhood. Individuals vary because of the presence of mutations and, in sexually reproducing species, because of the recombination of alleles and chromosomes due to the processes of meiosis and fertilization.

This chapter is about microevolution—that is, gene frequency changes within a population below the level of speciation. The field of population genetics, which uses the Hardy-Weinberg principle, shows us how the study of microevolution can be objective rather than subjective. A change in gene pool allele frequencies defines and signifies that microevolution has occurred. There are various agents of microevolutionary change, but only natural selection results in adaptation to the environment. Recent observations and experiments show that natural selection can occur rapidly. The emergence of MRSA, methicillin-resistant *Staphylococcus aureus* bacteria, only took about sixty years. Investigators who noted that guppies have a different appearance according to the presence of predators can also observe this change because it takes only a few months in the wild or even in the laboratory. So, we have to change our perception of natural selection as a process that cannot be observed to one that anyone can observe if they are so inclined.

Sexual selection should be considered a form of natural selection because it affects the reproductive capacity of the individual. Males that are selected to reproduce by females have more offspring than those that are not selected. Sexual selection teaches us that any trait that evolves through natural selection can be subjected to a cost-benefit analysis. It is obvious that some male traits arising through sexual selection bear a cost and may actually decrease the chance of survival. Still, if a trait helps a male leave more fertile offspring than other members of a population, it is beneficial in an evolutionary context.

We have seen that natural selection does not normally reduce variations to the point that no further evolutionary change is possible. Retention of variations is always desirable because a changing environment requires further evolutionary adjustments.

summary

16.1 Population Genetics

Microevolution requires diversity, and this chapter is interested in allele and genotype differences with a population. Diversity can even extend to SNPs, which are single nucleotide polymorphisms. Investigators are beginning to think that SNPs have significance because they may help regulate the expression of genes.

The Hardy-Weinberg equilibrium is a constancy of gene pool allele frequencies that remains from generation to generation if certain conditions are met. The conditions are no mutations, no gene flow, random mating, no genetic drift, and no selection. Since these conditions are rarely met, a change in gene pool frequencies is likely. When gene pool frequencies change, microevolution has occurred. Deviations from a Hardy-Weinberg equilibrium allow us to determine when evolution has taken place.

Mutations, gene flow, nonrandom mating, genetic drift, and natural selection all cause deviations from a Hardy-Weinberg equilibrium. Mutations are the raw material for evolutionary change. Recombinations help bring about adaptive genotypes. Gene flow occurs when a breeding individual (in animals) migrates to another population or when gametes and seeds (in plants) are carried into another population. Constant gene flow between two populations causes their gene pools to become similar. Nonrandom mating occurs when relatives mate (inbreeding) or assortative mating takes place. Both of these cause an increase in homozygotes. Genetic drift occurs when allele frequencies are altered only because some individuals, by chance, contribute more alleles to the next generation. Genetic drift can cause the gene pools of two isolated populations to become dissimilar as some alleles are lost and others are fixed. Genetic drift is particularly evident after a bottleneck, when severe inbreeding occurs, or when founders start a new population.

16.2 Natural Selection

Most of the traits of evolutionary significance are polygenic; the diversity in a population results in a bell-shaped curve. Three types of selection occur: (1) directional—the curve shifts in one direction, as when bacteria become resistant to antibiotics. (New observations and experiments of late have shown how quickly directional selection can occur. Within 12 months, guppies originally similar in appearance become more colorful if predation is absent and less colorful if predation is present.); (2) stabilizing—the peak of the curve increases, as when there is an optimum clutch size for survival of Swiss starling young; and (3) disruptive—the curve has two peaks, as when *Cepaea* snails vary because a wide geographic range causes selection to vary.

Traits that promote reproductive success are expected to be advantageous overall, despite any possible disadvantage. Males produce many sperm and are expected to compete to inseminate females. Females produce few eggs and are expected to be selective about their mates. Studies of satin bowerbirds and birds of paradise have been done to test hypotheses regarding female choice. A cost-benefit analysis can be applied to competition between males for mates, in reference to a dominance hierarchy (e.g., baboons) and territoriality (e.g., red deer).

It is possible that male competition and female choice also occur among humans. Biological differences between the sexes may promote certain mating behaviors because they increase fitness.

16.3 Maintenance of Diversity

Despite constant natural selection, genetic diversity is maintained. Mutations and recombination still occur; gene flow among small populations can introduce new alleles; and natural selection itself sometimes results in variation. In sexually reproducing diploid organisms, the heterozygote acts as a repository for recessive alleles whose frequency is low. In regard to sickle-cell disease, the heterozygote is more fit in areas where malaria occurs, and therefore both homozygotes are maintained in the population.

understanding the terms

assortative mating	287
bottleneck effect	288
cost-benefit analysis	291
directional selection	290
disruptive selection	290
dominance hierarchy	291
fitness	291
founder effect	288

gene flow	287
gene pool	285
genetic drift	287
Hardy-Weinberg principle	286
heterozygote advantage	295
industrial melanism	286
microevolution	285
mutation	287
nonrandom mating	287
population	284
population genetics	284
sexual selection	291
single nucleotide polymorphism (SNP)	284
stabilizing selection	289
territoriality	292
territory	291

Match the terms to these definitions:

a. ______________ Outcome of natural selection in which extreme phenotypes are eliminated and the average phenotype is conserved.

b. ______________ Marking and/or defending a particular area against invasion by another species member.

c. ______________ Change in the genetic makeup of a population due to chance (random) events; important in small populations or when only a few individuals mate.

d. ______________ Total of all the genes of all the individuals in a population.

e. ______________ Sharing of genes between two populations through interbreeding.

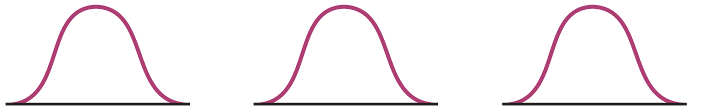
reviewing this chapter

1. The discovery of SNPs is of what significance? 284
2. What is the Hardy-Weinberg principle? 285–86
3. Name and discuss the five conditions of evolutionary change. 286–88
4. What is a population bottleneck, and what is the founder effect? Give examples of each. 288
5. Distinguish among directional, stabilizing, and disruptive selection by giving examples. 289–90
6. What is sexual selection, and why does it foster female choice and male competition during mating? 291–93
7. What is a cost-benefit analysis, and how does it apply to a dominance hierarchy and territoriality? Give examples. 291–92
8. State ways in which diversity is maintained in a population. 294–95

testing yourself

Choose the best answer for each question.

1. Assuming a Hardy-Weinberg equilibrium, 21% of a population is homozygous dominant, 50% is heterozygous, and 29% is homozygous recessive. What percentage of the next generation is predicted to be homozygous recessive?
   a. 21%
   b. 50%
   c. 29%
   d. 42%
   e. 58%
2. A human population has a higher-than-usual percentage of individuals with a genetic disorder. The most likely explanation is
   a. mutations and gene flow.
   b. mutations and natural selection.
   c. nonrandom mating and founder effect.
   d. nonrandom mating and gene flow.
   e. All of these are correct.
3. The offspring of better-adapted individuals are expected to make up a larger proportion of the next generation. The most likely explanation is
   a. mutations and nonrandom mating.
   b. gene flow and genetic drift.
   c. mutations and natural selection.
   d. mutations and genetic drift.
4. The continued occurrence of sickle-cell disease with malaria in parts of Africa is due to
   a. continual mutation.
   b. gene flow between populations.
   c. relative fitness of the heterozygote.
   d. disruptive selection.
   e. protozoan resistance to DDT.
5. Which of these is necessary to natural selection?
   a. diversity
   b. differential reproduction
   c. inheritance of differences
   d. differential adaptiveness
   e. All of these are correct.
6. When a population is small, there is a greater chance of
   a. gene flow.
   b. genetic drift.
   c. natural selection.
   d. mutations occurring.
   e. sexual selection.
7. Which of these is an example of stabilizing selection?
   a. Over time, *Equus* developed strength, intelligence, speed, and durable grinding teeth.
   b. British land snails mainly have two different phenotypes.
   c. Swiss starlings usually lay four or five eggs, thereby increasing their chances of more offspring.
   d. Drug resistance increases with each generation; the resistant bacteria survive, and the nonresistant bacteria get killed off.
   e. All of these are correct.
8. Which of these cannot occur if a population is to maintain an equilibrium of allele frequencies?
   a. People leave one country and relocate in another.
   b. A disease wipes out the majority of a herd of deer.
   c. Members of an Indian tribe only allow the two tallest people in a tribe to marry each spring.
   d. Large black rats are the preferred males in a population of rats.
   e. All of these are correct.
9. The homozygote Hb^SHb^S persists because
   a. it offers protection against malaria.
   b. the heterozygote offers protection against malaria.
   c. the genotype Hb^AHb^A offers protection against malaria.
   d. sickle-cell disease is worse than sickle-cell trait.
   e. Both b and d are correct.
10. The diagrams represent a distribution of phenotypes in a population. Superimpose another diagram on (a) to show that directional selection has occurred, on (b) to show that stabilizing selection has occurred, and on (c) to show that disruptive selection has occurred.



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

11. The observation that the most fit male bowerbirds are the ones that can keep their nests intact supports which hypothesis?
    a. good genes hypothesis—females choose mates based on their improved chances of survival
    b. runaway hypothesis—females choose mates based on their appearance
    c. Either hypothesis could be true.
    d. Neither hypothesis is true.

12. In some bird species, the female bird chooses a mate that is most similar to her in size. This supports
    a. the good genes hypothesis.
    b. the runaway hypothesis.
    c. Either hypothesis could be true.
    d. Neither hypothesis is true.
13. Which of the following are costs that a dominant male baboon must pay in order to gain a reproductive benefit?
    a. He requires more food and must travel larger distances.
    b. He requires more food and must care for his young.
    c. He is more prone to injury and requires more food.
    d. He is more prone to injury and must care for his young.
    e. He must care for his young and travel larger distances.
14. A red deer harem master typically dies earlier than other males because he is
    a. likely to get expelled from the herd and cannot survive alone.
    b. more prone to disease because he interacts with so many animals.
    c. in need of more food than other males.
    d. apt to place himself between a predator and the herd to protect the herd.
15. Which one of the following statements would *not* pertain to a Punnett square that involves the alleles of a gene pool?
    a. The results tell you the chances that an offspring can have a particular condition.
    b. The results tell you the genotype frequencies of the next generation.
    c. The eggs and sperm are the gamete frequencies of the previous generation.
    d. All of these are correct.
16. Which of the following applies to the Hardy-Weinberg expression: $p^2 + 2pq + q^2$?
    a. Knowing either p^2 or q^2, you can calculate all the other frequencies.
    b. applies to Mendelian traits that are controlled by one pair of alleles
    c. $2pq$ = heterozygous individuals
    d. can be used to determine the genotype and allele frequencies of the previous and the next generations
    e. All of these are correct.
17. Following genetic drift, the
    a. genotype and allele frequencies would not change.
    b. genotype and allele frequencies would change.
    c. adaptation would occur.
    d. population would have more phenotypic variation but less genotypic variation.
18. The high frequency of Huntington disease in a population could be due to
    a. mutation plus nonrandom mating.
    b. the founder effect.
    c. natural selection because Huntington disease has a benefit.
    d. pollution in the environment.
    e. Both a and b are correct.
19. For disruptive selection to occur,
    a. the population has to contain diversity.
    b. the environment has to contain diversity.
    c. pollution must be present.
    d. natural selection must occur.
    e. All but c are correct.
20. Which of these is mismatched?
    a. male competition—males produce many sperm
    b. female choice—females produce few eggs
    c. male choice—males with exaggerated traits get to choose
    d. male competition—dominance hierarchy
21. All vertebrate forelimbs contain the same bones because
    a. they form the best structures for all sorts of adaptations.
    b. they are pliable and able to adapt.
    c. their common ancestor had these bones.
    d. vertebrates have vertebrates in their spine.
    e. All of these are correct.

additional genetics problems*

1. If $p^2 = 0.36$, what percentage of the population has the recessive phenotype, assuming a Hardy-Weinberg equilibrium?
2. If 1% of a human population has the recessive phenotype, what percentage has the dominant phenotype, assuming a Hardy-Weinberg equilibrium?
3. In a population of snails, ten had no antennae (*aa*); 180 were heterozygous with antennae (*Aa*); and 810 were homozygous with antennae (*AA*). What is the frequency of the *a* allele in the population?

*Answers to Additional Genetics Problems appear in Appendix A.

thinking scientifically

1. A farmer uses a new pesticide. He applies the pesticide as directed by the manufacturer and loses about 15% of his crop to insects. A farmer in the next state learns of these results, uses three times as much pesticide, and loses only 3% of her crop to insects. Each farmer follows this pattern for five years. At the end of five years, the first farmer is still losing about 15% of his crop to insects, but the second farmer is losing 40% of her crop to insects. How could these observations be interpreted on the basis of natural selection?
2. You are observing a grouse population in which two feather phenotypes are present in males. One is relatively dark and blends into shadows well, and the other is relatively bright and so is more obvious to predators. The females are uniformly dark-feathered. Observing the frequency of mating between females and the two types of males, you have recorded the following:
    matings with dark-feathered males: 13
    matings with bright-feathered males: 32

   Propose a hypothesis to explain why females apparently prefer bright-feathered males. What selective advantage might there be in choosing a male with alleles that make it more susceptible to predation? What data would help test your hypothesis?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10