# 23

# The Evolution of Populations

▲ **Figure 23.1 Is this finch evolving?**

**EVOLUTION**

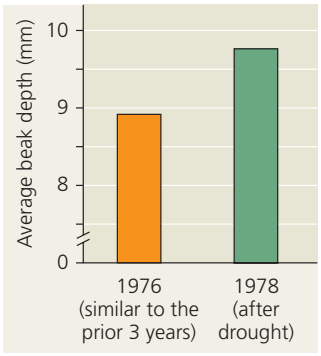
**KEY CONCEPTS**



**OVERVIEW**

## The Smallest Unit of Evolution

One common misconception about evolution is that individual organisms evolve. It is true that natural selection acts on individuals: Each organism's traits affect its survival and reproductive success compared with other individuals. But the evolutionary impact of natural selection is only apparent in the changes in a *population* of organisms over time.




◀ **Figure 23.2 Evidence of selection by food source.** The data represent adult beak depth measurements of medium ground finches hatched in the generations before and after the 1977 drought. Beak sizes remained large until 1983, when changing conditions no longer favored large-beaked birds.

MB See the related Experimental Inquiry Tutorial in MasteringBiology.

Consider the medium ground finch (*Geospiza fortis*), a seed-eating bird that inhabits the Galápagos Islands **(Figure 23.1)**. In 1977, the *G. fortis* population on the island of Daphne Major was decimated by a long period of drought: Of some 1,200 birds, only 180 survived. Researchers Peter and Rosemary Grant observed that during the drought, small, soft seeds were in short supply. The finches mostly fed on large, hard seeds that were more plentiful. Birds with larger, deeper beaks were better able to crack and eat these larger seeds, and they survived at a higher rate than finches with smaller beaks. Since beak depth is an inherited trait in these birds, the average beak depth in the next generation of *G. fortis* was greater than it had been in the pre-drought population **(Figure 23.2)**. The finch population had evolved by natural selection. However, the *individual* finches did not evolve. Each bird had a beak of a particular size, which did not grow larger during the drought. Rather, the proportion of large beaks in the population increased from generation to generation: The population evolved, not its individual members.

Focusing on evolutionary change in populations, we can define evolution on its smallest scale, called **microevolution**, as change in allele frequencies in a population over generations. As we will see in this chapter, natural selection is not the only cause of microevolution. In fact, there are three main mechanisms that can cause allele frequency change: natural selection, genetic drift (chance events that alter allele frequencies), and gene flow (the transfer of alleles between populations). Each of these mechanisms has distinctive effects on the genetic composition of populations. However, only natural selection consistently improves the match between organisms and their environment (adaptation). Before we examine natural selection and adaptation more closely, let's revisit a prerequisite for these processes in a population: genetic variation.

**CONCEPT 23.1**

## Genetic variation makes evolution possible

In *The Origin of Species*, Darwin provided abundant evidence that life on Earth has evolved over time, and he proposed natural selection as the primary mechanism for that change. He

observed that individuals differed in their inherited traits and that selection acted on such differences, leading to evolutionary change. Thus, Darwin realized that variation in heritable traits was a prerequisite for evolution, but he did not know precisely how organisms pass heritable traits to their offspring.

Just a few years after Darwin published *The Origin of Species*, Gregor Mendel wrote a groundbreaking paper on inheritance in pea plants (see Chapter 14). In that paper, Mendel proposed a particulate model of inheritance in which organisms transmit discrete heritable units (now called genes) to their offspring. Although Darwin did not know about genes, Mendel's paper set the stage for understanding the genetic differences on which evolution is based. Here we'll examine such genetic differences and how they are produced.

## Genetic Variation

You probably have no trouble recognizing your friends in a crowd. Each person is unique, exhibiting differences in their facial features, height, and voice. Indeed, individual variation occurs in all species. In addition to the differences that we can see or hear, individuals vary extensively at the molecular level. For example, you cannot identify a person's blood group (A, B, AB, or O) from his or her appearance, but this and many other molecular traits vary among individuals.

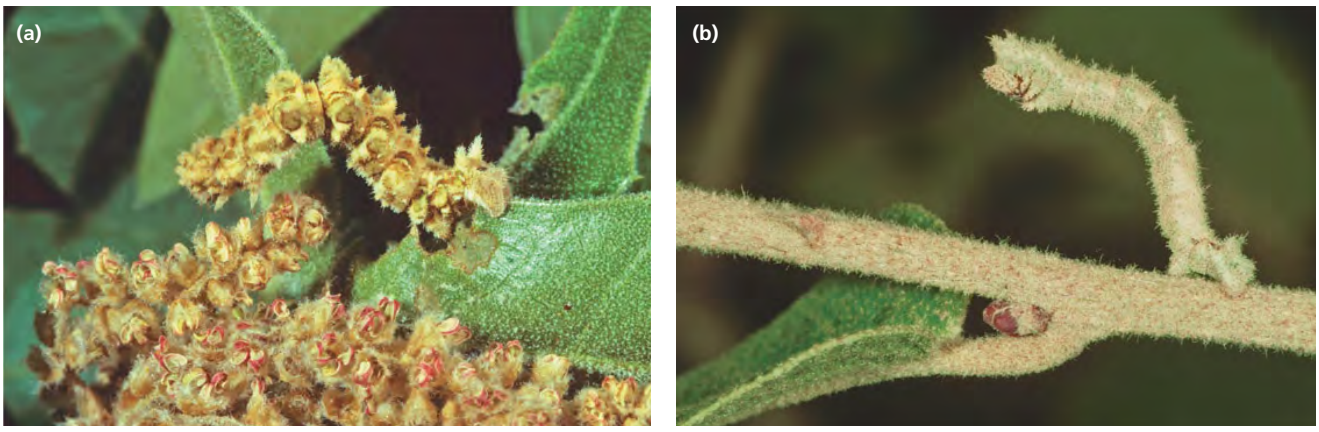
Individual variations often reflect **genetic variation**, differences among individuals in the composition of their genes or other DNA segments. As you read in earlier chapters, however, some phenotypic variation is not heritable (see **Figure 23.3** for a striking example in a caterpillar of the southwestern United States). Phenotype is the product of an inherited genotype and many environmental influences. In a human example, bodybuilders alter their phenotypes dramatically but do not pass their huge muscles on to the next generation. In general, only the genetically determined part of phenotypic variation can have evolutionary consequences. As such, genetic variation provides the raw material for evolutionary change: Without genetic variation, evolution cannot occur.

### *Variation Within a Population*

Characters that vary within a population may be discrete or quantitative. *Discrete characters*, such as the purple or white flower colors of Mendel's pea plants (see Figure 14.3), can be classified on an either-or basis (each plant has flowers that are either purple or white). Many discrete characters are determined by a single gene locus with different alleles that produce distinct phenotypes. However, most heritable variation involves *quantitative characters*, which vary along a continuum within a population. Heritable quantitative variation usually results from the influence of two or more genes on a single phenotypic character.

For both discrete and quantitative characters, biologists often need to describe how much genetic variation there is in a particular population. We can measure genetic variation at the whole-gene level (*gene variability*) and at the molecular level of DNA (*nucleotide variability*). Gene variability can be quantified as the **average heterozygosity**, the average percentage of loci that are heterozygous. (Recall that a heterozygous individual has two different alleles for a given locus, whereas a homozygous individual has two identical alleles for that locus.) As an example, on average the fruit fly *Drosophila melanogaster* is heterozygous for about 1,920 of its 13,700 loci (14%) and homozygous for all the rest. We can therefore say that a *D. melanogaster* population has an average heterozygosity of 14%. Analyses of this and many other species show that this level of genetic variation provides ample raw material for natural selection to operate, resulting in evolutionary change.

When determining gene variability, how do scientists identify heterozygous loci? One method is to survey the protein products of genes using gel electrophoresis (see Figure 20.9). However, this approach cannot detect silent mutations that




▲ **Figure 23.3 Nonheritable variation.** These caterpillars of the moth *Nemoria arizonaria* owe their different appearances to chemicals in their diets, not to differences in their genotypes. Caterpillars raised on a diet of oak flowers resembled the flowers **(a)**, whereas their siblings raised on oak leaves resembled oak twigs **(b)**.

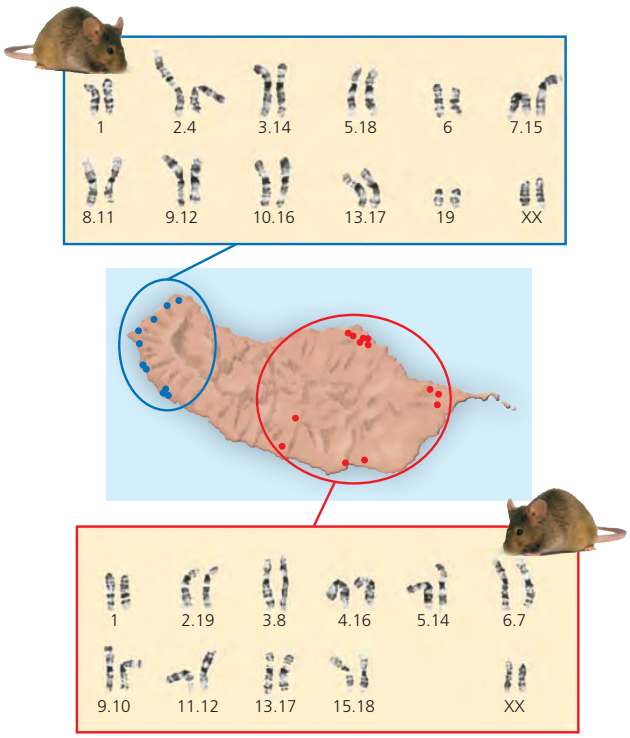
alter the DNA sequence of a gene but not the amino acid sequence of the protein (see Figure 17.24). To include such silent mutations in their estimates of average heterozygosity, researchers must use other approaches, such as PCR-based methods and restriction fragment analyses (see Chapter 20).

To measure nucleotide variability, biologists compare the DNA sequences of two individuals in a population and then average the data from many such comparisons. The genome of *D. melanogaster* has about 180 million nucleotides, and the sequences of any two fruit flies differ on average by approximately 1.8 million (1%) of their nucleotides. Thus, the nucleotide variability of *D. melanogaster* populations is about 1%.

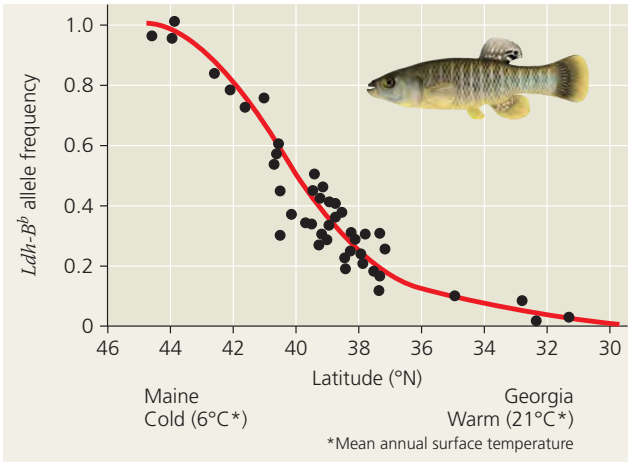
As in this example, gene variability tends to exceed nucleotide variability. Why is this true? Remember that a gene can consist of thousands of nucleotides. A difference at only one of these nucleotides can be sufficient to make two alleles of that gene different, increasing gene variability.

### *Variation Between Populations*

In addition to variation observed within a population, species also exhibit **geographic variation**, differences in the genetic composition of separate populations. **Figure 23.4** illustrates geographic variation in populations of house mice (*Mus musculus*) separated by mountains on the Atlantic island of Madeira. Inadvertently introduced by Portuguese settlers in the 15th century, several populations of mice have evolved in isolation from one another. Researchers have observed differences in the karyotypes (chromosome sets) of these isolated populations. In certain populations, some of the chromosomes have become fused. However, the patterns of fused chromosomes differ from one population to another. Because these chromosome-level changes leave genes intact, their phenotypic effects on the mice seem to be neutral. Thus, the variation between these populations appears to have resulted from chance events (drift) rather than natural selection.




▲ **Figure 23.4 Geographic variation in isolated mouse populations on Madeira.** The number pairs represent fused chromosomes. For example, "2.4" indicates fusion of chromosome 2 and chromosome 4. Mice in the areas indicated by the blue dots have the set of fused chromosomes in the blue box; mice in the red-dot locales have the set of fused chromosomes in the red box.




▲ **Figure 23.5 A cline determined by temperature.** In mummichog fish, the frequency of the *Ldh-B*$^b$ allele for the enzyme lactate dehydrogenase-B (which functions in metabolism) decreases in fish sampled from Maine to Georgia. The *Ldh-B*$^b$ allele codes for a form of the enzyme that is a better catalyst in cold water than are other versions of the enzyme. Individuals with the *Ldh-B*$^b$ allele can swim faster in cold water than can individuals with other alleles.

Other examples of geographic variation occur as a **cline**, a graded change in a character along a geographic axis. Some clines are produced by a gradation in an environmental variable, as illustrated by the impact of temperature on the frequency of a cold-adaptive allele in mummichog fish (*Fundulus heteroclitus*). Clines such as the one depicted in **Figure 23.5** probably result from natural selection—otherwise there would be no reason to expect a close association between the environmental variable and the frequency of the allele. But selection can only operate if multiple alleles exist for a given locus. Such variation in alleles can arise in several ways.

## Sources of Genetic Variation

The genetic variation on which evolution depends originates when mutation, gene duplication, or other processes produce new alleles and new genes. Many new genetic variants can be produced in short periods of time in organisms that reproduce rapidly. Sexual reproduction can also result in genetic variation as existing genes are arranged in new ways.

### Formation of New Alleles

As described in Chapters 17 and 21, new alleles can arise by *mutation*, a change in the nucleotide sequence of an organism's DNA. A mutation is like a shot in the dark—we cannot predict accurately which segments of DNA will be altered or in what way. In multicellular organisms, only mutations in cell lines that produce gametes can be passed to offspring. In plants and fungi, this is not as limiting as it may sound, since many different cell lines can produce gametes (see Figures 30.6 and 31.17). But in most animals, the majority of mutations occur in somatic cells and are lost when the individual dies.

A change of as little as one base in a gene, called a "point mutation," can have a significant impact on phenotype, as in sickle-cell disease (see Figure 17.23). Organisms reflect thousands of generations of past selection, and hence their phenotypes generally provide a close match to their environment. As a result, it's unlikely that a new mutation that alters a phenotype will improve it. In fact, most such mutations are at least slightly harmful. But much of the DNA in eukaryotic genomes does not code for protein products, and point mutations in these noncoding regions are often harmless. Also, because of the redundancy in the genetic code, even a point mutation in a gene that encodes a protein will have no effect on the protein's function if the amino acid composition is not changed. And even where there is a change in the amino acid, it may not affect the protein's shape and function. However, as will be discussed later in this chapter, a mutant allele may on rare occasions actually make its bearer better suited to the environment, enhancing reproductive success.

### Altering Gene Number or Position

Chromosomal changes that delete, disrupt, or rearrange many loci at once are usually harmful. However, when such large-scale changes leave genes intact, their effects on organisms may be neutral (as in the case of the Madeira mice described in Figure 23.4). In rare cases, chromosomal rearrangements may even be beneficial. For example, the translocation of part of one chromosome to a different chromosome could link DNA segments in a way that results in a positive effect.

An important source of variation begins when genes are duplicated due to errors in meiosis (such as unequal crossing over), slippage during DNA replication, or the activities of transposable elements (see Chapters 15 and 21). Duplications of large chromosome segments, like other chromosomal aberrations, are often harmful, but the duplication of smaller pieces of DNA may not be. Gene duplications that do not have severe effects can persist over generations, allowing mutations to accumulate. The result is an expanded genome with new genes that may take on new functions.

Such beneficial increases in gene number appear to have played a major role in evolution. For example, the remote ancestors of mammals had a single gene for detecting odors that has since been duplicated many times. As a result, humans today have about 1,000 olfactory receptor genes, and mice have 1,300. This dramatic proliferation of olfactory genes probably helped early mammals, enabling them to detect faint odors and to distinguish among many different smells. More recently, about 60% of human olfactory receptor genes have been inactivated by mutations, whereas mice have lost only 20% of theirs. Since mutation rates in humans and mice are similar, this difference is likely due to strong selection against mice with mutations that inactivate their olfactory genes. A versatile sense of smell appears to be much more important to mice than to humans!

### Rapid Reproduction

Mutation rates tend to be low in plants and animals, averaging about one mutation in every 100,000 genes per generation, and they are often even lower in prokaryotes. But prokaryotes typically have short generation spans, so mutations can quickly generate genetic variation in populations of these organisms. The same is true of viruses. For instance, HIV has a generation span of about two days. It also has an RNA genome, which has a much higher mutation rate than a typical DNA genome because of the lack of RNA repair mechanisms in host cells (see Chapter 19). For this reason, it is unlikely that a single-drug treatment would ever be effective against HIV; mutant forms of the virus that are resistant to a particular drug would no doubt proliferate in relatively short order. The most effective AIDS treatments to date have been drug "cocktails" that combine several medications. It is less likely that multiple mutations conferring resistance to *all* the drugs will occur in a short time period.

### Sexual Reproduction

In organisms that reproduce sexually, most of the genetic variation in a population results from the unique combination of alleles that each individual receives from its parents. Of course, at the nucleotide level, all the differences among these alleles have originated from past mutations and other processes that can produce new alleles. But it is the mechanism of sexual reproduction that shuffles existing alleles and deals them at random to produce individual genotypes.

As described in Chapter 13, three mechanisms contribute to this shuffling: crossing over, independent assortment of chromosomes, and fertilization. During meiosis, homologous chromosomes, one inherited from each parent, trade some of their alleles by crossing over. These homologous chromosomes and the alleles they carry are then distributed at random into gametes. Then, because myriad possible mating combinations exist in a population, fertilization brings together gametes that are likely to have different genetic backgrounds. The combined effects of these three mechanisms ensure that sexual reproduction rearranges existing alleles into fresh combinations each generation, providing much of the genetic variation that makes evolution possible.

## CONCEPT CHECK 23.1

1. (a) Explain why genetic variation within a population is a prerequisite for evolution. (b) What factors can produce genetic differences between populations?
2. Of all the mutations that occur in a population, why do only a small fraction become widespread?
3. **MAKE CONNECTIONS** If a population stopped reproducing sexually (but still reproduced asexually), how would its genetic variation be affected over time? Explain. (See Concept 13.4, pp. 257–259.)

For suggested answers, see Appendix A.

## CONCEPT 23.2

# The Hardy-Weinberg equation can be used to test whether a population is evolving

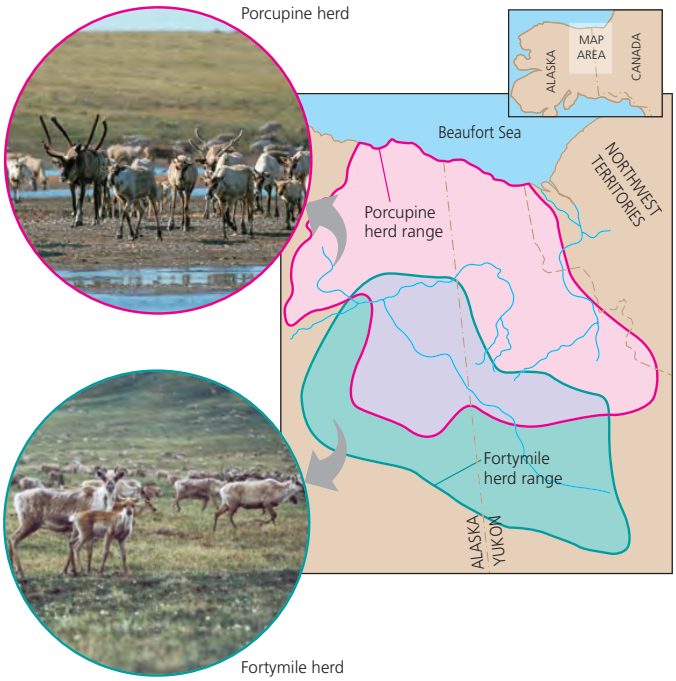
Although the individuals in a population must differ genetically for evolution to occur, the presence of genetic variation does not guarantee that a population will evolve. For that to happen, one of the factors that cause evolution must be at work. In this section, we'll explore one way to test whether evolution is occurring in a population. The first step in this process is to clarify what we mean by a population.

## Gene Pools and Allele Frequencies

A **population** is a group of individuals of the same species that live in the same area and interbreed, producing fertile offspring. Different populations of a single species may be isolated geographically from one another, thus exchanging genetic material only rarely. Such isolation is common for species that live on widely separated islands or in different lakes. But not all populations are isolated, nor must populations have sharp boundaries **(Figure 23.6)**. Still, members of a population typically breed with one another and thus on average are more closely related to each other than to members of other populations.

We can characterize a population's genetic makeup by describing its **gene pool**, which consists of all copies of every type of allele at every locus in all members of the population. If only one allele exists for a particular locus in a population, that allele is said to be *fixed* in the gene pool, and all individuals are homozygous for that allele. But if there are two or more alleles for a particular locus in a population, individuals may be either homozygous or heterozygous.

Each allele has a frequency (proportion) in the population. For example, imagine a population of 500 wildflower plants with two alleles, $C^R$ and $C^W$, for a locus that codes for flower pigment. These alleles show incomplete dominance (see Figure 14.10); thus, each genotype has a distinct phenotype.




▲ **Figure 23.6 One species, two populations.** These two caribou populations in the Yukon are not totally isolated; they sometimes share the same area. Still, members of either population are most likely to breed within their own population.

Plants homozygous for the $C^R$ allele ($C^RC^R$) produce red pigment and have red flowers; plants homozygous for the $C^W$ allele ($C^WC^W$) produce no red pigment and have white flowers; and heterozygotes ($C^RC^W$) produce some red pigment and have pink flowers.




In our population, suppose there are 320 plants with red flowers, 160 with pink flowers, and 20 with white flowers. Because these are diploid organisms, there are a total of 1,000 copies of the gene for flower color in the population of 500 individuals. The $C^R$ allele accounts for 800 of these copies ($320 \times 2 = 640$ for $C^RC^R$ plants, plus $160 \times 1 = 160$ for $C^RC^W$ plants).

When studying a locus with two alleles, the convention is to use $p$ to represent the frequency of one allele and $q$ to represent the frequency of the other allele. Thus, $p$, the frequency of the $C^R$ allele in the gene pool of this population, is 800/1,000 = 0.8 = 80%. And because there are only two alleles for this gene, the frequency of the $C^W$ allele, represented by $q$, must be 200/1,000 = 0.2 = 20%. For loci that have more than two alleles, the sum of all allele frequencies must still equal 1 (100%).

Next we'll see how allele and genotype frequencies can be used to test whether evolution is occurring in a population.

## The Hardy-Weinberg Principle

One way to assess whether natural selection or other factors are causing evolution at a particular locus is to determine

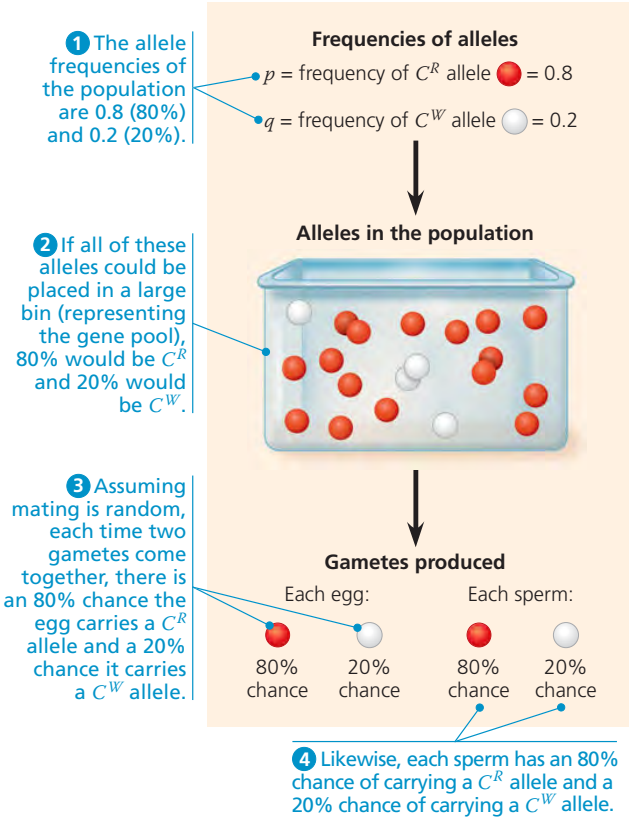
what the genetic makeup of a population would be if it were *not* evolving at that locus. We can then compare that scenario with data from a real population. If there are no differences, we can conclude that the real population is not evolving. If there are differences, this suggests that the real population may be evolving—and then we can try to figure out why.

### Hardy-Weinberg Equilibrium

The gene pool of a population that is not evolving can be described by the **Hardy-Weinberg principle**, named for the British mathematician and German physician, respectively, who independently derived it in 1908. This principle states that the frequencies of alleles and genotypes in a population will remain constant from generation to generation, provided that only Mendelian segregation and recombination of alleles are at work. Such a gene pool is in *Hardy-Weinberg equilibrium*.

To use the Hardy-Weinberg principle, it is helpful to think about genetic crosses in a new way. Previously, we used Punnett squares to determine the genotypes of offspring in a genetic cross (see Figure 14.5). Here, instead of considering the possible allele combinations from one cross, consider the combination of alleles in *all* of the crosses in a population.

Imagine that all the alleles for a given locus from all the individuals in a population were placed in a large bin **(Figure 23.7)**.




▲ **Figure 23.7 Selecting alleles at random from a gene pool.**

We can think of this bin as holding the population's gene pool for that locus. "Reproduction" occurs by selecting alleles at random from the bin; somewhat similar events occur in nature when fish release sperm and eggs into the water or when pollen (containing plant sperm) is blown about by the wind. By viewing reproduction as a process of randomly selecting and combining alleles from the bin (the gene pool), we are in effect assuming that mating occurs at random—that is, that all male-female matings are equally likely.

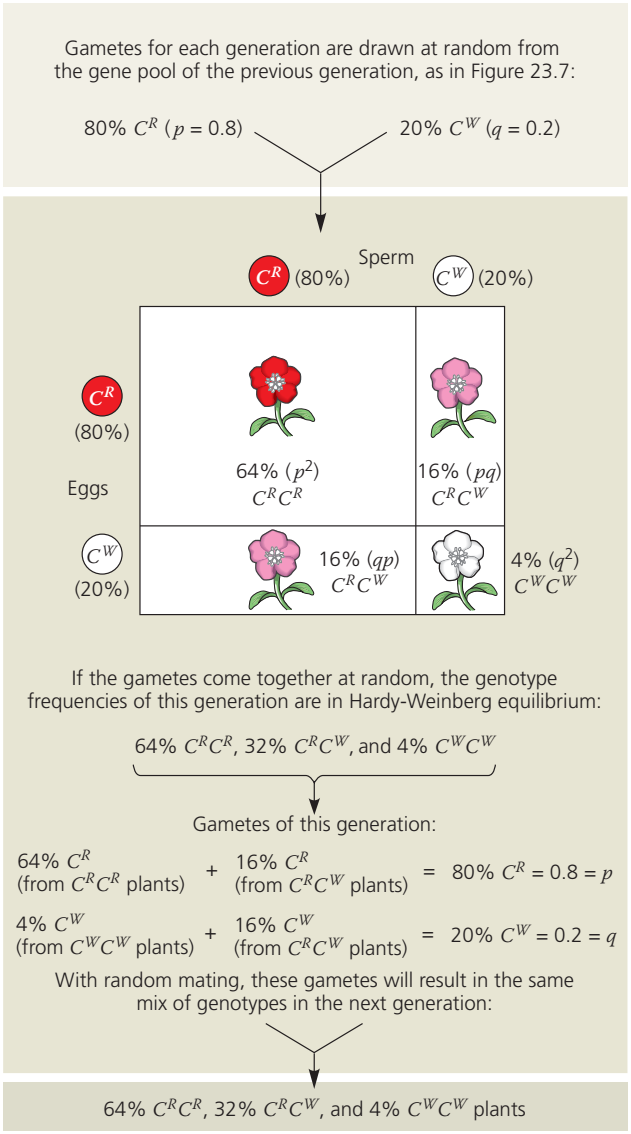
Let's apply the bin analogy to the hypothetical wildflower population discussed earlier. In that population of 500 flowers, the frequency of the allele for red flowers ($C^R$) is $p = 0.8$, and the frequency of the allele for white flowers ($C^W$) is $q = 0.2$. Thus, a bin holding all 1,000 copies of the flower-color gene in the population contains 800 $C^R$ alleles and 200 $C^W$ alleles. Assuming that gametes are formed by selecting alleles at random from the bin, the probability that an egg or sperm contains a $C^R$ or $C^W$ allele is equal to the frequency of these alleles in the bin. Thus, as shown in Figure 23.7, each egg has an 80% chance of containing a $C^R$ allele and a 20% chance of containing a $C^W$ allele; the same is true for each sperm.

Using the rule of multiplication (see Figure 14.9), we can now calculate the frequencies of the three possible genotypes, assuming random unions of sperm and eggs. The probability that two $C^R$ alleles will come together is $p \times p = p^2 = 0.8 \times 0.8 = 0.64$. Thus, about 64% of the plants in the next generation will have the genotype $C^RC^R$. The frequency of $C^WC^W$ individuals is expected to be about $q \times q = q^2 = 0.2 \times 0.2 = 0.04$, or 4%. $C^RC^W$ heterozygotes can arise in two different ways. If the sperm provides the $C^R$ allele and the egg provides the $C^W$ allele, the resulting heterozygotes will be $p \times q = 0.8 \times 0.2 = 0.16$, or 16% of the total. If the sperm provides the $C^W$ allele and the egg the $C^R$ allele, the heterozygous offspring will make up $q \times p = 0.2 \times 0.8 = 0.16$, or 16%. The frequency of heterozygotes is thus the sum of these possibilities: $pq + qp = 2pq = 0.16 + 0.16 = 0.32$, or 32%.

As shown in **Figure 23.8** on the facing page, the genotype frequencies in the next generation must add up to 1 (100%). Thus, the equation for Hardy-Weinberg equilibrium states that at a locus with two alleles, the three genotypes will appear in the following proportions:

| $p^2$ | + | $2pq$ | + | $q^2$ | = | 1 |
|---|---|---|---|---|---|---|
| Expected frequency of genotype $C^RC^R$ | | Expected frequency of genotype $C^RC^W$ | | Expected frequency of genotype $C^WC^W$ | | |

Note that for a locus with two alleles, only three genotypes are possible (in this case, $C^RC^R$, $C^RC^W$, and $C^WC^W$). As a result, the sum of the frequencies of the three genotypes must equal 1 (100%) in *any* population—regardless of whether the population is in Hardy-Weinberg equilibrium. A population is in Hardy-Weinberg equilibrium only if the genotype frequencies are such that the actual frequency of




▲ **Figure 23.8 The Hardy-Weinberg principle.** In our wildflower population, the gene pool remains constant from one generation to the next. Mendelian processes alone do not alter frequencies of alleles or genotypes.

? *If the frequency of the $C^R$ allele is 60%, predict the frequencies of the $C^RC^R$, $C^RC^W$, and $C^WC^W$ genotypes.*

one homozygote is $p^2$, the actual frequency of the other homozygote is $q^2$, and the actual frequency of heterozygotes is $2pq$. Finally, as suggested by Figure 23.8, if a population such as our wildflowers is in Hardy-Weinberg equilibrium and its members continue to mate randomly generation after generation, allele and genotype frequencies will remain constant. The system operates somewhat like a deck of cards: No matter how many times the deck is reshuffled to deal out new hands, the deck itself remains the same. Aces do not grow more numerous than jacks. And the repeated shuffling of a population's gene pool over the generations cannot, in itself, change the frequency of one allele relative to another.

### Conditions for Hardy-Weinberg Equilibrium

The Hardy-Weinberg principle describes a hypothetical population that is not evolving. But in real populations, the allele and genotype frequencies often *do* change over time. Such changes can occur when at least one of the following five conditions of Hardy-Weinberg equilibrium is not met:

1. **No mutations.** The gene pool is modified if mutations alter alleles or if entire genes are deleted or duplicated.
2. **Random mating.** If individuals mate preferentially within a subset of the population, such as their close relatives (inbreeding), random mixing of gametes does not occur, and genotype frequencies change.
3. **No natural selection.** Differences in the survival and reproductive success of individuals carrying different genotypes can alter allele frequencies.
4. **Extremely large population size.** The smaller the population, the more likely it is that allele frequencies will fluctuate by chance from one generation to the next (a process called genetic drift).
5. **No gene flow.** By moving alleles into or out of populations, gene flow can alter allele frequencies.

Departure from these conditions usually results in evolutionary change, which, as we've already described, is common in natural populations. But it is also common for natural populations to be in Hardy-Weinberg equilibrium for specific genes. This apparent contradiction occurs because a population can be evolving at some loci, yet simultaneously be in Hardy-Weinberg equilibrium at other loci. In addition, some populations evolve so slowly that the changes in their allele and genotype frequencies are difficult to distinguish from those predicted for a nonevolving population.

### Applying the Hardy-Weinberg Principle

The Hardy-Weinberg equation is often used as an initial test of whether evolution is occurring in a population (you'll encounter an example in Concept Check 23.2, question 3). The equation also has medical applications, such as estimating the percentage of a population carrying the allele for an inherited disease. For example, consider phenylketonuria (PKU), a metabolic disorder that results from homozygosity for a recessive allele and occurs in about one out of every 10,000 babies born in the United States. Left untreated, PKU results in mental disability and other problems. (Newborns are now tested for PKU, and symptoms can be largely avoided with a diet very low in phenylalanine. For this reason, products that contain phenylalanine, such as diet colas, carry warning labels.)

To apply the Hardy-Weinberg equation, we must assume that no new PKU mutations are being introduced into the population (condition 1), and that people neither choose their mates on the basis of whether or not they carry this gene nor generally mate with close relatives (condition 2). We must also ignore any effects of differential survival and reproductive success among PKU genotypes (condition 3) and assume that there are no effects of genetic drift (condition 4) or of gene flow from other populations into the United States (condition 5). These assumptions are reasonable: The mutation rate for the PKU gene is low, inbreeding is not common in the United States, selection occurs only against the rare homozygotes (and then only if dietary restrictions are not followed), the U.S. population is very large, and populations outside the country have PKU allele frequencies similar to those seen in the United States. If all these assumptions hold, then the frequency of individuals in the population born with PKU will correspond to $q^2$ in the Hardy-Weinberg equation ($q^2$ = frequency of homozygotes). Because the allele is recessive, we must estimate the number of heterozygotes rather than counting them directly as we did with the pink flowers. Since we know there is one PKU occurrence per 10,000 births ($q^2$ = 0.0001), the frequency of the recessive allele for PKU is

$$q = \sqrt{0.0001} = 0.01$$

and the frequency of the dominant allele is

$$p = 1 - q = 1 - 0.01 = 0.99$$

The frequency of carriers, heterozygous people who do not have PKU but may pass the PKU allele to offspring, is

$$2pq = 2 \times 0.99 \times 0.01 = 0.0198$$
(approximately 2% of the U.S. population)

Remember, the assumption of Hardy-Weinberg equilibrium yields an approximation; the real number of carriers may differ. Still, our calculations suggest that harmful recessive alleles at this and other loci can be concealed in a population because they are carried by healthy heterozygotes.

### CONCEPT CHECK 23.2

1. Suppose a population of organisms with 20,000 gene loci is fixed at half of these loci and has two alleles at each of the other loci. How many different types of alleles are found in its entire gene pool? Explain.
2. If $p$ is the frequency of allele $A$, use the Hardy-Weinberg equation to predict the frequency of individuals that have at least one $A$ allele.
3. **WHAT IF?** A locus that affects susceptibility to a degenerative brain disease has two alleles, $A$ and $a$. In a population, 16 people have genotype $AA$, 92 have genotype $Aa$, and 12 have genotype $aa$. Is this population evolving? Explain.

For suggested answers, see Appendix A.

## CONCEPT 23.3

# Natural selection, genetic drift, and gene flow can alter allele frequencies in a population

Note again the five conditions required for a population to be in Hardy-Weinberg equilibrium. A deviation from any of these conditions is a potential cause of evolution. New mutations (violation of condition 1) can alter allele frequencies, but because mutations are rare, the change from one generation to the next is likely to be very small. Nevertheless, as we'll see, mutation ultimately can have a large effect on allele frequencies when it produces new alleles that strongly influence fitness in a positive or negative way. Nonrandom mating (violation of condition 2) can affect the frequencies of homozygous and heterozygous genotypes but by itself usually has no effect on allele frequencies in the gene pool. The three mechanisms that alter allele frequencies directly and cause most evolutionary change are natural selection, genetic drift, and gene flow (violations of conditions 3–5).

## Natural Selection

As you read in Chapter 22, Darwin's concept of natural selection is based on differential success in survival and reproduction: Individuals in a population exhibit variations in their heritable traits, and those with traits that are better suited to their environment tend to produce more offspring than those with traits that are not as well suited.

In genetic terms, we now know that selection results in alleles being passed to the next generation in proportions that differ from those in the present generation. For example, the fruit fly *D. melanogaster* has an allele that confers resistance to several insecticides, including DDT. This allele has a frequency of 0% in laboratory strains of *D. melanogaster* established from flies collected in the wild in the early 1930s, prior to DDT use. However, in strains established from flies collected after 1960 (following 20 or more years of DDT use), the allele frequency is 37%. We can infer that this allele either arose by mutation between 1930 and 1960 or that it was present in 1930, but very rare. In any case, the rise in frequency of this allele most likely occurred because DDT is a powerful poison that is a strong selective force in exposed fly populations.

As the *D. melanogaster* example shows, an allele that confers insecticide resistance will increase in frequency in a population exposed to that insecticide. Such changes are not coincidental. By consistently favoring some alleles over others, natural selection can cause *adaptive evolution* (evolution that results in a better match between organisms and their environment). We'll explore this process in more detail a little later in this chapter.

## Genetic Drift

If you flip a coin 1,000 times, a result of 700 heads and 300 tails might make you suspicious about that coin. But if you flip a coin only 10 times, an outcome of 7 heads and 3 tails would not be surprising. The smaller the number of coin flips, the more likely it is that chance alone will cause a deviation from the predicted result. (In this case, the prediction is an equal number of heads and tails.) Chance events can also cause allele frequencies to fluctuate unpredictably from one generation to the next, especially in small populations—a process called **genetic drift**.

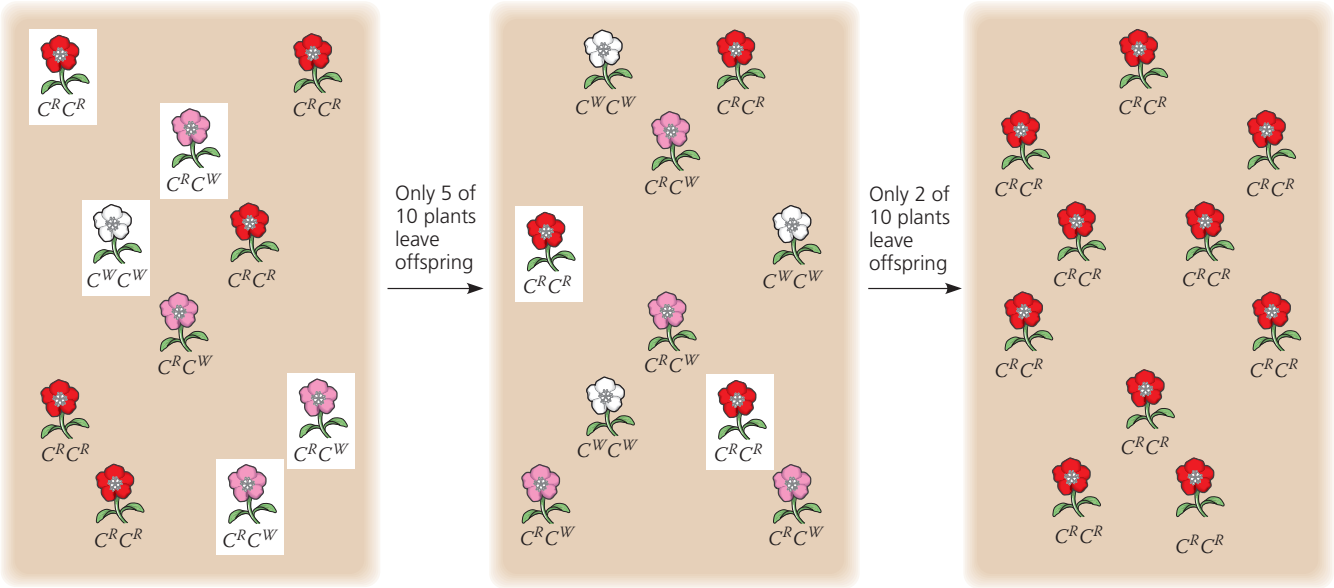
**Figure 23.9** models how genetic drift might affect a small population of our wildflowers. In this example, an allele is lost from the gene pool, but it is a matter of chance that the $C^W$ allele is lost and not the $C^R$ allele. Such unpredictable changes in allele frequencies can be caused by chance events associated with survival and reproduction. Perhaps a large animal such as a moose stepped on the three $C^WC^W$ individuals in generation 2, killing them and increasing the chance that only the $C^R$ allele would be passed to the next generation. Allele frequencies can also be affected by chance events that occur during fertilization. For example, suppose two individuals of genotype $C^RC^W$ had a small number of offspring. By chance alone, every egg and sperm pair that generated offspring could happen to have carried the $C^R$ allele and not the $C^W$ allele.

Certain circumstances can result in genetic drift having a significant impact on a population. Two examples are the founder effect and the bottleneck effect.

### *The Founder Effect*

When a few individuals become isolated from a larger population, this smaller group may establish a new population whose gene pool differs from the source population; this is called the **founder effect**. The founder effect might occur, for example, when a few members of a population are blown by a storm to a new island. Genetic drift, in which chance events alter allele frequencies, will occur in such a case if the storm indiscriminately transports some individuals (and their alleles), but not others, from the source population.

The founder effect probably accounts for the relatively high frequency of certain inherited disorders among isolated human populations. For example, in 1814, 15 British colonists founded a settlement on Tristan da Cunha, a group of small islands in the Atlantic Ocean midway between Africa and South America. Apparently, one of the colonists carried a recessive allele for retinitis pigmentosa, a progressive form of blindness that afflicts homozygous individuals. Of the founding colonists' 240 descendants on the island in the late 1960s, 4 had retinitis pigmentosa. The frequency of the allele that causes this disease is ten times




▲ **Figure 23.9 Genetic drift.** This small wildflower population has a stable size of ten plants. Suppose that by chance only five plants of generation 1 (those in white boxes) produce fertile offspring. (This could occur, for example, if only those plants happened to grow in a location that provided enough nutrients to support the production of offspring.) Again by chance, only two plants of generation 2 leave fertile offspring. As a result, by chance the frequency of the $C^W$ allele first increases in generation 2, then falls to zero in generation 3.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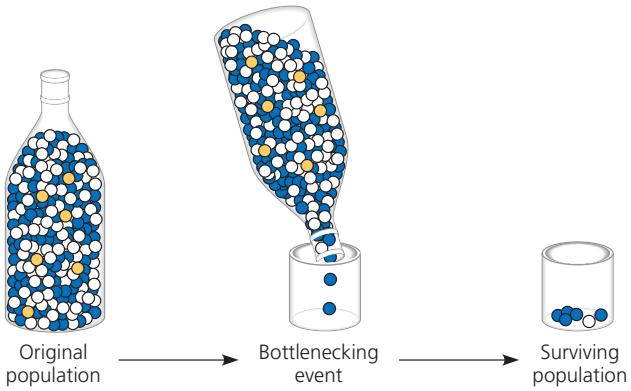



▲ **Figure 23.10 The bottleneck effect.** Shaking just a few marbles through the narrow neck of a bottle is analogous to a drastic reduction in the size of a population. By chance, blue marbles are overrepresented in the surviving population and gold marbles are absent.

higher on Tristan da Cunha than in the populations from which the founders came.

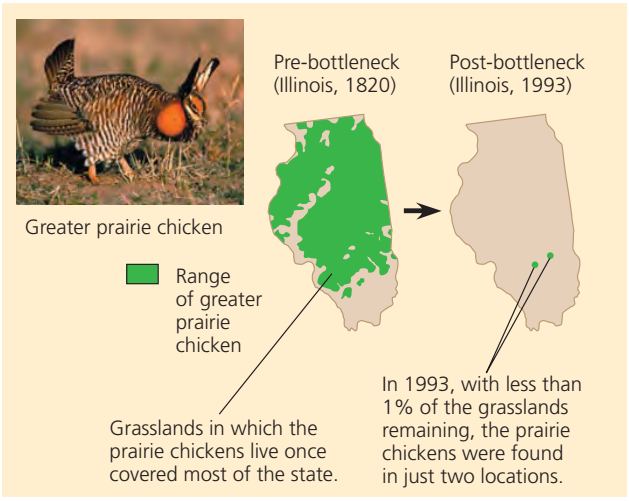
### *The Bottleneck Effect*

A sudden change in the environment, such as a fire or flood, may drastically reduce the size of a population. A severe drop in population size can cause the **bottleneck effect**, so named because the population has passed through a "bottleneck" that reduces its size **(Figure 23.10)**. By chance alone, certain alleles may be overrepresented among the survivors, others may be underrepresented, and some may be absent altogether. Ongoing genetic drift is likely to have substantial effects on the gene pool until the population becomes large enough that chance events have less impact. But even if a population that has passed through a bottleneck ultimately recovers in size, it may have low levels of genetic variation for a long period of time—a legacy of the genetic drift that occurred when the population was small.

One reason it is important to understand the bottleneck effect is that human actions sometimes create severe bottlenecks for other species, as the following example shows.

### Case Study: *Impact of Genetic Drift on the Greater Prairie Chicken*

Millions of greater prairie chickens (*Tympanuchus cupido*) once lived on the prairies of Illinois. As these prairies were converted to farmland and other uses during the 19th and 20th centuries, the number of greater prairie chickens plummeted **(Figure 23.11a)**. By 1993, only two Illinois populations remained, which together harbored fewer than 50 birds. The few surviving birds had low levels of genetic variation, and less than 50% of their eggs hatched, compared with much higher hatching rates of the larger populations in Kansas and Nebraska **(Figure 23.11b)**.




**(a)** The Illinois population of greater prairie chickens dropped from millions of birds in the 1800s to fewer than 50 birds in 1993.

| Location | Population size | Number of alleles per locus | Percentage of eggs hatched |
|---|---|---|---|
| Illinois | | | |
| 1930–1960s | 1,000–25,000 | 5.2 | 93 |
| 1993 | <50 | 3.7 | <50 |
| Kansas, 1998 (no bottleneck) | 750,000 | 5.8 | 99 |
| Nebraska, 1998 (no bottleneck) | 75,000–200,000 | 5.8 | 96 |

**(b)** As a consequence of the drastic reduction in the size of the Illinois population, genetic drift resulted in a drop in the number of alleles per locus (averaged across six loci studied) and a decrease in the percentage of eggs that hatched.

▲ **Figure 23.11 Genetic drift and loss of genetic variation.**

These data suggest that genetic drift during the bottleneck may have led to a loss of genetic variation and an increase in the frequency of harmful alleles. To investigate this hypothesis, Juan Bouzat, of Bowling Green State University, Ohio, and his colleagues extracted DNA from 15 museum specimens of Illinois greater prairie chickens. Of the 15 birds, 10 had been collected in the 1930s, when there were 25,000 greater prairie chickens in Illinois, and 5 had been collected in the 1960s, when there were 1,000 greater prairie chickens in Illinois. By studying the DNA of these specimens, the researchers were able to obtain a minimum, baseline estimate of how much genetic variation was present in the Illinois population *before* the population shrank to extremely low numbers. This baseline estimate is a key piece of information that is not usually available in cases of population bottlenecks.

The researchers surveyed six loci and found that the 1993 Illinois greater prairie chicken population had lost nine alleles that were present in the museum specimens. The 1993 population also had fewer alleles per locus than the pre-bottleneck Illinois or the current Kansas and Nebraska populations (see Figure 23.11b). Thus, as predicted, drift had reduced the genetic variation of the small 1993 population. Drift may also have increased the frequency of harmful alleles, leading to the low egg-hatching rate. To counteract these negative effects, 271 birds from neighboring states were added to the Illinois population over four years. This strategy succeeded: New alleles entered the population, and the egg-hatching rate improved to over 90%. Overall, studies on the Illinois greater prairie chicken illustrate the powerful effects of genetic drift in small populations and provide hope that in at least some populations, these effects can be reversed.

### *Effects of Genetic Drift:* A Summary

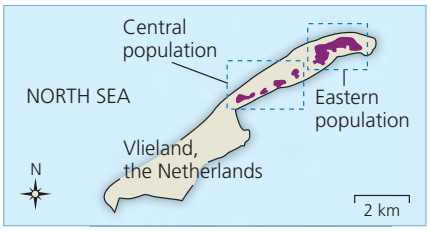
The examples we've described highlight four key points:

1. **Genetic drift is significant in small populations.** Chance events can cause an allele to be disproportionately over- or underrepresented in the next generation. Although chance events occur in populations of all sizes, they tend to alter allele frequencies substantially only in small populations.
2. **Genetic drift can cause allele frequencies to change at random.** Because of genetic drift, an allele may increase in frequency one year, then decrease the next; the change from year to year is not predictable. Thus, unlike natural selection, which in a given environment consistently favors some alleles over others, genetic drift causes allele frequencies to change at random over time.
3. **Genetic drift can lead to a loss of genetic variation within populations.** By causing allele frequencies to fluctuate randomly over time, genetic drift can eliminate alleles from a population. Because evolution depends on genetic variation, such losses can influence how effectively a population can adapt to a change in the environment.
4. **Genetic drift can cause harmful alleles to become fixed.** Alleles that are neither harmful nor beneficial can be lost or become fixed entirely by chance through genetic drift. In very small populations, genetic drift can also cause alleles that are slightly harmful to become fixed. When this occurs, the population's survival can be threatened (as for the greater prairie chicken).

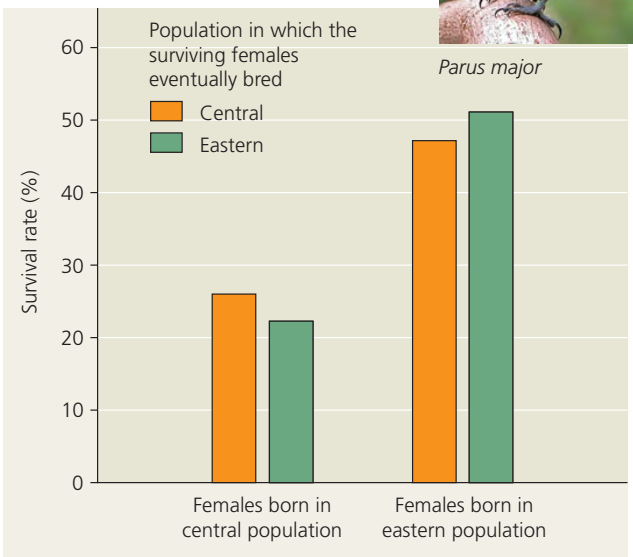
## Gene Flow

Natural selection and genetic drift are not the only phenomena affecting allele frequencies. Allele frequencies can also change by **gene flow**, the transfer of alleles into or out of a population due to the movement of fertile individuals or their gametes. For example, suppose that near our original hypothetical wildflower population there is another population consisting primarily of white-flowered individuals ($C^WC^W$). Insects carrying pollen from these plants may fly to and pollinate plants in our original population. The introduced $C^W$ alleles would modify our original population's allele frequencies in the next generation. Because alleles are exchanged between populations, gene flow tends to reduce the genetic differences between populations. In fact, if it is extensive enough, gene flow can result in two populations combining into a single population with a common gene pool.

Alleles transferred by gene flow can also affect how well populations are adapted to local environmental conditions. Researchers studying the songbird *Parus major* (great tit) on the small Dutch island of Vlieland noted survival differences between two populations on the island. Females born in the eastern population survive twice as well as females born in the central population, regardless of where the females eventually settle and raise offspring **(Figure 23.12)**. This finding suggests that females born in the eastern population are better adapted to life on the island than females born in the




*Parus major*




**▲ Figure 23.12 Gene flow and local adaptation.** In *Parus major* populations on Vlieland, the yearly survival rate of females born in the eastern population is higher than that of females born in the central population. Gene flow from the mainland to the central population is 3.3 times higher than it is to the eastern population, and birds from the mainland are selected against in both populations. These data suggest that gene flow from the mainland has prevented the central population from adapting fully to its local conditions.

central population. But extensive field studies also showed that the two populations are connected by high levels of gene flow (mating), which should reduce genetic differences between them. So how can the eastern population be better adapted to life on Vlieland than the central population? The answer lies in the unequal amounts of gene flow from the mainland. In any given year, 43% of the first-time breeders in the central population are immigrants from the mainland, compared with only 13% in the eastern population. Birds with mainland genotypes survive and reproduce poorly on Vlieland, and in the eastern population, selection reduces the frequency of these genotypes. In the central population, however, gene flow from the mainland is so high that it overwhelms the effects of selection. As a result, females born in the central population have many immigrant genes, reducing the degree to which members of that population are adapted to life on the island. Researchers are currently investigating why gene flow is so much higher in the central population and why birds with mainland genotypes have low fitness on Vlieland.

Gene flow can also transfer alleles that improve the ability of populations to adapt to local conditions. For example, gene flow has resulted in the worldwide spread of several insecticide-resistance alleles in the mosquito *Culex pipiens*, a vector of West Nile virus and other diseases. Each of these alleles has a unique genetic signature that allowed researchers to document that it arose by mutation in one or a few geographic locations. In their population of origin, these alleles increased because they provided insecticide resistance. These alleles were then transferred to new populations, where again, their frequencies increased as a result of natural selection.

Finally, gene flow has become an increasingly important agent of evolutionary change in human populations. Humans today move much more freely about the world than in the past. As a result, mating is more common between members of populations that previously had very little contact, leading to an exchange of alleles and fewer genetic differences between those populations.

### CONCEPT CHECK 23.3

1. In what sense is natural selection more "predictable" than genetic drift?
2. Distinguish genetic drift from gene flow in terms of (a) how they occur and (b) their implications for future genetic variation in a population.
3. **WHAT IF?** Suppose two plant populations exchange pollen and seeds. In one population, individuals of genotype *AA* are most common (9,000 *AA*, 900 *Aa*, 100 *aa*), while the opposite is true in the other population (100 *AA*, 900 *Aa*, 9,000 *aa*). If neither allele has a selective advantage, what will happen over time to the allele and genotype frequencies of these populations?

For suggested answers, see Appendix A.

## CONCEPT 23.4

# Natural selection is the only mechanism that consistently causes adaptive evolution

Evolution by natural selection is a blend of chance and "sorting": chance in the creation of new genetic variations (as in mutation) and sorting as natural selection favors some alleles over others. Because of this favoring process, the outcome of natural selection is *not* random. Instead, natural selection consistently increases the frequencies of alleles that provide reproductive advantage and thus leads to adaptive evolution.

## A Closer Look at Natural Selection

In examining how natural selection brings about adaptive evolution, we'll begin with the concept of relative fitness and the different ways that an organism's phenotype is subject to natural selection.

### *Relative Fitness*

The phrases "struggle for existence" and "survival of the fittest" are commonly used to describe natural selection, but these expressions are misleading if taken to mean direct competitive contests among individuals. There *are* animal species in which individuals, usually the males, lock horns or otherwise do combat to determine mating privilege. But reproductive success is generally more subtle and depends on many factors besides outright battle. For example, a barnacle that is more efficient at collecting food than its neighbors may have greater stores of energy and hence be able to produce a larger number of eggs. A moth may have more offspring than other moths in the same population because its body colors more effectively conceal it from predators, improving its chance of surviving long enough to produce more offspring. These examples illustrate how in a given environment, certain traits can lead to greater **relative fitness**: the contribution an individual makes to the gene pool of the next generation *relative to* the contributions of other individuals.

Although we often refer to the relative fitness of a genotype, remember that the entity that is subjected to natural selection is the whole organism, not the underlying genotype. Thus, selection acts more directly on the phenotype than on the genotype; it acts on the genotype indirectly, via how the genotype affects the phenotype.

### *Directional, Disruptive, and Stabilizing Selection*

Natural selection can alter the frequency distribution of heritable traits in three ways, depending on which phenotypes in a population are favored. These three modes of selection are

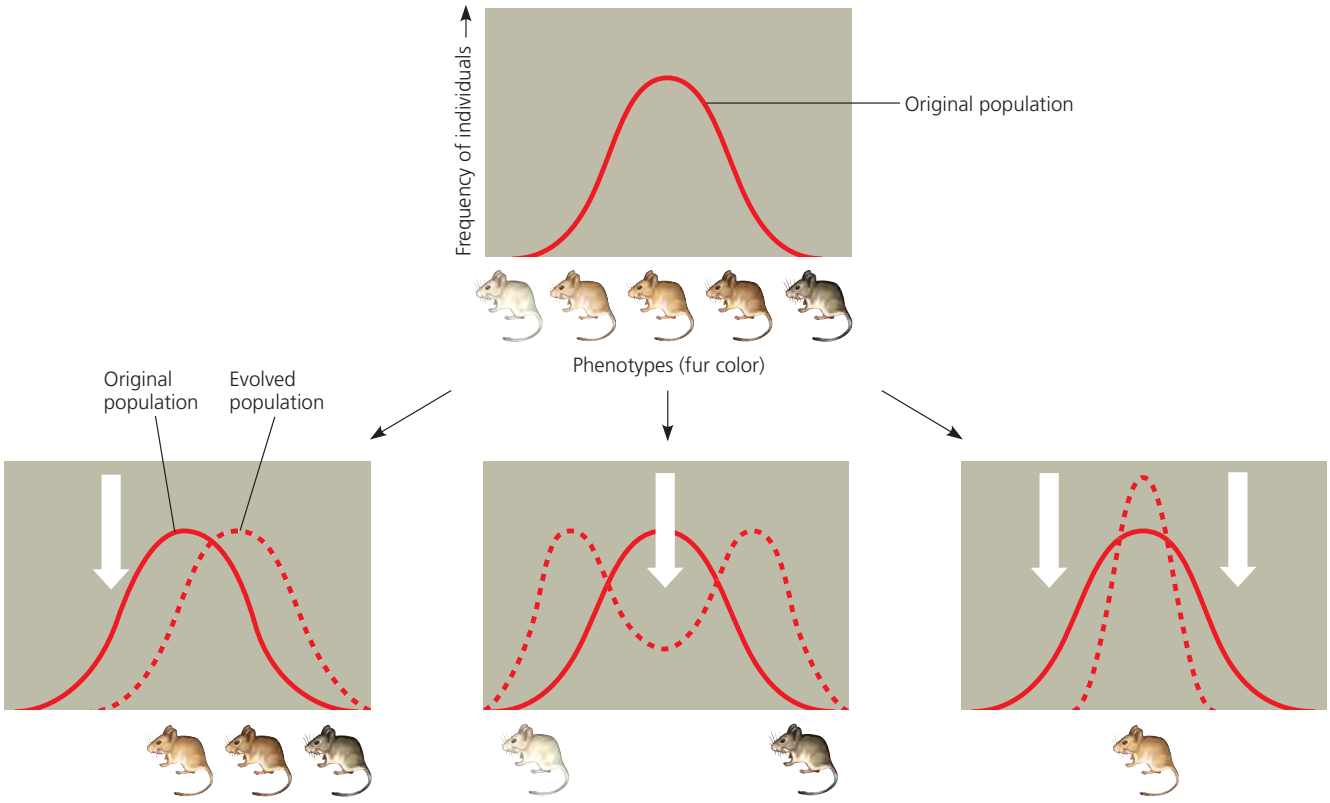
called directional selection, disruptive selection, and stabilizing selection.

**Directional selection** occurs when conditions favor individuals exhibiting one extreme of a phenotypic range, thereby shifting a population's frequency curve for the phenotypic character in one direction or the other **(Figure 23.13a)**. Directional selection is common when a population's environment changes or when members of a population migrate to a new (and different) habitat. For instance, an increase in the relative abundance of large seeds over small seeds led to an increase in beak depth in a population of Galápagos finches (see Figure 23.2).

**Disruptive selection** **(Figure 23.13b)** occurs when conditions favor individuals at both extremes of a phenotypic range over individuals with intermediate phenotypes. One example is a population of black-bellied seedcracker finches in Cameroon whose members display two distinctly different beak sizes. Small-billed birds feed mainly on soft seeds, whereas large-billed birds specialize in cracking hard seeds. It appears that birds with intermediate-sized bills are relatively inefficient at cracking both types of seeds and thus have lower relative fitness.

**Stabilizing selection** **(Figure 23.13c)** acts against both extreme phenotypes and favors intermediate variants. This mode of selection reduces variation and tends to maintain the status quo for a particular phenotypic character. For example, the birth weights of most human babies lie in the range of 3–4 kg (6.6–8.8 pounds); babies who are either much smaller or much larger suffer higher rates of mortality.

Regardless of the mode of selection, however, the basic mechanism remains the same. Selection favors individuals whose heritable phenotypic traits provide higher reproductive success than do the traits of other individuals.




**(a) Directional selection** shifts the overall makeup of the population by favoring variants that are at one extreme of the distribution. In this case, lighter mice are selected against because they live among dark rocks, making it harder for them to hide from predators.

**(b) Disruptive selection** favors variants at both ends of the distribution. These mice have colonized a patchy habitat made up of light and dark rocks, with the result that mice of an intermediate color are selected against.

**(c) Stabilizing selection** removes extreme variants from the population and preserves intermediate types. If the environment consists of rocks of an intermediate color, both light and dark mice will be selected against.

▲ **Figure 23.13 Modes of selection.** These cases describe three ways in which a hypothetical deer mouse population with heritable variation in fur coloration from light to dark might evolve. The graphs show how the frequencies of individuals with different fur colors change over time. The large white arrows symbolize selective pressures against certain phenotypes.

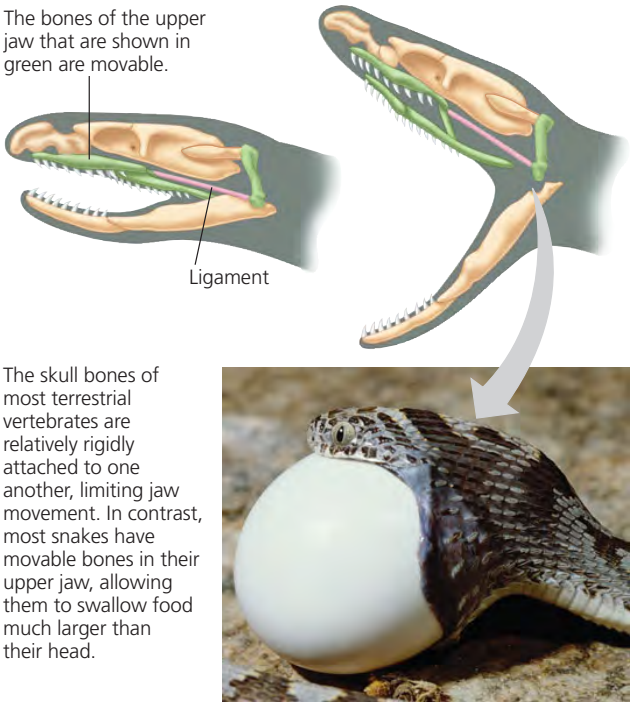
**MAKE CONNECTIONS** *Review Figure 22.13 on p. 461. Which mode of selection has occurred in soapberry bug populations that feed on the introduced goldenrain tree? Explain.*

## The Key Role of Natural Selection in Adaptive Evolution

The adaptations of organisms include many striking examples. Cuttlefish, for example, have the ability to change color rapidly, enabling them to blend into different backgrounds. Another example is the remarkable jaws of snakes **(Figure 23.14)**, which allow them to swallow prey much larger than their own head (a feat analogous to a person swallowing a whole watermelon). Other adaptations, such as a version of an enzyme that shows improved function in cold environments (see Figure 23.5), may be less visually dramatic but just as important for survival and reproduction.

Such adaptations can arise gradually over time as natural selection increases the frequencies of alleles that enhance survival and reproduction. As the proportion of individuals that have favorable traits increases, the match between a species and its environment improves; that is, adaptive evolution occurs. However, as we saw in Chapter 22, the physical and biological components of an organism's environment may change over time. As a result, what constitutes a "good match" between an organism and its environment can be a moving target, making adaptive evolution a continuous, dynamic process.

And what about the two other important mechanisms of evolutionary change in populations, genetic drift and gene flow? Both can, in fact, increase the frequencies of alleles that improve the match between organisms and their environment, but neither does so consistently. Genetic drift can cause the frequency of a slightly beneficial allele to increase, but it also can cause the frequency of such an allele to decrease. Similarly, gene flow may introduce alleles that are advantageous or ones that are disadvantageous. Natural selection is the only evolutionary mechanism that consistently leads to adaptive evolution.




▲ **Figure 23.14 Movable jaw bones in snakes.**

## Sexual Selection

Charles Darwin was the first to explore the implications of **sexual selection**, a form of selection in which individuals with certain inherited characteristics are more likely than other individuals to obtain mates. Sexual selection can result in **sexual dimorphism**, a difference between the two sexes in secondary sexual characteristics **(Figure 23.15)**. These distinctions include differences in size, color, ornamentation, and behavior.

How does sexual selection operate? There are several ways. In **intrasexual selection**, meaning selection within the same sex, individuals of one sex compete directly for mates of the opposite sex. In many species, intrasexual selection occurs among males. For example, a single male may patrol a group of females and prevent other males from mating with them. The patrolling male may defend his status by defeating smaller, weaker, or less fierce males in combat. More often, this male is the psychological victor in ritualized displays that discourage would-be competitors but do not risk injury that would reduce his own fitness (see Figure 51.17). Intrasexual selection has also been observed among females in a variety of species, including ring-tailed lemurs and broad-nosed pipefish.

In **intersexual selection**, also called *mate choice*, individuals of one sex (usually the females) are choosy in selecting

▲ **Figure 23.15 Sexual dimorphism and sexual selection.** Peacocks (above left) and peahens (above right) show extreme sexual dimorphism. There is intrasexual selection between competing males, followed by intersexual selection when the females choose among the showiest males.

their mates from the other sex. In many cases, the female's choice depends on the showiness of the male's appearance or behavior (see Figure 23.15). What intrigued Darwin about mate choice is that male showiness may not seem adaptive in any other way and may in fact pose some risk. For example, bright plumage may make male birds more visible to predators. But if such characteristics help a male gain a mate, and if this benefit outweighs the risk from predation, then both the bright plumage and the female preference for it will be reinforced because they enhance overall reproductive success.

How do female preferences for certain male characteristics evolve in the first place? One hypothesis is that females prefer male traits that are correlated with "good genes." If the trait preferred by females is indicative of a male's overall genetic quality, both the male trait and female preference for it should increase in frequency. **Figure 23.16** describes one experiment testing this hypothesis in gray tree frogs (*Hyla versicolor*).

Other researchers have shown that in several bird species, the traits preferred by females are related to overall male health. Here, too, female preference appears to be based on traits that reflect "good genes," in this case alleles indicative of a robust immune system.

## The Preservation of Genetic Variation

Some of the genetic variation in populations represents **neutral variation**, differences in DNA sequence that do not confer a selective advantage or disadvantage. But variation is also found at loci affected by selection. What prevents natural selection from reducing genetic variation at those loci by culling all unfavorable alleles? The tendency for directional and stabilizing selection to reduce variation is countered by mechanisms that preserve or restore it.

### *Diploidy*

In diploid eukaryotes, a considerable amount of genetic variation is hidden from selection in the form of recessive alleles. Recessive alleles that are less favorable than their dominant counterparts, or even harmful in the current environment, can persist by propagation in heterozygous individuals. This latent variation is exposed to natural selection only when both parents carry the same recessive allele and two copies end up in the same zygote. This happens only rarely if the frequency of the recessive allele is very low. Heterozygote protection maintains a huge pool of alleles that might not be favored under present conditions, but which could bring new benefits if the environment changes.

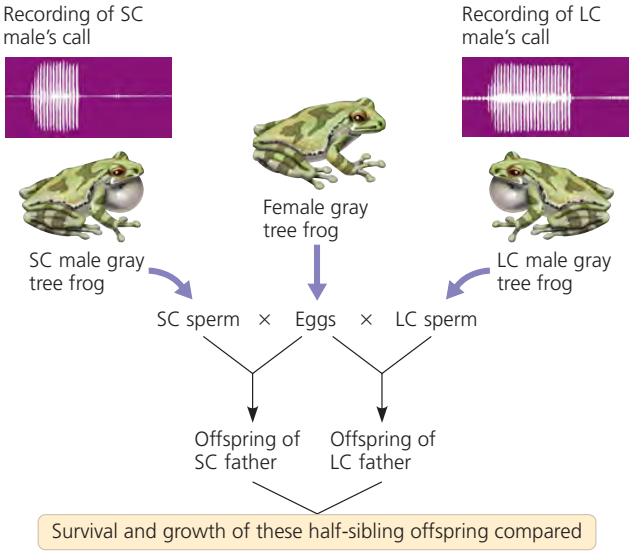
### *Balancing Selection*

Selection itself may preserve variation at some loci. **Balancing selection** occurs when natural selection maintains two or

**▼ Figure 23.16** **INQUIRY**

**Do females select mates based on traits indicative of "good genes"?**

**EXPERIMENT** Female gray tree frogs (*Hyla versicolor*) prefer to mate with males that give long mating calls. Allison Welch and colleagues, at the University of Missouri, tested whether the genetic makeup of long-calling (LC) males is superior to that of short-calling (SC) males. The researchers fertilized half the eggs of each female with sperm from an LC male and fertilized the remaining eggs with sperm from an SC male. The resulting half-sibling offspring were raised in a common environment, and several measures of their "performance" were tracked for two years.




**RESULTS**

| Offspring Performance | 1995 | 1996 |
|---|---|---|
| Larval survival | LC better | NSD |
| Larval growth | NSD | LC better |
| Time to metamorphosis | LC better (shorter) | LC better (shorter) |

NSD = no significant difference; LC better = offspring of LC males superior to offspring of SC males.

**CONCLUSION** Because offspring fathered by an LC male outperformed their half-siblings fathered by an SC male, the team concluded that the duration of a male's mating call is indicative of the male's overall genetic quality. This result supports the hypothesis that female mate choice can be based on a trait that indicates whether the male has "good genes."

**SOURCE** A. M. Welch et al., Call duration as an indicator of genetic quality in male gray tree frogs, *Science* 280:1928–1930 (1998).

**INQUIRY IN ACTION** Read and analyze the original paper in *Inquiry in Action: Interpreting Scientific Papers*.

**WHAT IF?** Why did the researchers split each female frog's eggs into two batches for fertilization by different males? Why didn't they mate each female with a single male frog?

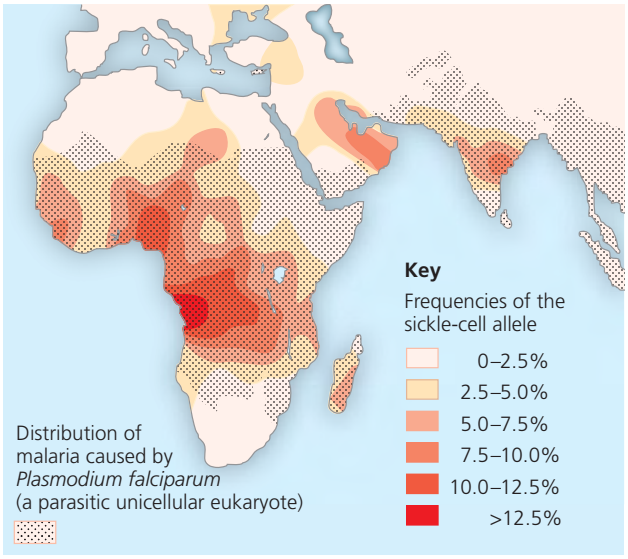
more forms in a population. This type of selection includes heterozygote advantage and frequency-dependent selection.

**Heterozygote Advantage** If individuals who are heterozygous at a particular locus have greater fitness than do both kinds of homozygotes, they exhibit **heterozygote advantage**. In such a case, natural selection tends to maintain two or more alleles at that locus. Note that heterozygote advantage is defined in terms of *genotype*, not phenotype. Thus, whether heterozygote advantage represents stabilizing or directional selection depends on the relationship between the genotype and the phenotype. For example, if the phenotype of a heterozygote is intermediate to the phenotypes of both homozygotes, heterozygote advantage is a form of stabilizing selection.

An example of heterozygote advantage occurs at the locus in humans that codes for the β polypeptide subunit of hemoglobin, the oxygen-carrying protein of red blood cells. In homozygous individuals, a certain recessive allele at that locus causes sickle-cell disease. The red blood cells of people with sickle-cell disease become distorted in shape, or *sickled*, under low-oxygen conditions (see Figure 5.21), as occurs in the capillaries. These sickled cells can clump together and block the flow of blood in the capillaries, resulting in serious damage to organs such as the kidney, heart, and brain. Although some red blood cells become sickled in heterozygotes, not enough become sickled to cause sickle-cell disease.

Heterozygotes for the sickle-cell allele are protected against the most severe effects of malaria, a disease caused by a parasite that infects red blood cells (see Figure 28.10). This partial protection occurs because the body destroys sickled red blood cells rapidly, killing the parasites they harbor (but not affecting parasites inside normal red blood cells). Protection against malaria is important in tropical regions where the disease is a major killer. In such regions, selection favors heterozygotes over homozygous dominant individuals, who are more vulnerable to the effects of malaria, and also over homozygous recessive individuals, who develop sickle-cell disease. The frequency of the sickle-cell allele in Africa is generally highest in areas where the malaria parasite is most common (**Figure 23.17**). In some populations, it accounts for 20% of the hemoglobin alleles in the gene pool, a very high frequency for such a harmful allele.

**Frequency-Dependent Selection** In **frequency-dependent selection**, the fitness of a phenotype depends on how common it is in the population. Consider the scale-eating fish (*Perissodus microlepis*) of Lake Tanganyika, in Africa. These fish attack other fish from behind, darting in to remove a few scales from the flank of their prey. Of interest here is a peculiar feature of the scale-eating fish: Some are "left-mouthed" and some are "right-mouthed." Simple Mendelian inheritance determines these phenotypes, with the right-mouthed allele being dominant to the left-mouthed allele. Because their mouth twists to the left, left-mouthed fish always attack their prey's right flank **(Figure 23.18)**. (To see why, twist your lower jaw and lips to the left and imagine trying to take a bite from the left side of a fish, approaching it from behind.) Similarly, right-mouthed fish always attack from the left. Prey species guard against attack from whatever phenotype of scale-eating fish is most common in the lake. Thus, from year to year, selection favors whichever mouth phenotype is least common. As a result, the frequency of left- and right-mouthed fish oscillates over time, and balancing selection (due to frequency dependence) keeps the frequency of each phenotype close to 50%.

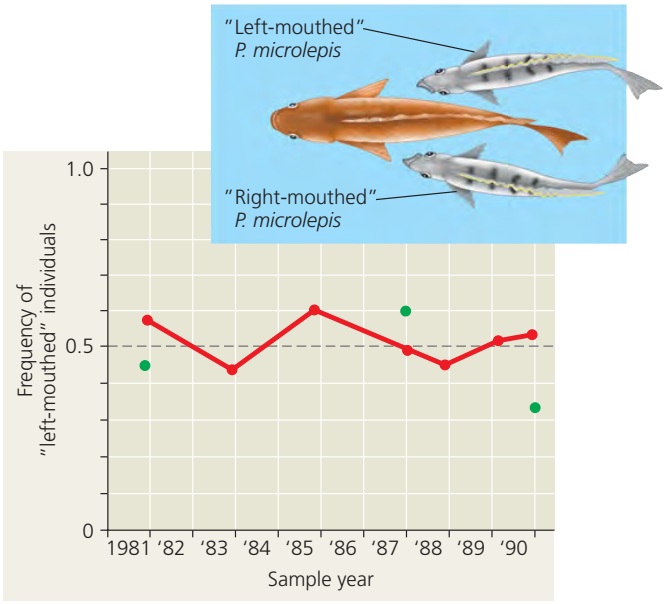



**▲ Figure 23.17 Mapping malaria and the sickle-cell allele.** The sickle-cell allele is most common in Africa, but it is not the only case of heterozygote advantage providing protection against malaria. Alleles at other loci (not shown on this map) are also favored by heterozygote advantage in populations near the Mediterranean Sea and in southeast Asia where malaria is widespread.

## Why Natural Selection Cannot Fashion Perfect Organisms

Though natural selection leads to adaptation, nature abounds with examples of organisms that are less than ideally "engineered" for their lifestyles. There are several reasons why.

1. **Selection can act only on existing variations.** Natural selection favors only the fittest phenotypes among those currently in the population, which may not be the ideal traits. New advantageous alleles do not arise on demand.
2. **Evolution is limited by historical constraints.** Each species has a legacy of descent with modification from ancestral forms. Evolution does not scrap the




**▲ Figure 23.18 Frequency-dependent selection in scale-eating fish (*Perissodus microlepis*).** Michio Hori, of Kyoto University, Japan, noted that the frequency of left-mouthed individuals rises and falls in a regular manner. At each of three time periods when the phenotypes of breeding adults were assessed, adults that reproduced (represented by green dots) had the opposite phenotype of that which was most common in the population. Thus, it appeared that right-mouthed individuals were favored by selection when left-mouthed individuals were more common, and vice versa.

**?** *What did the researchers measure to determine which phenotype was favored by selection? Are any assumptions implied by this choice? Explain.*

ancestral anatomy and build each new complex structure from scratch; rather, evolution co-opts existing structures and adapts them to new situations. We could imagine that if a terrestrial animal were to adapt to an environment in which flight would be advantageous, it might be best just to grow an extra pair of limbs that would serve as wings. However, evolution does not work this way; instead, it operates on the traits an organism already has. Thus, in birds and bats, an existing pair of limbs took on new functions for flight as these organisms evolved from nonflying ancestors.

3. **Adaptations are often compromises.** Each organism must do many different things. A seal spends part of its time on rocks; it could probably walk better if it had legs instead of flippers, but then it would not swim nearly as well. We humans owe much of our versatility and athleticism to our prehensile hands and flexible limbs, but these also make us prone to sprains, torn ligaments, and dislocations: Structural reinforcement has been compromised for agility. **Figure 23.19** depicts another example of evolutionary compromise.

**▲ Figure 23.19 Evolutionary compromise.** The loud call that enables a Túngara frog to attract mates also attracts more dangerous characters in the neighborhood—in this case, a bat about to seize a meal.

4. **Chance, natural selection, and the environment interact.** Chance events can affect the subsequent evolutionary history of populations. For instance, when a storm blows insects or birds hundreds of kilometers over an ocean to an island, the wind does not necessarily transport those individuals that are best suited to the new environment. Thus, not all alleles present in the founding population's gene pool are better suited to the new environment than the alleles that are "left behind." In addition, the environment at a particular location may change unpredictably from year to year, again limiting the extent to which adaptive evolution results in a close match between the organism and current environmental conditions.

With these four constraints, evolution does not tend to craft perfect organisms. Natural selection operates on a "better than" basis. We can, in fact, see evidence for evolution in the many imperfections of the organisms it produces.

## CONCEPT CHECK 23.4

1. What is the relative fitness of a sterile mule? Explain.
2. Explain why natural selection is the only evolutionary mechanism that consistently leads to adaptive evolution.
3. **WHAT IF?** Consider a population in which heterozygotes at a certain locus have an extreme phenotype (such as being larger than homozygotes) that confers a selective advantage. Does such a situation represent directional, disruptive, or stabilizing selection? Explain your answer.
4. **WHAT IF?** Would individuals who are heterozygous for the sickle-cell allele be selected for or against in a region free from malaria? Explain.

For suggested answers, see Appendix A.

# 23 CHAPTER REVIEW

## SUMMARY OF KEY CONCEPTS

### CONCEPT 23.1

**Genetic variation makes evolution possible (pp. 469–473)**

- **Genetic variation** refers to genetic differences among individuals within a population.
- The nucleotide differences that provide the basis of genetic variation arise by mutation and other processes that produce new alleles and new genes.
- New genetic variants are produced rapidly in organisms with short generation times. In sexually reproducing organisms, most of the genetic differences among individuals result from crossing over, the independent assortment of chromosomes, and fertilization.

? *Why do biologists estimate gene variability and nucleotide variability, and what do these estimates represent?*

### CONCEPT 23.2

**The Hardy-Weinberg equation can be used to test whether a population is evolving (pp. 473–476)**

- A **population**, a localized group of organisms belonging to one species, is united by its **gene pool**, the aggregate of all the alleles in the population.
- The **Hardy-Weinberg principle** states that the allele and genotype frequencies of a population will remain constant if the population is large, mating is random, mutation is negligible, there is no gene flow, and there is no natural selection. For such a population, if $p$ and $q$ represent the frequencies of the only two possible alleles at a particular locus, then $p^2$ is the frequency of one kind of homozygote, $q^2$ is the frequency of the other kind of homozygote, and $2pq$ is the frequency of the heterozygous genotype.

? *Is it circular reasoning to calculate* p *and* q *from observed genotype frequencies and then use those values of* p *and* q *to test if the population is in Hardy-Weinberg equilibrium? Explain your answer. (Hint: Consider a specific case, such as a population with 195 individuals of genotype* AA*, 10 of genotype* Aa*, and 195 of genotype* aa*.)*

### CONCEPT 23.3

**Natural selection, genetic drift, and gene flow can alter allele frequencies in a population (pp. 476–480)**

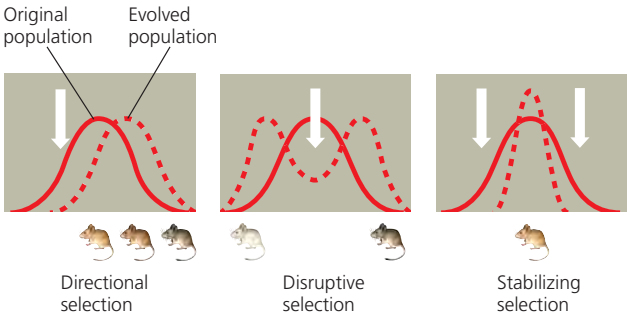
- In natural selection, individuals that have certain inherited traits tend to survive and reproduce at higher rates than other individuals *because of* those traits.
- In **genetic drift**, chance fluctuations in allele frequencies over generations tend to reduce genetic variation.
- **Gene flow**, the transfer of alleles between populations, tends to reduce genetic differences between populations over time.

? *Would two small, geographically isolated populations in very different environments be likely to evolve in similar ways? Explain.*

### CONCEPT 23.4

**Natural selection is the only mechanism that consistently causes adaptive evolution (pp. 480–485)**

- One organism has greater **relative fitness** than a second organism if it leaves more fertile descendants than the second organism. The modes of natural selection differ in how selection acts on phenotype (the white arrows in the summary diagram below represent selective pressure on a population).




- Unlike genetic drift and gene flow, natural selection consistently increases the frequencies of alleles that enhance survival and reproduction, thus improving the match between organisms and their environment.
- **Sexual selection** influences evolutionary change in secondary sex characteristics that can give individuals advantages in mating.
- Despite the winnowing effects of selection, populations have considerable genetic variation. Some of this variation represents **neutral variation**; additional variation can be maintained by diploidy and balancing selection.
- There are constraints to evolution: Natural selection can act only on available variation; structures result from modified ancestral anatomy; adaptations are often compromises; and chance, natural selection, and the environment interact.

? *How might secondary sex characteristics differ between males and females in a species in which females compete for mates?*

## TEST YOUR UNDERSTANDING

### LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Natural selection changes allele frequencies because some _____ survive and reproduce more successfully than others.
   a. alleles  c. gene pools  e. individuals
   b. loci  d. species

2. No two people are genetically identical, except for identical twins. The main source of genetic variation among human individuals is
   a. new mutations that occurred in the preceding generation.
   b. genetic drift due to the small size of the population.
   c. the reshuffling of alleles in sexual reproduction.
   d. geographic variation within the population.
   e. environmental effects.

3. Sparrows with average-sized wings survive severe storms better than those with longer or shorter wings, illustrating
   a. the bottleneck effect.
   b. disruptive selection.
   c. frequency-dependent selection.
   d. neutral variation.
   e. stabilizing selection.

## LEVEL 2: APPLICATION/ANALYSIS

4. If the nucleotide variability of a locus equals 0%, what is the gene variability and number of alleles at that locus?
   a. gene variability = 0%; number of alleles = 0
   b. gene variability = 0%; number of alleles = 1
   c. gene variability = 0%; number of alleles = 2
   d. gene variability > 0%; number of alleles = 2
   e. Without more information, gene variability and number of alleles cannot be determined.

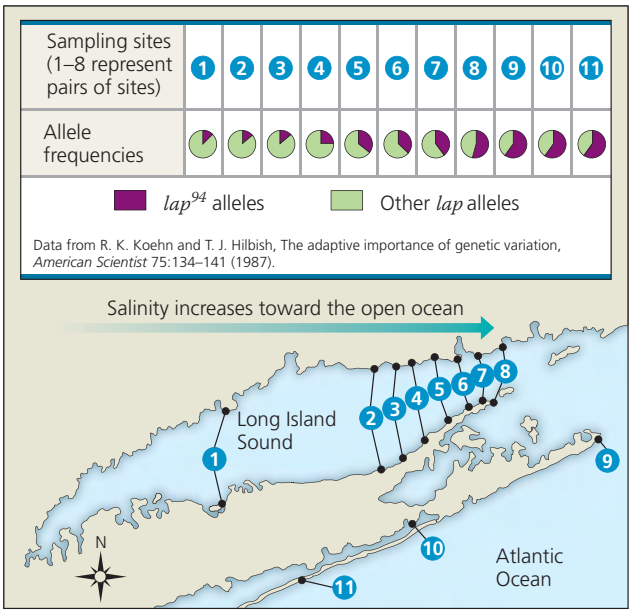
5. There are 40 individuals in population 1, all with genotype *A1A1*, and there are 25 individuals in population 2, all with genotype *A2A2*. Assume that these populations are located far from each other and that their environmental conditions are very similar. Based on the information given here, the observed genetic variation is most likely an example of
   a. genetic drift.
   b. gene flow.
   c. disruptive selection.
   d. discrete variation.
   e. directional selection.

6. A fruit fly population has a gene with two alleles, *A1* and *A2*. Tests show that 70% of the gametes produced in the population contain the *A1* allele. If the population is in Hardy-Weinberg equilibrium, what proportion of the flies carry both *A1* and *A2*?
   a. 0.7 b. 0.49 c. 0.21 d. 0.42 e. 0.09

## LEVEL 3: SYNTHESIS/EVALUATION

7. **EVOLUTION CONNECTION**
   How is the process of evolution revealed by the imperfections of living organisms?

8. **SCIENTIFIC INQUIRY**
   **DRAW IT** Richard Koehn, of the State University of New York, Stony Brook, and Thomas Hilbish, of the University of South Carolina, studied genetic variation in the marine mussel *Mytilus edulis* around Long Island, New York. They measured the frequency of a particular allele ($lap^{94}$) for an enzyme involved in regulating the mussel's internal saltwater balance. The researchers presented their data as a series of pie charts linked to sampling sites within Long Island Sound, where the salinity is highly variable, and along the coast of the open ocean, where salinity is constant:




*(Question 8, continued)*

Create a data table for the 11 sampling sites by estimating the frequency of $lap^{94}$ from the pie charts. (*Hint*: Think of each pie chart as a clock face to help you estimate the proportion of the shaded area.) Then graph the frequencies for sites 1–8 to show how the frequency of this allele changes with increasing salinity in Long Island Sound (from southwest to northeast). How do the data from sites 9–11 compare with the data from the sites within the Sound?

Construct a hypothesis that explains the patterns you observe in the data and that accounts for the following observations: (1) the $lap^{94}$ allele helps mussels maintain osmotic balance in water with a high salt concentration but is costly to use in less salty water; and (2) mussels produce larvae that can disperse long distances before they settle on rocks and grow into adults.

9. **WRITE ABOUT A THEME**
   **Emergent Properties** Heterozygotes at the sickle-cell locus produce both normal and abnormal (sickle-cell) hemoglobin (see Concept 14.4). When hemoglobin molecules are packed into a heterozygote's red blood cells, some cells receive relatively large quantities of abnormal hemoglobin, making these cells prone to sickling. In a short essay (approximately 100–150 words), explain how these molecular and cellular events lead to emergent properties at the individual and population levels of biological organization.

*For selected answers, see Appendix A.*

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